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Scientific Results of The Danish Deep-Sea Expedition Round the World 1950-52

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SYSTEMATICS AND BIOLOGY OF THE DEEP-SEA HOLOTHURIANS

Part 1. Elasipoda

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CONTENTS

I. INTRODUCTION

Among the five orders of the class Holothurioidea, the Elasipoda are unique in being confined to the deep sea, i. e. to depths exceeding 200–400 meters.

The four remaining orders (Aspidochirota, Molpadonia, Dendrochirota, and Apoda) all include sublittoral as well as deep-sea groups. These orders will be dealt with in subsequent volumes of the Galathea Report.

The Holothurioidea comprise about 1100 described species (Madsen 1954). Approximately 380 species belong to the deep sea.

Previous to the present revision, the Elasipoda comprised 171 species. Of these, 165 belonged to the benthic families Deimatidae, Laetmogonidae, Psychropotidae, and Elpidiidae, while the remaining six belonged to the pelagic family Pelagothuriidae. The present investigation deals with the four benthic families only. Eleven species are erected, while 18 previously described species are left out, being insufficiently described. The total number of recognized benthic species is reduced from 165 to 106.

In addition to the material brought home by the Galathea Expedition (1950–1952), the investigation also includes the Elasipoda taken during three collecting voyages of the late Dr. Th. Mortensen during the years 1913–1930.

The working up of this global material made necessary a comparison with the described materials from earlier deep-sea expeditions. With this purpose visits were paid to the museums of London, Amsterdam, Paris, Monaco, Washington, and Cambridge (Mass.).

The present work discusses all the 106 known species of benthic Elasipoda, 75 of which have been examined.

Among the many people who have contributed with aid and advice to the present work I owe a particular debt to the late Dr. Anton Fr. Bruun, the inspiring scientific leader of the Galathea Expedition, who gave me the opportunity to participate in the expedition and afterwards placed at my disposal the rich material of holothurians.

I am indebted to all my deep-sea colleagues in the Zoological Museum, of whom I may mention Dr. F. J. Madsen, curator of echinoderms, and Dr. T. Wolff, editor of the Galathea Report.

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Most of the drawings, apart from the simple line drawings, were made by the late Poul H. Winther (PHW), while a few are due to Mrs. Lise Jersing (LJ) and Mrs. Julie Tesch (JT). The diagrams in Figs. 99–103 were made by Mr. E. Leenders.

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History of exploration

Descriptions of deep-sea holothurians are almost exclusively found in the reports from the various deep-sea expeditions. A review of these expeditions and of the work dealing with their collections of holothurians, therefore, is at the same time a history of exploration of this group.

The Challenger Expedition 1872–1876 founded the knowledge of the deep-sea holothurians, as well as that of most other deep-sea animal groups. The holothurians from this famous expedition were treated by Théel (1882, 1886 a) who erected the order Elasipoda, comprising 52 species. Only one of the species, *Elpidia glacialis,* was known before, described by the same author in an earlier paper (Théel 1876).

While the *Challenger* brought home material from the three main oceans, the subsequent deep-sea expeditions explored restricted regions.

The Norwegian North-Atlantic Expedition 1876–1878, with the research vessel *Vöringen,* explored the Norwegian Sea and the adjacent regions of the North Atlantic (Danielssen & Koren 1882). The genera *Irpa* and *Kolga* were erected on this material.

The *Ingolf* 1895–1896 explored the northernmost part of the North Atlantic and the south-western part of the Norwegian Sea (Heding 1935, 1942). The *Godthaab* 1928 explored the West Greenland seas (Mortensen 1932).

The area investigated by the *Ingolf* is bordered to the south by a large unexplored area. Farther south, the North Atlantic has been explored by a number of expeditions. The eastern and central parts were explored by the *Travailleur* and the *Talisman* 1880–1883 (R. Perrier 1902) and by the expeditions of Prince Albert I of Monaco with the *Princesse Alice* and the *Hirondelle II* (von Marenzeller 1893a, Hérouard 1902, 1923). The Bay of Biscay by the *Caudan* 1895 (Koehler 1896). The western North Atlantic was covered by the *Albatross* 1893 (Verrill 1885), the *Blake* 1877–1880 (Théel 1886 b), and the *Atlantis* 1938–1939 (Deichmann 1940). The *Michael Sars* crossed the North Atlantic (Grieg 1921). The Swedish Deep-Sea Expedition 1947–1948 made a few deep-sea trawlings in the mid-Atlantic, including one at hadal depth (7625–7900 m) in the Puerto Rico Trench (Madsen 1953).

The German Deep-Sea Expedition 1898–1899 with the *Valdivia* explored the eastern South Atlantic, the Antarctic Ocean, and the Indian Ocean (Ludwig & Heding 1935, Heding 1940).

The *Investigator* 1887–1901 explored the Bay of Bengal and the Arabian Sea (Koehler & Vaney 1905). The *Siboga* 1899–1900 explored the Indonesian Seas (Sluiter 1901 b).

A number of expeditions with the *Albatross* explored regions of the Pacific Ocean; most of them were working close to the coasts: West coast of Central America 1891 (Ludwig 1894);

Hawaiian Islands 1902 (Fisher 1907); North Pacific coast of North America 1903 (Edwards 1907); Japan 1906 (Ohshima 1915, 1916–1919), and Baja California 1911 (Clark 1913, 1923 a). Only the expeditions 1899–1900 and 1903–1905 to the eastern Tropical Pacific had a number of stations far from the coast. The holothurians from the two last-mentioned expeditions were treated by H. L. Clark (1920).

The Antarctic Ocean was investigated, besides by the *Challenger* and the *Valdivia,* by the French Antarctic Expeditions 1903–1905 and 1908–1910 (Vaney 1906, 1914); the *Belgica* 1897–1899 (Hérouard 1906); the *Scotia* 1902–1904 (Vaney 1908); the Swedish Antarctic Expedition 1901–1903 (Ekman 1925); the German Antarctic Expedition 1901–1903 (Ekman 1927), and the *Eltanin* 1962–1964 (Agatep 1967 a, b).

Since 1949, Russian expeditions, in particular with the *Vitiaz,* have explored various parts of the world ocean. The holothurian genera *Myriotrochus* and *Elpidia* have so far been worked up (Belyaev 1970, 1971).

The degree of exploration of the different geographic regions (Figs. 107–108) is further considered in connection with the discussion of the geographic distribution of the species (p. 219).

The Galathea collections

The *Galathea,* like the *Challenger,* undertook a circumnavigation of the world. A special object was to explore the fauna of the deep-sea trenches – the fauna which Bruun (1956) termed the hadal fauna. Prior to the Galathea Expedition, this fauna was known only from one haul made by the Swedish Deep-Sea Expedition at 7625–7900 m in the Puerto Rico Trench.

The *Galathea* brought up benthic animals from 98 trawling and dredging stations at depths greater than 400 m, 83 of them exceeding 1000 m.

While holothurians were taken at only 7 of the 15 stations at depths of 400–1000 m, they were present at 79 of the 83 stations at depths greater than 1000 m. Three of the stations which did not yield holothurians were from hard bottom in the Indian Ocean off South Africa (depth: 4390–5340 m). The hauls made at two of the stations (175 and 178) failed almost totally, yielding very little benthic material. The third one (St. 182) brought up blocks of lava and a typical epifauna, especially of Bryozoa.

Only one soft-bottom trawling-station at depths exceeding 1000 m failed to bring up holothurians: St. 302 in the Bay of Bengal (depth: 1190 m, bottom: clay). The station yielded 51 bivalves and some other benthic invertebrates.

In addition to the exploration of the trenches, the *Galathea* concentrated on the exploration of the abyssal fauna, while the bathyal fauna was investigated to a more limited extent.

The equipment of the *Galathea* made possible the use of large fishing gear. Shrimp Otter Trawl (SOT) and Herring Otter Trawl (HOT) of the types used by Danish fishermen were used at great depths – the HOT at a depth down to 7160 m in the Sunda Trench. A 6 m wide Sledge Trawl (ST 600) was used down to 8210–8300 m in the Kermadec Trench, and a 3 m wide Sledge Trawl (ST 300) down to 10200 m in the Philippine Trench.

The *Galathea* collections, including the type specimens, are kept in the Zoological Museum of Copenhagen.

The advantage of large gear in catching holothurians

The large gear used by the *Galathea* brought up rich catches of the larger animals of the sea floor. But the wide meshes of the nets did not permit an effective collecting of the smaller ones. Groups of small-sized animals (e. g. Crustacea) are not represented in such proportions as to give a correct impression of their density on the sea floor.

Trawls with a large opening have a particular advantage in catching holothurians. Bathyscaphe observations have shown that many deep-sea holothurians are so buoyant that they may be swept off the bottom by the water movements caused by the sampling gear. Barham *et al.* (1967) relate, from a depth of 1060–1243 m in the San Diego Trough, that "the motion of the passing bathyscaphe sweeps *Scotoplanes* sp. off their feet and tumbles them around". They pointed to the remarkable fact that extensive grab-sample explorations in the same area (Hartman 1963, Hartman & Barnard 1958–1960) failed to bring up a single specimen of *Scotoplanes.* Apparently, *Scotoplanes* is so buoyant that it escapes the bottom grab.

Wolff (1971), during dives of the bathyscaphe *Archimède* to 4160 m off Madeira, observed a sausage-shaped holothurian (agreeing in shape with *Benthodytes* and with some genera of the Aspidochirota) which, at the approach of the grab of the bathyscaphe, changed rapidly into a loaf-shape and, due to its buoyancy, escaped the grab.

The unfitness of small nets for catching these highly buoyant animals is illustrated by the fact that the haul made with the Herring Otter Trawl at the *Galathea* St. 716 (3570 m depth off Costa Rica showed a much greater dominance of holothurians than did the hauls with the small dredge (100 cm wide and 10 cm high) used by the *Vema* in the same area (Wolff 1961).

The poor representation of juvenile stages of holothurians (p. 182) may be due not only to the large mesh size of the gear used by the *Galathea.* Possibly, the holothurians of the deep sea are long-lived and spend a comparatively short period of their life as juveniles. In addition, the juveniles may be even more buoyant than the adult individuals, or they lead a semipelagic life. It is noteworthy that the smallest specimens taken belong to the genera *Elpidia,* of which the hadal forms, in particular, are heavily armoured, and to *Myriotrochus* which, in contrast to the Elasipoda, live buried in the substratum.

List by station of the Elasipoda collected by the Galathea

Abbreviations of gear: HOT: Herring Otter Trawl. SOT: Shrimp Otter Trawl. SBT: Shrimp Beam Trawl. ST 200, ST 300 and ST 600: Sledge (Agassiz, Sigsbee) Trawl, 2 m, 3 m, and 6 m wide.

Temperature records preceded by "c." are from closely situated stations.

For further information of the stations, see Bruun (1958) and Kiilerich (1964).

32. Monrovia–Takoradi (4°05'N, 2°13'W), 2100 m, 20.XI.1950, SBT
    Benthodytes lingua Perrier, 4
    Psychropotes depressa (Théel), 13
    Scotoplanes globosa Théel, 37

52. San Tomé–Cameroon (1°42'N, 7°51'E), 2550 m, muddy clay, c. 3.0° C., 30.XI.1950, SOT
    Psychropotes depressa (Théel), 5
    Peniagone diaphana (Théel), 3

63. Off Gabon (2°00'N, 9°14'E), 1520 m, blue clay, c. 3.8° C., 2.XII.1950, SOT
    Peniagone diaphana (Théel), 1

65. Off Gabon (2°17'S, 8°10'E), 2770 m, bluish clay, 3.0° C., 4.XII.1950, ST 300
    Psychropotes depressa (Théel), 2

186. Cape Town–Durban (32°33'S, 32°01'E), 3620 m, Globigerina ooze, 1.2° C., 31.I.1951, SOT
    Benthodytes plana n. sp., 1
    Benthodytes typica Théel, 4

190. Off Durban (29°42'S, 33°19'E), 2720 m, Globigerina ooze, 3.II.1951, ST 300
    Deima validum validum Théel, 2
    Benthodytes typica Théel, 2

192. Off Durban (32°00'S, 32°41'E), 3430 m (ST 300) and 3530 m (SOT), Globigerina ooze, 1.2° C., 5.II.1951
    Oneirophanta mutabilis mutabilis Théel, 3
    Benthodytes typica Théel, 5
    Psychropotes verrucosa (Ludwig), 1

193. Off Durban (32°34'S, 31°52'E), 3680 m, Globigerina ooze, 1.1° C., 6.II.1951, SOT
    Deima validum validum Théel, 5

217. Mozambique Channel (14°20'S, 45°09'E), 3390 m, Globigerina ooze, 1.6° C., 27.II.1951, HOT
    Deima validum validum Théel, 1
    Oneirophanta mutabilis mutabilis Théel, 1
    Benthodytes typica Théel, 24
    Psychropotes sp., 1

231. Madagascar–Mombasa (8°52'S, 49°25'E), 5020 m, 7.III.1951, ST 300
    Psychropotes belyaevi n. sp., 2
    Ellipinion solidum n. sp., 1
    Peniagone sp., 1

232. Madagascar–Mombasa (9°03'S, 49°22'E), 4930 m, c. 1.3° C., 8.III.1951, HOT
    Psychropotes belyaevi n. sp., 1
    Ellipinion solidum n. sp., 1
    Peniagone sp., 3

234. Madagascar–Mombasa (5°25'S, 47°09'E), 4820 m, Globigerina ooze, 10.III.1951, HOT
    Deima validum validum Théel, 7
    Psycheotrephes magna n. sp., 4
    Psychropotes belyaevi n. sp., 3
    Psychropotes verrucosa (Ludwig), 2
    Psychropotes longicauda Théel, 6
    Peniagone convexa n. sp., 1

235. Madagascar–Mombasa (4°47'S, 46°19'E), 4810 m, Globigerina ooze, c. 1.7° C., 11.III.1951, HOT
    Deima validum validum Théel, 1
    Psychropotes belyaevi n. sp., 19

Psychropotes semperiana Théel, 4
Psychropotes longicauda Théel, 5

241\. Off Kenya (4°00'S, 41°27'E), 1510 m, pure Globigerina, c. 4.3° C., 15.III.1951, HOT
Benthogone rosea Koehler, 1

279\. Seychelles–Ceylon (1°00'N, 76°17'E), 4320 m, Globigerina ooze, 8.IV.1951, ST 300
Deima validum validum Théel, 2
Psychropotes semperiana Théel, 1

281\. Seychelles–Ceylon (3°38'N, 78°15'E), 3310 m, Globigerina ooze, 10.IV.1951, ST 300
Deima validum validum Théel, 1
Benthodytes plana n. sp., 1
Benthodytes typica Théel, 1

282\. Seychelles–Ceylon (5°32'N, 78°41'E), 4040 m, blackish mud, c. 1.4° C., 11.IV.1951, HOT
Benthodytes typica Théel, 1
Peniagone convexa n. sp., 1
Peniagone rigida (Théel), 1

299\. Bay of Bengal (17°10'N, 84°30'E), 2820 m, mud, 24.IV.1951, HOT
Benthodytes typica Théel, 26
Psychropotes mirabilis n. sp., 1

314\. Bay of Bengal (15°54'N, 90°17'E), 2600 m, brownish ooze, 3.V.1951, HOT
Benthodytes typica Théel, 1

324\. Strait of Malacca (6°38'N, 96°00'E), 1140 m, brownish Globigerina ooze, 9.V.1951, ST 300
Benthogone fragilis (Koehler & Vaney), 1

435\. Philippine Trench (10°20'N, 126°41'E), 9820–10000 m, very stiff clay, 2.6° C., 7.VIII. 1951, ST 300
Ellipinion galatheae (Hansen), 1

465\. Sunda Trench (10°20'S, 109°55'E), 6900–7000 m, 1.5° C., 5.IX.1951, ST 300
Elpidia glacialis sundensis Hansen, 7

466\. Sunda Trench (10°21'S, 110°12'E), 7160 m, bluish clay, c. 1.5° C., 6.IX.1951, HOT
Peniagone sp., 8
Amperima naresi (Théel), 114
Elpidia glacialis sundensis Hansen, c. 3000

474\. Sunda Trench (9°49'S, 114°13'E), 3810–3840 m, 1.2° C., 11.IX.1951, ST 300
Benthodytes sp., 1

490\. Bali Sea (5°25'S, 117°03'E), 545–570 m, sand and clay, c. 6.5° C., 14.IX.1951, ST 300
Orphnurgus glaber Walsh, 5

495\. Banda Trench (5°26'S, 130°58'E), 7250–7290 m, clay, 3.6° C., 22.IX.1951, HOT
Benthodytes sanguinolenta Théel, 5
Psychropotes verrucosa (Ludwig), 3
Peniagone sp., 1

497\. Banda Trench (5°18'S, 131°18'E), 6490–6650 m, soft clay, 23.IX.1951, HOT
Benthodytes sanguinolenta Théel, 3
Psychropotes verrucosa (Ludwig), 1

517\. New Britain Trench (6°31'S, 153°58'E), 8940 m, clay, 13.X.1951, ST 300
Elpidia glacialis solomonensis Hansen, 14

521\. New Britain Trench (5°59'S, 153°28'E), 8780–8830 m, clay, 16.X.1951, ST 200
Elpidia glacialis solomonensis Hansen, 63

550\. Tasman Sea (31°27'S, 153°33'E), 4530 m, very stiff clay, c. 1.0° C., 12.XI.1951, ST 200
Deima validum validum Théel, 1

574\. Tasman Sea (39°45'S, 159°39'E), 4670 m, 18.XII.1951, ST 600
Deima validum validum Théel, 1
Psychropotes verrucosa (Ludwig), 1
Peniagone diaphana (Théel), 2

575\. Tasman Sea (40°11'S, 163°35'E), 3710 m, pteropod ooze, c. 1.1° C., 19.XII.1951, SOT
Benthodytes typica Théel, 21
Psychropotes verrucosa (Ludwig), 3

601\. Tasman Sea (45°51'S, 164°32'E), 4400 m, Globigerina ooze, c. 1.1° C., 14.I.1952, HOT
Psychropotes longicauda Théel, 5

602\. Tasman Sea (43°58'S, 165°24'E), 4510 m, bluish clay, c. 1.1° C., 15.I.1952, ST 300
Elpidia theeli Hansen, 14
Psychropotes verrucosa (Ludwig), 1

607\. Tasman Sea (44°18'S, 166°46'E), 3580 m, clay, c. 1.3° C., 17.I.1952, HOT
Benthodytes sanguinolenta Théel, 2

626\. Tasman Sea (42°10'S, 170°10'E), 610 m, Globigerina ooze, 20.I.1952, ST 300
Peniagone sp., 4 juveniles

649\. Kermadec Trench (35°16'S, 178°40'W), 8210–8300 m, grey clay with pumice, 1.5° C., 14.II.1952, ST 600
Peniagone azorica von Marenzeller, 160
Elpidia glacialis kermadecensis Hansen, c. 1800

650\. Kermadec Trench (32°20'S, 176°54'W), 6620–6730 m, brown clay with pumice, 1.3° C., 15.II.1952, ST 600
Apodogaster sp., c. 10
Peniagone azorica von Marenzeller, 260
Scotoplanes globosa Théel, 31
Elpidia glacialis kermadecensis Hansen, 1
Psychropotes verrucosa (Ludwig), 1

651. Kermadec Trench (32°10'S, 177°14'W), 6960–7000 m, brown clay with pumice, 1.3° C., 16.II.1952, HOT
Peniagone azorica von Marenzeller, 6

653. Kermadec Trench (32°09'S, 176°35'W), 6180 m, brown clay with pumice, 17.II.1952, HOT
Peniagone azorica von Marenzeller, 1
Scotoplanes globosa Théel, 1

654. Kermadec Trench (32°10'S, 175°54'W), 5850–5900 m, brown clay with pumice, 1.2° C., 18.II.1952, HOT
Oneirophanta mutabilis mutabilis Théel, 14
Apodogaster sp., 3
Peniagone azorica von Marenzeller, 11
Scotoplanes globosa Théel, 16

658. Kermadec Trench (35°51'S, 178°31'W), 6660–6770 m, brown sand with clay and stones, 1.3° C., 20.II.1952, ST 600
Peniagone azorica von Marenzeller, c. 600
Peniagone sp., 1
Scotoplanes globosa Théel, 17

661. Kermadec Trench (36°07'S, 178°32'W), 5230–5340 m, pumice in abundance, 1.1° C., 23.II.1952, ST 600
Peniagone azorica von Marenzeller, 60
Ellipinion sp., 3

663. Kermadec Trench (36°31'S, 178°38'W), 4410 m, brown sandy clay with pumice, 1.2° C., 24.II.1952, HOT
Oneirophanta mutabilis mutabilis Théel, 1
Apodogaster sp., 6
Laetmogone wyvillethomsoni Théel, 1
Benthodytes sanguinolenta Théel, 1
Psycheotrephes magna n. sp., 3
Psychropotes longicauda Théel, 14
Psychropotes loveni Théel, 1
Peniagone humilis n. sp., 1
Peniagone azorica von Marenzeller, 267
Achlyonice ecalcarea Théel, 1
Ellipinion bucephalum n. sp., 1
Scotoplanes globosa Théel, 5

664. Kermadec Trench (36°34'S, 178°57'W), 4540 m, brown sandy clay with pumice, 1.1° C., 24.II.1952, HOT
Oneirophanta mutabilis mutabilis Théel, 5
Oneirophanta setigera (Ludwig), 1
Apodogaster sp., 1
Benthodytes sp., 1
Psychropotes longicauda Théel, 33
Peniagone azorica von Marenzeller, 179

665. Kermadec Trench (36°38'S, 178°21'E), 2470 m, grey clay, 2.1° C., 25.II.1952, HOT
Benthodytes sp., 1
Scotoplanes globosa Théel, 1

668. Kermadec Trench (36°23'S, 177°41'E), 2640 m, clay, 2.0° C., 29.II.1952, HOT
Deima validum validum Théel, 1
Benthodytes typica Théel, 1
Psychropotes loveni Théel, 2
Peniagone azorica von Marenzeller, 5
Amperima robusta (Théel), 1
Scotoplanes globosa Théel, 66

716. Acapulco–Panama (9°23'N, 89°32'W), 3570 m, dark muddish clay, c. 1.9° C., 6.V.1952, HOT
Oneirophanta mutabilis affinis Ludwig, 30
Benthodytes incerta Ludwig, 16
Benthodytes sanguinolenta Théel, 1
Psychropotes longicauda Théel, 5
Peniagone papillata n. sp., 41
Peniagone vitrea Théel, 1
Scotoplanes clarki n. sp., c. 100

724. Gulf of Panama (5°44'N, 79°20'W), 2950–3190 m, dark clay and stones, c. 2.0° C., 12.V.1952, ST 600
Apodogaster sp., 1

726. Gulf of Panama (5°49'N, 78°52'W), 3270–3670 m, clay, c. 2.0° C., 13.V.1952, HOT
Oneirophanta mutabilis affinis Ludwig, 1
Oneirophanta setigera (Ludwig), 1
Benthodytes typica Théel, 1

739. Gulf of Panama (7°22'N, 79°32'W), 915–975 m, green clay, c. 5° C., 15.V.1952, HOT
Pannychia moseleyi Théel, 13

758. Puerto Rico Trench (18°45'N, 66°27'W), 2840 m, c. 3–4° C., 30.V.1952, ST 600
Benthodytes typica Théel, 3

List by station of the Elasipoda collected by Dr. Th. Mortensen

The Pacific Expedition 1913–1916

27.III.1914. 15 miles W. 1/2 S. of Jolo (Philippines), 458 m, soft bottom
Orphnurgus glaber Walsh, 3

10.VI.1914. Sagami Bay (Japan), 450 m
Laetmogone fimbriata (Sluiter), 5

2.VII.1914. Sagami Bay (Japan), 732 m
Laetmogone maculata (Théel), 1
Laetmogone fimbriata (Sluiter), 2

15.IX.1914. N.E. of Tasmania (39°10'S, 149°55'E), 366–458 m, soft bottom
Laetmogone maculata (Théel), 9
16.IX.1914. N.E. of Tasmania (38°12'S, 149°40'E), 183–293 m
Laetmogone maculata (Théel), 1

The Danish Expedition to the Kei Islands 1922 (cf. Mortensen 1923)

St. 41. Kei Islands (5°29'S, 132°28'E), 245 m, mud
Orphnurgus glaber Walsh, 1
Laetmogone maculata (Théel), 1
Laetmogone fimbriata (Sluiter), 1
St. 42. Kei Islands (5°35'S, 132°29'E), 225 m
Laetmogone maculata (Théel), 1
St. 51. Kei Islands (5°46'S, 132°51'E), 348 m, mud
Orphnurgus glaber Walsh, 1
St. 52. Kei Islands (5°46'S, 132°50'E), 352 m
Orphnurgus glaber Walsh, 1
St. 56. Kei Islands (5°31'S, 132°51'E), 345 m
Orphnurgus glaber Walsh, 1

The Java – South Africa Expedition 1929–1930

St. 25. Off Durban (29°56'S, 31°19'E), 412 m, sandy mud
Laetmogone fimbriata (Sluiter), 10
St. 78. Off St. Helena (8 miles W. by N. of Sugarloaf), 2400–2780 m (collected by the *Dana*)
Achlyonice ecalcarea Théel, 1

In addition, seven specimens of *Benthodytes lingua* R.Perrier from South Africa, probably originating from The Java–South Africa Expedition, are described in the present work.

Re-examined material

A re-examination was made of the collections in the following museums:

The British Museum (Natural History). The greater part of the *Challenger* collections are kept here, although a number of specimens from this expedition were distributed to other museums (Amsterdam, Copenhagen, Paris).

The Zoological Museum, Amsterdam. The *Siboga* holothurians are kept here, in a fine state of preservation.

The Muséum National d'Histoire Naturelle, Paris, keeps the complete collections of the *Travailleur* and the *Talisman*. Unfortunately, the specimens are in a rather poor state as regards their external morphology. The deposits, however, are well preserved in most of them.

The Musée Océanographique de Monaco keeps the collections made by the *Princesse Alice* and the *Hirondelle II*.

The Zoological Museum, University of Copenhagen. In addition to the collections from the *Galathea* and from Dr. Mortensen's expeditions this museum keeps the collections made by the *Ingolf* and the *Godthaab*. The holothurians of the German Deep-Sea Expedition *(Valdivia)* are also at the present time kept in Copenhagen.

The Museum of Comparative Zoology, Cambridge (Massachusetts), keeps the *Blake* and a smaller part of the *Albatross* collections.

The United States National Museum, Washington, keeps the greater part of the collections from the various expeditions of the *Albatross*. However, the holothurians obtained during the Japanese cruise (Ohshima 1915, 1916–1919) seem to be almost entirely lost.

In the above-mentioned seven museums are stored the greater part of the previously described material of deep-sea holothurians.

The re-examination of the specimens in the museums mentioned concerned the external morphology, while skin samples had to be taken to the Zoological Museum of Copenhagen for an examination of the deposits. For this reason the revision of the materials did not include the selection of lectotypes, despite the fact that type specimens were usually not selected by the original authors. Whenever a specimen was found to be labelled «Type», it has been stated here.

Abbreviations of museum names

BM:	British Museum (Natural History), London
MCZ:	Museum of Comparative Zoology, Cambridge, Massachusetts
MNHN:	Muséum National d'Histoire Naturelle, Paris
MOM:	Musée Océanographique, Monaco
USNM:	United States National Museum, Washington, D.C.
ZMA:	Zoological Museum, Amsterdam
ZMUC:	Zoological Museum, University of Copenhagen

Methods of examination

In order to state the variation of the taxonomic characters all available specimens of each species were as a rule examined. The taxonomically important calcareous deposits (p. 182) were examined in about 1200 specimens, representing 75 species and originating from the *Galathea* as well as from previous expeditions. The examination was made by means of slide preparations of the dorsal and ventral skin, and usually also of a tentacle, a tubefoot, and a papilla. The deposits of the internal organs are less important taxonomically, and were not examined in all species. The preparations were made by dehydrating a piece of skin in absolute alcohol, with subsequent clearing in xylene and mounting in Canada balsam. The preparations are all kept in the Zoological Museum of Copenhagen.

Permanent mounts for deposit studies are of the greatest importance, when the variation of the deposits and the synonymy of the species are investigated.

The *Galathea* specimens were preserved on board in 4 % formalin neutralized with borax, or in 70 % alcohol. The former specimens were transferred to 70 % alcohol after the return of the expedition. The calcareous deposits are well preserved in practically all the specimens. Unneutralized formalin dissolves the deposits and should never be used for specimens to be studied taxonomically. When specimens are fixed for histological investigations, the borax should be replaced by $CaCO_3$ to avoid maceration of the tissues.

Specimens first kept in formalin in some instances proved to have retained their natural shape better than specimens transferred directly to alcohol. Thus, in *Scotoplanes globosa* the marginal lobes on the tentacle discs were visible only in specimens which had been through formalin.

II. SYSTEMATIC PART

Order Elasipoda Théel, 1882

Diagnosis: Mesentery with dorsal attachment throughout its length. Respiratory trees absent.

Remarks: The taxonomy and relationship of the Elasipoda, including the basis of the proposed division of the order into two suborders, are discussed in the General Part (pp. 206–207).

Key to the suborders

1. Deposits perforated plates, spatulated crosses, rods, or wheels .... Deimatina (p. 14)
1. Deposits, when present, primary crosses (or primary cross derivatives) with arrested development of dichotomous divisions .... Psychropotina (p. 75)

Suborder Deimatina nov. subordo

Diagnosis: Deposits perforated plates (or derivatives from these) or wheels; no primary crosses with arrested development of dichotomous divisions. Papillae usually numerous and large.

Key to the families

1. Deposits perforated plates, spatulated crosses, and spatulated rods, or transformed into spindle-shaped, rounded, or amorphous bodies. Wheels absent. Each gonad composed of a single cluster of unbranched sacs .... Deimatidae (p. 15)
1. Deposits wheels. In addition only scattered rods, or (in *Laetmogone violacea)* spinous crosses occur. Each gonad composed of numerous branched ducts and tubules .... Laetmogonidae (p. 47)

Family **DEIMATIDAE** sensu Ekman, 1926

Diagnosis: Deposits varying from perforated plates and spatulated primary crosses to spatulated, or reduced and deformed rods. Wheels absent. Gonads consisting of few, sac-shaped tubules.

Taxonomy: Ekman (1926) separated the Laetmogonidae from Théel's family Deimatidae. The taxonomic position of the family is considered elsewhere (p. 206).

The Deimatidae, as defined by Ekman, included five genera and 20 species. One of the species (*Scotodeima parvispiculatum* Clark, 1920), on re-examination of the type specimen in USNM, proved to be based on a defective specimen of the aspidochirote holothurian *Synallactes aenigma* Ludwig, 1894. Other 11 nominal species are considered synonyms of formerly described ones.

The previously recognized genera were, in part, based on doubtful taxonomic characters. The former division of the family is, therefore, abandoned and the family is divided into three genera only, based on the shape of the tentacle discs and the presence or absence of circum-oral papillae.

The genera were distinguished as follows:

Deima Théel, 1879, was defined by its large, perforated plates, and by its tentacles being retractile into the oral cavity.

Oneirophanta Théel, 1879, had plates similar to those of *Deima,* but the tentacles were unretractile.

Orphnurgus Théel, 1879, was originally clearly distinguished from *Deima* and *Oneirophanta* by the small, spinous rods which characterize the type species, *O. asper*. However, these rods were absent from the species subsequently referred to the genus. These had various kinds of deposits, such as spatulated crosses, spatulated rods, dichotomously divided crosses, and ellipsoid, spindle-shaped, or spherical bodies.

Scotodeima Ludwig, 1894, was distinguished from *Orphnurgus* by the presence of midventral tubefeet. Although the validity of the genus was doubted by Ohshima (1915), it remained to be treated as a separate genus.

Amphideima Koehler & Vaney, 1905, was distinguished from *Orphnurgus* (and from other deimatids) by the absence of ventrolateral papillae.

The following criticism may be made against this division of the family:

The genus *Orphnurgus* differed from *Oneirophanta* by the absence of perforated plates and not by a deposit type of its own. The spatulated rods and the spatulated and ramified crosses are not confined to species of *Orphnurgus,* but may be found also in *Oneirophanta mutabilis* – here being interconnected with the perforated plates by all intermediates. While the ramified crosses merely represent early stages of perforated plates, the spatulated rods and crosses derive from these plates through an enlargement of the primary rod or the primary cross, concurrently with a reduction of the terminal ramifications. The occasional occurrence of these deposits among the perforated plates in *Oneirophanta mutabilis* (and even in a specimen of *Deima validum)* shows that they are types easily realized, and unsuitable, therefore, as generic characters. Thus, the species *Scotodeima setigerum* and *S. protectum,* both having exclusively spatulated crosses in the body wall and spatulated rods in the papillae, might have reached their similarity by convergence. (In the present paper they are referred to the genera *Oneirophanta* and *Orphnurgus,* respectively).

The inadvisability of using the presence or absence of perforated plates as a generic character is especially emphasized by the presence in *Oneirophanta mutabilis* of specimens having only a few deposits closed to form perforated plates – the majority remaining with open, dichotomous ramifications. These deposits were predominant in most of the specimens of *O. mutabilis* from *Galathea* St. 654 – specimens rather referable to *Orphnurgus* than to *Oneirophanta,* according to the former definitions of the genera.

Midventral tubefeet, formerly said to distinguish *Scotodeima,* were also found to occur occasionally in *Deima validum, Oneirophanta mutabilis, O. setigera,* and *Orphnurgus glaber.* As their presence or absence do not even distinguish species, the genus *Scotodeima* cannot be upheld. The species of *Scotodeima* are replaced in *Orphnurgus* and *Oneirophanta.*

Probably, the absence of ventrolateral papillae, said to distinguish the genus *Amphideima,* likewise represents no more than an individual variation. The single species, *A. investigatoris,* is here considered a synonym of *Orphnurgus glaber.*

Among the features used to distinguish the former genera of the Deimatidae, alone the retractility of the tentacles into the oral cavity in the genus *Deima* appears to be taxonomically valid. All the six described species of *Deima* (which are here merged into one species) proved on re-examination to possess this feature. Furthermore, the feature was always combined with the presence of a ring of circum-oral papillae. All other species of the Deimatidae have unretractile tentacles and lack circum-oral papillae. On the other hand, the genus *Benthogone* of the family Laetmogonidae and the genus *Benthodytes* of the family Psychropotidae are similar to *Deima* in both these features.

The tentacle discs in the family belong to two distinctly different types (Pl. VIII: 1–7). A division of the family according to these types and to the presence or absence of circum-oral papillae and retractility of the tentacles seems to be more in agreement with the natural affinities of the species than the previous division.

Deima possesses retractile tentacles and circum-oral papillae. The tentacle discs are circular in outline and the margin provided with 4–10 rounded knobs or elongated lobes.

Oneirophanta has tentacle discs similar to those of *Deima* (although sometimes with reduced knobs), but the tentacles are unretractile and there are no circum-oral papillae. Intra-ovarian young of *O. mutabilis affinis,* however, have slightly ramified discs. The genus comprises three species, *O. mutabilis, O. setigera* (= *Scotodeima setigerum*) and, with some doubt, *O. conservata,* in which the shape of the tentacles is unknown.

Orphnurgus differs from *Deima* and *Oneirophanta* by the presence of ramified processes on the margin of the tentacle discs. Like *Oneirophanta* it has unretractile tentacles and lacks circum-oral papillae.

Ramified tentacle discs were described by Théel for *Orphnurgus asper,* and by Fisher for *O. insignis* (= *O. glaber*). All the examined specimens of *O. glaber* had ramified tentacle discs, and the same applied to the re-examined species *O. protectus* and *O. vitreus.*

Unfortunately, the ramified processes on the tentacle discs are often so contracted that they appear merely as small lobes on the edge. In most of the specimens here described of *O. glaber* the tentacles had such an appearance; a comparison with specimens in which the tentacle discs were fully extended revealed, however, that the lobes were in actual fact contracted ramifications. Since the ramifications are conspicuous only in the extended state, it is hardly surprising that these have been reported from only one (*Orphnurgus insignis*) of the six nominal species here united under *O. glaber*. A re-examination of the other five species will probably reveal the presence of contracted ramifications on the tentacle discs.

Key to the genera of Deimatidae

1. Tentacle discs retractile into the oral cavity. Circum-oral papillae present. *Deima* (p. 16)
1. Tentacles unretractile. Circum-oral papillae absent 2
2. Tentacle discs circular in outline, usually with rounded knobs on the margin, but never with ramified processes .... *Oneirophanta* (p. 24)
2. Tentacle discs with ramified (but often contracted) processes on the margin .... *Orphnurgus* (p. 38)

Genus ***Deima*** Théel, 1879

Théel 1879, pp. 4–5; Théel 1882, p. 68. – Type species, designated by Deichmann (1930): *Deima validum* Théel, 1879.

Diagnosis: Tentacles 18–20, retractile into the oral cavity; discs with rounded knobs on the margin. Circum-oral papillae present. Deposits perforated plates, consisting of one or several layers of meshwork.

Remarks: The six species formerly referred to this genus are here united into one with two subspecies.

Deima validum Théel, 1879

Figs. 1, 109, pls. XI: 1, XIII: 1–2

Diagnosis: Ventrolateral tubefeet 10–13 pairs, single-rowed. Midventral tubefeet absent or represented by a reduced pre-anal pair only. Dorsal papillae 5–16 pairs, single-rowed and usually rigid. Ventrolateral papillae 3–7 pairs, usually rigid.

Distribution: *Deima validum* has a worldwide distribution although it appears to be absent from many regions. The bathymetric range of the species varies strikingly from one region to another. No other deep-sea holothurian shows a similar combination of geographic and bathymetric occurrence.

Based on differences in the number of dorsal papillae, and to some degree in the type of deposit, Hansen (1967) proposed a division of the species into two subspecies, the almost cosmopolitan *Deima validum validum* and the eastern Pacific *D. v. pacificum*.

Deima v. validum is in the eastern North Atlantic known from depths of 2779–4360 m (2.5–2.9° C.), and off the West Indies from depths of 1049–1783 m (3.7–6.0° C.).

The only record from the South Atlantic is from 1227 m (3.3° C.) off Rio de Janeiro.

The subspecies may have a wider distribution in the Atlantic Ocean. However, the absence of records from the well-explored northernmost part of the North Atlantic and along the east coast of North America indicates a real absence of the species in these two regions.

In the western Indian Ocean the known bathymetric range is 2720–4820 m (1.1–1.7° C.), thus very similar to the range in the eastern North Atlantic. However, due to insufficient exploration at shallower depths, the upper limit of bathymetric range is uncertain in this region.

In the northern Indian Ocean (including the Arabian Sea and the Bay of Bengal) the bathymetric range is 1224–4320 m (1.7–6.1° C.), thus comprising almost the whole known depth range of the species.

In Indonesian seas the subspecies is known from 724–1158 m (c. 4–7° C.). Here, the upper limit is remarkably shallow. The lower limit is uncertain, because this region has been investigated by only few stations with greater depths. North of New Guinea the species (under the name *Deima fastosum*) was recorded from 3658 m (0.9° C.).

The Japanese records are from 1317–1680 m (2.7–3.7° C.); the lower limit is uncertain, owing to the almost total absence of deeper stations.

In the remaining parts of the Pacific the subspecies is known only from true abyssal depths: Kermadec Trench, 2640 m (2.2° C.). Tasman Sea, 4530–4670 m (1.0° C.). North Pacific, 3749 m (1.3° C.).

Thus, the subspecies seems to have a limited bathymetric range in the eastern North Atlantic (2779–4360 m), while in the northern Indian Ocean the range is wide (1224–4320 m). In the remaining regions either the upper or the lower limit of bathymetric range is uncertain.

Deima v. pacificum is known only from the Gulf of Panama at depths of 1618–2487 m (2.2–2.9° C.). This interval seems to represent fairly well the true range of the species in this region, since the many stations at lower and greater depths failed to bring up the species. In this region with its steep continental slope the distribution of the species is apparently limited to a narrow zone close to the coast.

A wide gap separates the known distributional area of the subspecies *pacificum* from the nearest records off Japan of the subspecies *validum*. As yet, the intervening region is too little explored to permit a conclusion from the absence of records to the absence of the species. However, it is remarkable that the species has not been recorded from the region off the coasts of Mexico and Baja California, where depths corresponding to the range of the subspecies *pacificum* have been covered by several stations (Clark 1923a, Parker 1964).

The region south of the Gulf of Panama is unexplored at these depths.

Deima validum validum Théel, 1879

Deima validum Théel, 1879, p. 5, figs. 36–38; Théel 1882, pp. 68–70, pls. XVIII, XIX, XXXI: 4–9, XXXVI: 4, XXXVII: 8, XLIII: 7, XLIV: 13, XLVI: 5; Sluiter 1901b, p. 60.

Deima validum validum Théel, Hansen 1967, pp. 488–490, fig. 5.

Deima fastosum Théel, 1879, pp. 5–6, figs. 1–3; Théel 1882, pp. 71–73, pls. XX, XXI: 1, XXXI: 10–13, XXXV: 7–10, XXXVI: 7, XXXVII: 3, XLIII: 2–3, 5, XLVI: 8.

Deima blakei Théel, 1886b, pp. 1–2, figs. 1–2; Koehler & Vaney 1905, pp. 55–57, pl. XI: 13–15; Hérouard 1923, pp. 40–41, pls. V: 7, VI: 5; Deichmann 1930, pp. 115–116, pls. X: 7–11, XI: 1–3; Deichmann 1936, p. 9; Deichmann 1940, pp. 198–199.

Deima atlanticum Hérouard, 1898, pp. 88–89, figs. 1–2; Hérouard 1902, pp. 32–35, pls. III: 3, IV: 18, V: 1–5, VIII: 26–29; Grieg 1921, p. 4, pl. I: 2–3.

Deima mosaicum Ohshima, 1915, pp. 233–234; Ohshima 1916–1919, with two figures.

Diagnosis: Ventrolateral tubefeet 10–13 pairs. Pre-anal tubefeet rarely present. Dorsal papillae 5–10 pairs. Ventrolateral papillae 3–7 pairs. Perforated plates usually large and composed of several layers; diameter of dorsal ones 1.5–7.0 mm, of ventral ones 0.5–4.0 mm.

Material:

St. 190, off Durban (29°42'S, 33°19'E), 2720 m. – 2 specimens.

St. 193, off Durban (32°34'S, 31°52'E), 3680 m. – 5 specimens.

St. 217, Mozambique Channel (14°20'S, 45°09'E), 3390 m. – 1 specimen.

St. 234, Madagascar–Mombasa (5°25'S, 47°09'E), 4820 m. – 7 specimens.

St. 235, Madagascar–Mombasa (4°47'S, 46°19'E), 4810 m. – 1 specimen.

St. 279, Seychelles–Ceylon (1°00'N, 76°17'E), 4320 m. – 2 specimens.

St. 281, Seychelles–Ceylon (3°38'N, 78°15'E), 3310 m. – 1 specimen.

St. 550, Tasman Sea (31°27'S, 153°33'E), 4530 m. – 1 specimen.

St. 574, Tasman Sea (39°45'S, 159°39'E), 4670 m. – 1 specimen.

St. 668, Kermadec Trench (36°23'S, 177°41'E), 2640 m. – 1 specimen.

In addition, two hitherto undescribed specimens (in USNM) are included from *Albatross* St. 2763 (year 1887), off Rio de Janeiro (24°17'S, 42°48'W), 1227 m, temp. 3.3° C.

Description of the *Galathea* specimens:

The general features of the species are well known from earlier descriptions – in particular from Théel's excellent treatment of the *Challenger* specimens. The present description is made with special reference to an evaluation of synonymous species and to an analysis of the variation in the taxonomic characters.

Body with flat ventrum and strongly vaulted dorsum. Ratio of length to breadth about 5:3 in all the specimens.

Tentacles with soft discs having 4–8 (usually 6) rounded processes on the edge. The processes are always clearly visible – although they are usually somewhat contracted – and often give a cup-shaped appearance to the discs. In all the specimens most of the tentacles are retracted into the oral cavity.

Circum-oral papillae. As described by Théel the mouth is placed in the centre of a radially furrowed circular field, surrounded by a circle of minute papillae. The papillae are clearly visible only in the *Galathea* specimen from St. 668. However, in some of the specimens a number of small pits indicate retracted circum-oral papillae.

Table 1. *Deima validum validum.* Number of tubefeet and papillae in the *Galathea* specimens.

Station	Length (cm)	Ventro-lateral tubefeet	Dorsal papillae	Ventro-lateral papillae
190	5.0	11–11	–	–
–	6.5	12–12	6–6	(3–3)
193	7.0	11–11	5–5	3–3
–	7.5	11–11	5–6	3–3
–	7.5	11–11	5–5	3–3
–	8.0	11–11	6–6	3–3
–	9.5	11–11	5–5	3–3
217	5.0	12–12	7–7	6–
234	4.0	11–11	5–5	3–3
–	6.0	11–11	5–5	3–3
–	7.0	11–11	6–6	7–6
–	8.0	11–11	–	4–
–	11.0	12–11	5–5	3–3
–	12.0	11–11	5–5	3–3
235	9.0	10–10	–	–
279	5.0	11–	7–7	(6–6)
–	6.5	11–11	–	(6–6)
281	9.0	12–14	5–5	5–5
574	8.5	10–10	7–7	6–7
668	4.0	10–10	–	–

Ventrolateral tubefeet single-rowed. The variation in number is shown in Table 1.

Pre-anal tubefeet absent in all the specimens.

Dorsal and ventrolateral papillae rigid and conical. They are nearly always broken, and few can be measured. They probably vary in length from $^{1}/_{4}$ to $^{1}/_{2}$ body length. Very small papillae (only a few millimeter long) are present in the 5 cm long specimen from St. 217.

The variation in number of papillae appears in Table 1.

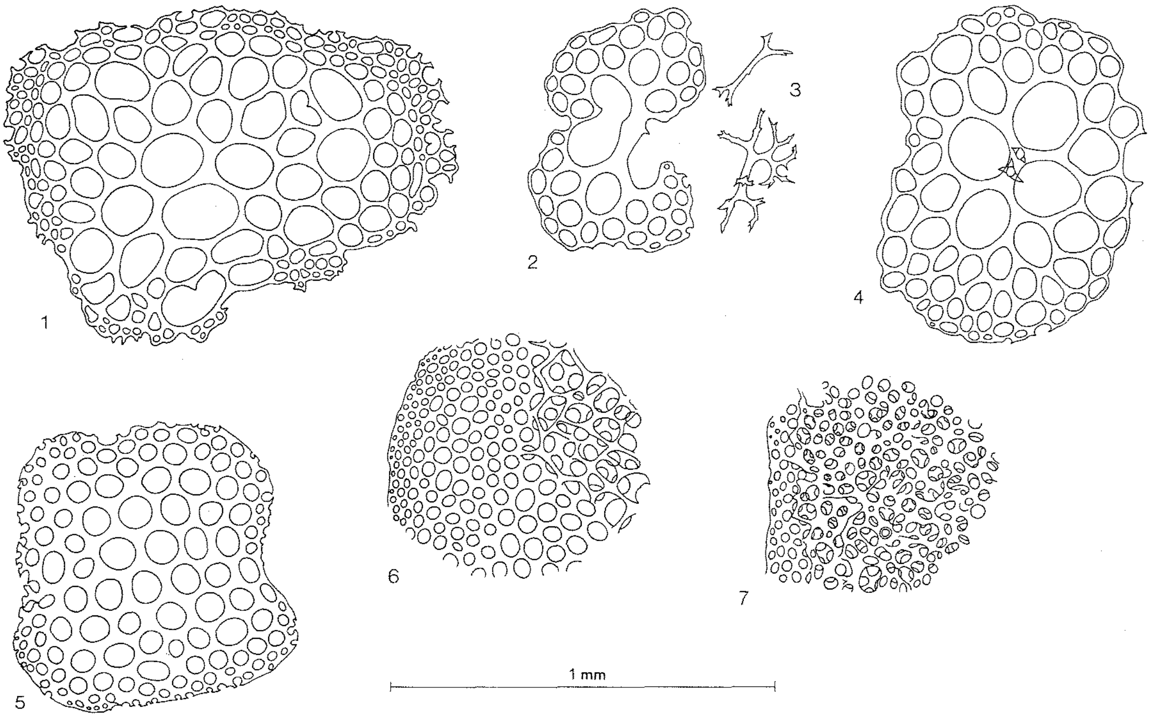


Fig. 1. *Deima validum validum* (1–4, 6–7) and *D. v. pacificum* (5). Deposits. 1, *Galathea* St. 668, dorsum; 2–4, *Blake* Exp., off St. Vincent, West Indies *(D. blakei)*, ventrum (2–3) and dorsum (4); 5, *Albatross* St. 3362 *(D. pacificum)*, dorsum; 6, *Albatross* St. 4956 *(D. mosaicum)*, dorsum; 7, *Galathea* St. 190, dorsum.

Deposits (Fig. 1) large, imbricating, perforated plates, the diameters of which vary greatly within the single specimen. In the specimens from the Indian Ocean the dorsal plates attain a diameter of 4–7 mm, while the ventral ones measure 2–3, occasionally 4 mm. The two specimens from the Tasman Sea have smaller plates; in the specimen from St. 550 the plates measure up to 2 mm both dorsally and ventrally, while in the specimen from St. 574 the dorsal plates reach about 2.5 mm, and the ventral ones only 1 mm in diameter. In the specimen from the Kermadec Trench the dorsal and ventral plates are up to 1.5 mm in diameter.

The plates consist of a basal layer with rather small, rounded holes which diminish somewhat in size towards the periphery, and one or more additional layers with irregular meshes. The first additional layer starts from vertical spines on the basal plate, the ends of the spines developing horizontal ramifications, which merge with those from other spines. The successive additional layers arise in a more irregular manner, the layering of the plates thus becoming more and more effaced. The additional layers become gradually smaller. In the specimen from St. 281 the additional layers amount in the centre of the dorsal plates to four or five, forming a low, conical knob. The other specimens from the Indian Ocean (Fig. 1:7) have two or three (sometimes only one) additional layers in the dorsal plates. The ventral deposits in the specimens from the Indian Ocean have one additional layer, occasionally with indications of a second additional layer.

The two specimens from the Tasman Sea have, in agreement with the small size of the plates, only one additional layer in the dorsal plates, and practically none in the ventral ones. As in the Indian Ocean specimens the holes of the basal plate are numerous, regularly rounded, and rather small also in the central part of the plate. The specimen from St. 668 in the Kermadec Trench has exclusively one-layered plates (Fig. 1:1) which resemble those of *Oneirophanta mutabilis.*

External to the perforated plates in the two specimens from the Tasman Sea, and in most of the specimens from the Indian Ocean, are found a number of small, dichotomously branched rods, similar to those figured by Théel for *D. validum*. Their occurrence is fortuitous – being present in the preparations from some specimens, and absent from those of others from one and the same station.

The peritoneal layer of the skin and the walls of the gonadal tubules usually contain ramified spicules, which may be closed to form perforated plates with a few large, irregular meshes, similar to those figured by Théel for *D. validum*. The occurrence of these inner spicules is, like that of the outer branched spicules, accidental and without taxonomic significance.

Description of the specimens from *Albatross* St. 2763: The two specimens from St. 2763 (off Rio de Janeiro) were labelled "*Deima validum*" (identified by W. K. Fisher). Body length 7.0 and 8.5 cm. Tentacles (mostly retracted) cup-shaped with marginal digits. Oral field with radial furrows and surrounded by a circular wall (circum-oral papillae not seen). Ventrolateral tubefeet 11 pairs. Pre-anal tubefeet one pair. Dorsal papillae 7 pairs. Ventrolateral papillae 4 pairs. The papillae are flexible, with somewhat rounded ends; they are 2–3 cm long in the large specimen, and 1.0–1.5 cm in the small specimen. Perforated plates one-layered ("*Oneirophanta*-like"), 0.7–1.0 mm in diameter both in dorsum and ventrum (the ventral plates are more robust than the dorsal ones). (The description of the perforated plates refers to the large specimen only, while the statements of the external features refer to both specimens). Rods absent from the papillae in both specimens.

Review and re-examination of previously described material: The six nominal species here merged to a single, cosmopolitan species were separated almost exclusively on purely quantitative characters such as the number and size of the dorsal papillae, and the diameter and number of layers in the perforated plates. Some taxonomic significance has likewise been attributed to the presence or absence of ramified outer and inner spicules of the skin. The examination of the *Galathea* material proved this to be unwarranted.

Although the species were based on an overestimation of the taxonomic characters, the differences reported between the species are not without taxonomic interest. They indicate to some degree a geographic or local variation in *Deima validum*. This applies most clearly to the eastern Pacific *D. pacificum,* where the number of dorsal papillae exceeds the variation otherwise found in *D. validum* without any overlapping. The species is here retained as a geographic subspecies of *Deima validum*. The Japanese species *D. mosaicum,* the species *D. fastosum* from north of New Guinea, and the West Indian representatives of *D. blakei* likewise differ from the typical *Deima validum,* although less clearly than *D. pacificum*. They have not been considered of subspecific rank but are united with *D. atlanticum* and *D. validum* to form the subspecies *Deima validum validum.*

The five species included under *D. validum validum* are here briefly described in order to make possible a discussion of the variation within the subspecies.

Deima validum Théel was erected on two specimens from *Challenger* St. 246 at 3749 m in the North Pacific. The type specimen (in BM) was re-examined. Ventrolateral tubefeet 11 pairs. Pre-anal tubefeet absent. Dorsal papillae (7–)9 pairs. Ventrolateral papillae 6 pairs. (Théel stated a different number of papillae, owing to the first pair of dorsal papillae being counted as ventrolateral ones. However, this was changed by Ludwig (1894), whose terminology is adopted in the present work). Perforated plates reaching 7 mm, with the basal plate covered by an additional meshwork. They are indistinguishable from those of the *Galathea* specimens from the Indian Ocean. *D. validum* was later reported from Indonesia by Sluiter (1901b) who referred four specimens from three *Siboga* stations at 724–1158 m to this species, without giving a description of them. Re-examination of the specimens revealed an interesting variation.

The specimen from *Siboga* St. 85 (Makassar Strait) is 5.5 cm long. Tentacles partly unretracted, apparently all having six well-developed marginal knobs. Dorsal papillae slender and pointed, reaching 4 cm. Perforated plates dorsally 1–2 mm, ventrally 0.5 mm; the plates are strictly single-layered, with large central, and small peripheral holes, and sometimes with a few rudimentary spines.

The two specimens from *Siboga* St. 286 (south of Timor) are 6.0 and 11.5 cm long, respectively. Tentacles retracted in both specimens. Small specimen: Ventrolateral tubefeet 10 pairs. Pre-anal tubefeet one pair. Dorsal papillae 7–8 pairs, all shorter than 1 cm. Large specimen: Ventrolateral tubefeet 11 pairs. Pre-anal tubefeet one pair. Dorsal papillae 7 pairs, up to 3 cm long. A preparation from the dorsal skin of the small specimen contained plates similar to those from St. 85.

The specimen from *Siboga* St. 211 (south of Celebes) is 2.7 cm long, and very defective, with nearly all the perforated plates lying at the bottom of the vial. A preparation showed plates up to 2.5 mm in diameter, which, in their structure, were intermediate between those found in the two other examined *Siboga* specimens and those of the *Galathea* specimens from the Indian Ocean: The basal plate had rather small perforations from centre to periphery and was covered by an additional, feebly developed, reticulated layer.

Deima fastosum Théel was taken in two specimens at *Challenger* St. 216 north of New Guinea at 3658 m (the type specimen in BM, the other in ZMUC). Ventrolateral tubefeet 11–13 pairs. Pre-anal tubefeet absent. Dorsal papillae 5 pairs. Ventrolateral papillae 3 pairs. Perforated plates reaching 5 mm, with a large, reticulated, conical knob.

The knobbed plates are not, in principle, different from the usual plates in *D. validum,* which by the addition of successively smaller secondary layers often approach the shape of a low pyramid. Nevertheless, the plates in the two specimens of *D. fastosum* represent an extreme case in the variation of the plates, hardly ever approached in other known specimens. Both specimens were re-examined by means of preparations and the knobs were seen to be very high, often rising vertically from the plate and giving the skin an almost spinous appearance.

Apart from the peculiar plates, the two specimens agree with a typical *D. validum.*

Deima blakei Théel has been recorded several times from off the West Indies at 1049–1783 m (Théel 1886b, Deichmann 1930, 1936, 1940). Reexamination was made of four specimens from a *Blake* station off St. Vincent, one from a *Blake* station south of Jamaica, one from the *Atlantis* St. 3358, and one from the *Atlantis* St. 3366 (all in MCZ).

Tentacles with 4–10 (usually 7–10) marginal knobs. Circum-oral papillae visible in several specimens. Ventrolateral tubefeet 11 pairs (two specimens had 12 tubefeet on one side). Pre-anal tubefeet present. Dorsal papillae 5–10 pairs. Ventrolateral papillae 4–5 pairs. (Deichmann (1940) found 3–7 pairs of ventrolateral papillae in her material). The papillae varied greatly in shape, from rigid and conical to flexible and slender.

The perforated plates of the re-examined specimens (Fig. 1: 2–4) were small, usually less than 1.5 mm across in the dorsum and 1.2 mm in the ventrum. A secondary layer was absent, or at the most feebly indicated. The holes of the central part of the plates were remarkably large, and often rather angular in outline. In one specimen almost all the ventral plates had an elongated primary rod (Fig. 1: 2). As noted by Deichmann the plates are reminiscent of those of *Oneirophanta mutabilis.*

Hérouard (1923) reported a specimen of *D. blakei* from 2779 m off Cape Finisterre (Spain). The specimen (not re-examined) had 11 pairs of ventrolateral tubefeet, one pair of small pre-anal tubefeet, 7 pairs of dorsal, and 4 pairs of ventrolateral papillae; perforated plates usually 2–3-layered, measuring 2–3 mm dorsally, 0.6–0.7 mm ventrally. Apart from their smaller size the plates probably agreed with those of the *Galathea* specimens from the western Indian Ocean and those of the *Challenger* specimens of *D. validum* from the northern Pacific. They differed distinctly from the plates of the West Indian specimens of *D. blakei.*

Koehler & Vaney (1905) recorded nine specimens of *D. blakei* from eight *Investigator* stations at 1224–3365 m in the Bay of Bengal and the Arabian Sea. Ventrolateral tubefeet 10–12(13) pairs. Midventral tubefeet present or absent. Dorsal papillae 6–9 pairs. Ventrolateral papillae 4–7(9) pairs. Perforated plates varying from 2–3 to 5–6 mm (the size was not specified for dorsum and ventrum). Some specimens were almost without an additional layer, the basal plate having only a few spines with some horizontal ramifications; in other specimens 2–3-layered plates predominated. No correlation was present between the number of layers and the size of the specimens.

The determination of the specimens was apparently based on the feeble development of the secondary layers in many of the plates. A figured plate shows (like those of the West Indian specimens of *D. blakei* and two of the reexamined *Siboga* specimens) a remarkable similarity to *O. mutabilis* plates in the large central and small peripheral holes and the minute spines.

Deima atlanticum Hérouard was taken in five specimens at 4360 m between the Azores and Portugal. Ventrolateral tubefeet 11 pairs. (Midventral tubefeet not mentioned). Dorsal papillae 5 pairs. Ventrolateral papillae 3 pairs. Perforated plates 2-layered (their size not mentioned). A figure of a part of a plate indicates that the plates are similar in type to those of the *Galathea* specimens from the western Indian Ocean and the *Challenger* specimens of *D. validum*.

Hérouard (1923) later stated that the two Atlantic species *D. atlanticum* and *D. blakei* differed from each other in the number of papillae and in the position of the first pair of tubefeet in relation to the mouth. However, the variation present in the *Galathea* specimens shows that both differences are individual variations only.

Grieg (1921) reported one specimen from a depth of 2800–3000 m west of the Canary Islands, having, like Hérouard's specimens, 11 pairs of ventrolateral tubefeet, 5 pairs of dorsal, and 3 pairs of ventrolateral papillae.

Deima mosaicum Ohshima is known from six specimens taken at two Japanese stations, at 1317 and 1680 m. Tentacles 18, with 7–10 marginal knobs. Circum-oral papillae present. Ventrolateral tubefeet 11–13 pairs. Pre-anal tubefeet one pair. Dorsal papillae 8–10 pairs. Ventrolateral papillae 4–5 pairs. The papillae were very long, measuring up to 8 cm (the largest specimen was stated to be 11 cm long). Dorsal perforated plates 3–4 mm, 2-layered. Ventral perforated plates 0.8–2.0 mm, single-layered. Re-examination of the deposits of two specimens (in USNM) confirmed that the plates (Fig. 1:6) had a feebly developed secondary layer.

The long papillae and the presence of only 18 tentacles were regarded as the distinguishing characters of the species. As will be seen, the long papillae, as well as the relatively high number of dorsal papillae, appear to be rather characteristic of Japanese specimens, although these features do not justify the erection of a species. On the other hand, the tentacle number reported for *D. mosaicum* represents hardly more than an individual variation. In *Oneirophanta mutabilis*, in which the tentacles are unretractile and easily counted, the number was seen to vary from 18 to 20 even among specimens from a single station.

Variation:

After examination of the *Galathea* material and the review of previous materials, an analysis of the variation in the taxonomic characters may be attempted.

Tentacles 18–20, with 4–10 marginal knobs. The variation in tentacle number as well as in number of knobs seems to be an individual one only.

Circum-oral papillae probably always present. They have been found in specimens of all the six species here synonymized.

Ventrolateral tubefeet single-rowed and remarkably constant in number. The variation is 10–13 pairs – 11 pairs being the most common number all over the distributional area of the species (including the subspecies *pacificum*).

Midventral tubefeet absent, or represented by a reduced pre-anal pair only. Their absence in all the specimens from the western Indian Ocean suggests that some geographic variation exists in their presence or absence.

Dorsal papillae 5–10 pairs. Although the whole range of variation in number may be found in West Indian specimens, some geographic variation appears to exist within the subspecies. While the specimens from the eastern Atlantic and the western Indian Ocean had 5–7 pairs, those from other regions had higher numbers (northern Indian Ocean 6–9, Indonesia 7–8, Japan 8–10, and northern Pacific 7–9 pairs). Only the specimens of *D. fastosum* from north of New Guinea had a low number of papillae (5 pairs).

The relatively high number of dorsal papillae in the specimens from Japan and the North Pacific points towards the conditions in the subspecies *pacificum* from the Gulf of Panama, in which 11–16 pairs are present. Unfortunately, no specimens are known from intermediate regions.

Ventrolateral papillae 3–7 pairs (only one specimen from the northern Indian Ocean provided an exception, having 9 left and 7 right papillae). The specimens from the *Galathea* St. 234 comprised almost the total variation found in the species. No geographic variation is present in the number – not even between the two subspecies.

Unusually long papillae were found in *D. mosaicum* and in one of the re-examined *Siboga* specimens from Indonesia. The fact that two other *Siboga* specimens had very short papillae calls for circumspection in the taxonomic use of the length of the papillae. A remarkable variation in length of the papillae was also found in the *Galathea* specimens from the western Indian Ocean.

Deposits. The variation in the perforated plates comprises their diameter, the development of additional layers of meshwork, and the size and size-distribution of holes in the basal plate. Bathymetric as well as geographic features are present in the variation, but no age variation could be distinguished.

Perforated plates with one or more additional layers of meshwork, and with numerous regular holes in the basal plate characterize the *Galathea* specimens from the western Indian Ocean (2720–4820 m), and the two *Challenger* specimens from the northern Pacific (3749 m). The specimens from the eastern North Atlantic (2779–4360 m) probably belong to the same type. The deposits of *D. fastosum* (north of New Guinea, 3658 m) represent an extreme development of this "abyssal" type of plate.

The specimens from the Tasman Sea (4530–4670 m) are the only specimens taken deeper than 2700 m which have a feebly developed additional meshwork on the plates; the plates of these specimens resemble those found in *D. mosaicum* (Japan, 1317–1680 m), and in the specimen from *Siboga* St. 211 (south of Celebes, 1158 m).

Perforated plates completely or almost completely devoid of additional meshwork were found in West Indian specimens (1049–1783 m), the specimen taken off Rio de Janeiro (1227 m), the specimen from the Kermadec Trench (2640 m), in three Indonesian *Siboga* specimens (Makassar Strait, 724 m; south of Timor, 883 m), and in the subspecies *D. validum pacificum* (eastern Pacific, 1618–2487 m).

Geographic differences are represented by the slenderly built plates with large central holes characteristic of West Indian specimens, and the robust plates with rather small holes even in the central part which are characteristic of the eastern Pacific subspecies.

Although on the whole one-layered plates are characteristic of bathyal specimens and many-layered plates of abyssal specimens, the presence of a transitional type of plate in the abyssal Tasman Sea specimens and in the bathyal Japanese specimens prevents a clear distinction between a bathyal and an abyssal type of deposit.

The excessive development of additional layers of meshwork in abyssal specimens, which is usually correlated with a large size of the plates, may represent a phenotypic feature. If this is true one might expect, in regions where the species has a wide bathymetric range, a gradual increase in the development of additional layers of meshwork with increasing depth. So far, such a region is known only in the Bay of Bengal (1224–3365 m). According to Koehler & Vaney (1905) the deposits here comprised 1-, 2-, and 3-layered plates; however, the types of plate were not specified for specimens from different depths.

Conclusion. A *geographic variation* within the subspecies is suggested by an increase in the average number of dorsal papillae from the eastern Atlantic and the western Indian Ocean towards the northern Pacific, where the number approaches that found in the subspecies *pacificum* from the Gulf of Panama. On the other hand, the variation shown by West Indian specimens comprises the whole variation in number of dorsal papillae found within the subspecies *validum*.

Absence of midventral tubefeet may be characteristic of specimens from the western Indian Ocean.

No geographic variation was found in the number of ventrolateral papillae or ventrolateral tubefeet.

Papillae of unusual length characterize the known Japanese specimens. However, the variation in length of papillae may be large at other localities; this points to a limited value of the feature in taxonomy.

Slenderly built perforated plates with large central holes are characteristic of West Indian specimens. They represent the type which is farthest from the sturdy and small-holed plates found in the subspecies *pacificum*.

A *bathymetric variation* is indicated by an increase with depth in the development of the additional meshwork on the perforated plates.

An *individual variation* appeared in the number of dorsal papillae in West Indian specimens, and in the length of dorsal and ventrolateral papillae in specimens from Indonesia and the western Indian Ocean.

Type: BM, labelled "Type".
Type locality: *Challenger* St. 246 (36°10'N, 178° 00'E).

Deima validum pacificum Ludwig, 1894

Deima pacificum Ludwig, 1894, pp. 63–70, pls. VIII: 5–8, IX: 1–4.
Deima validum pacificum Ludwig, Hansen 1967, pp. 488–490, fig. 5.

Diagnosis: Ventrolateral tubefeet 11 pairs. Preanal tubefeet, one pair. Dorsal papillae 11–16 pairs. Ventrolateral papillae 4–5 pairs. Perforated plates small and single-layered, dorsally 1.5–2.0 mm in diameter, ventrally half as large.

Remarks: Known only from 16 specimens taken by the *Albatross*. Of these, 7 specimens were reexamined (4 in USNM, 1 in MCZ, 1 in BM, 1 in ZMUC).

The subspecies is characterized, in particular, by the large number of dorsal papillae. The presence of pre-anal tubefeet and the small, single-layered perforated plates (Fig. 1: 5) are less characteristic features, being occasionally found also in *D. validum validum*. The relationships between the two subspecies were discussed under *D. validum validum*.

Type: USNM, labelled "Type".
Type locality: *Albatross* St. 3407 (0°04'S, 90°24'W).

Genus ***Oneirophanta*** Théel, 1879
Fig. 110

Théel 1879, p. 6; Théel 1882, p. 62. – Type species: *Oneirophanta mutabilis* Théel, 1879, by monotypy.

Diagnosis: Tentacles 15–20, unretractile; discs usually with rounded knobs on the margin but never with ramified processes. Circum-oral papillae absent. Deposits spatulated crosses or perforated, one-layered plates; spatulated rods present, at least in the papillae.

Remarks: *Oneirophanta conservata* may prove to have ramified tentacle discs, and thus actually belong to *Orphnurgus*.

Key to the species of *Oneirophanta*

1\. Body wall with spatulated crosses. Papillae with a bristle-like cluster of spatulated rods . . . . *setigera* (p. 36)
1\. Body wall with perforated plates. Papillae with perforated plates and occasional spatulated rods 2
2\. Each side with 8–28 ventrolateral tubefeet, 4–35 dorsal papillae (in single or double rows), and 4–17 ventrolateral papillae . . . . *mutabilis* (p. 24)
2\. Each side with about 33 ventrolateral tubefeet, 30 dorsal papillae (in double rows), and 13 ventrolateral papillae . . . . *conservata* (p. 36)

Oneirophanta mutabilis Théel, 1879
Figs. 2–9, 94: 2, 96, pls. VIII: 1–4, XI: 2–8, XIII: 3–9

Diagnosis: Tentacles 18–20. Each body side with 8–28 ventrolateral tubefeet (in single or alternating double rows), 4–35 dorsal papillae (in single or double rows), and 4–17 ventrolateral papillae. All papillae usually slender and flexible. Midventral tubefeet few, or absent. Deposits perforated plates, single-layered or with a feebly developed additional layer.

Distribution: *Oneirophanta mutabilis* is characteristic of the deep-abyssal zone, practically all records being from depths between 3200 and 6000 m. The species has been found in almost all regions where these depths have been explored.

Based on differences in the shape of the tentacles, the type of deposit, and the number of dorsal papillae a division of the species into two geographic subspecies was proposed by Hansen (1967). *O. mutabilis affinis* is restricted to a relatively small area in the eastern Pacific where it replaces the otherwise cosmopolitan *O. m. mutabilis*.

Oneirophanta mutabilis mutabilis Théel, 1879

Oneirophanta mutabilis Théel, 1879, pp. 6–7, figs. 4–6; Théel 1882, pp. 62–68, pls. XXI: 2, XXII, XXXI: 1–3, XXXVI: 1–2, 8–11, XXXVII: 4, 13, XXXVIII: 11–12, XL: 1–3, XLI: 1–2, 4, XLII: 9, XLIII: 1, 6, XLV, XLVI: 6–7; R. Perrier 1902, pp. 374–380, pl.

XVIII: 10–15; Clark 1913, p. 232; Grieg 1921, p. 5, pl. II: 1–2; Hérouard 1923, pp. 39–40, pls. IV: 10, V: 3–4; Ekman 1927, pp. 364–366, figs. 1–2; Agatep 1967b, pp. 63–65, pl. X: 1–7.

Oneirophanta mutabilis mutabilis Théel, Hansen 1967, pp. 485–488, figs. 3–4.

Oneirophanta alternata R. Perrier, 1900, pp. 117–118; R. Perrier 1902, pp. 380–386, pls. XIV: 3–4, XVIII: 16–22.

Oneirophanta alternata var. *talismani* R. Perrier, 1902, pp. 386–388, fig. 6.

Diagnosis: Tentacle discs with marginal, rounded knobs. Each body side with 8–28 (36) ventrolateral tubefeet, 4–19 dorsal papillae (in single rows), and 4–17 ventrolateral papillae. Deposits rather slenderly built perforated plates; occasionally, deposits with open ramifications predominate.

Material:

St. 192, off Durban (32°00'S, 32°41'E), 3430 and 3530 m (two hauls). – 3 specimens.

St. 217, Mozambique Channel (14°20'S, 45°09'E), 3390 m. – 1 specimen.

St. 654, Kermadec Trench (32°10'S, 175°54'W), 5850–5900 m. – 14 specimens.

St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 1 specimen.

St. 664, Kermadec Trench (36°34'S, 178°57'W), 4540 m. – 5 specimens.

Description:

The *Galathea* material of *O. m. mutabilis* came from the western Indian Ocean and the Kermadec Trench. Remarkable differences were found between the specimens from these two regions, possibly indicating a geographic variation. In addition, a considerable individual variation, as well as local differences between specimens from closely situated stations in the same region were found. In order to distinguish between the different types of variation, the material from the different stations (and to some degree the single specimens), is treated separately.

St. 192. – Specimen No. 1 (Fig. 2).

Body size 10×4 cm.

Tentacles 20, with 8 (occasionally 6) rounded knobs on the edge of the disc.

Ventrolateral tubefeet 17 on each side, in alternating double rows.

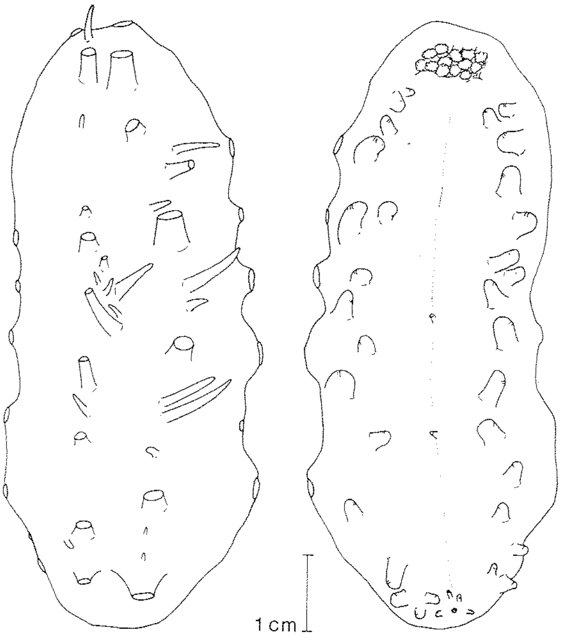


Fig. 2. *Oneirophanta mutabilis mutabilis*. St. 192. Specimen No. 1 in dorsal and ventral view.

Midventral tubefeet 4, rudimentary.

Dorsal papillae 17–18 on each side, without bilateral symmetry. Only very few are preserved intact in their full length; however, none probably exceeded 2 cm in length. The papillae show a remarkably irregular variation in diameter. Thus, the longer papillae vary from 2 to 5 mm in diameter at the base. Short and long, stout and slender papillae follow each other without regular sequence.

Ventrolateral papillae approximately 8–10 on each side. All the papillae are torn off at the base.

Deposits perforated plates, 2–3 mm in diameter, with a rather slender meshwork. The plates carry a number of small, vertical spines, but never a secondary layer of meshwork.

Papillae with perforated plates only – even in the slenderer ones rods are absent.

Tubefeet with perforated plates which are progressively reduced towards the sucking-discs.

Tentacles with irregularly placed rods which are usually stout and somewhat branched.

The total absence of spatulated rods in the specimen is noteworthy.

St. 192. – Specimen No. 2.

Body size 9×3.5 cm.

Tentacles (Pl. VIII: 2) varying in shape and remarkably different from those of specimen No. 1. The discs are sometimes asymmetrical, one side carrying processes so long and closely placed that they resemble the fingers of a hand, whilst on the opposite edge the processes can hardly be distinguished. Some of the discs are regularly star-shaped.

Ventrolateral tubefeet probably about 12–14 on each side, in alternating double rows.

Midventral tubefeet one pair, rudimentary, pre-anal; possibly more have been present.

Dorsal papillae very slender and short, the longest reaching only 7–8 mm. They are remarkably few in number: Four or five can be counted on each side, and the dorsal skin is so intact that only a few more can have been present.

Ventrolateral papillae few in number: Only two or three, a few millimeter long, are seen on each side.

Deposits as specimen No. 1. No deposits preserved in papillae.

St. 192. – Specimen No. 3.

Body size 8×4 cm.

Tentacles intermediate in shape between those of specimens Nos. 1–2.

Ventrolateral tubefeet probably about 12 on each side, in uneven single rows.

Midventral tubefeet absent.

Dorsal papillae apparently as few and as reduced as in specimen No. 2. Only three are seen on the whole dorsal side, the largest measuring 6 mm. Scar-markings indicate that more papillae have been present – a few of them probably rather stout.

Ventrolateral papillae mostly indicated by scar-markings, rudimentary and probably amounting to 5–6 pairs.

Deposits as specimens 1–2. No deposits preserved in papillae.

St. 217. – The specimen is 10 cm long and very defective, all the papillae being torn off. Only a few papillae scars are to be seen; the number of papillae probably did not exceed that in specimens 1–2 from St. 192. Ventrolateral tubefeet about 14 on each side, in alternating double rows. Midventral tubefeet few, rudimentary. Tentacles with 8 rounded knobs. Deposits as in the specimens from St. 192.

St. 654. – The 14 specimens are 3.5–9.5 cm long, and of a very uniform appearance (Fig. 3).

Tentacles (Pl. VIII: 1) usually 20, but at least one specimen has only 18. The discs carry 6–10 (usually 8) rounded knobs on the edge, and fall within the variation of the specimens from the Indian Ocean.

Tubefeet and papillae well preserved. They could be counted in nearly all cases (Table 2).

Table 2. *Oneirophanta mutabilis mutabilis.*
Number of tubefeet and papillae
in the specimens from St. 654.

	Length (cm)	Ventro-lateral tubefeet	Mid-ventral tubefeet	Dorsal papillae	Ventro-lateral papillae
Specimen 1	3.5	–	–	–	–
– 2	4.0	10–11	4	5–5	–
– 3	4.0	11–11	4	5–5	4–4
– 4	5.0	12–12	3	5–5	4–5
– 5	5.5	11–11	2	5–5	5–5
– 6	6.0	12–12	4	5–5	4–4
– 7	6.5	13–12	4	7–7	5–5
– 8	6.5	11–11	4	–	–
– 9	7.0	12–12	4	5–5	7–7
– 10	7.0	13–12	3	5–5	5–4
– 11	7.5	12–12	3	5–5	4–4
– 12	7.5	13–13	4	5–5	5–5
– 13	7.5	13–12	4	7–7	6–6
– 14	9.0	14–13	4	7–7	7–7

A striking similarity between the specimens is shown by the arrangement and type of reduction of the papillae. It is possible to establish the homology of the individual papillae and to ascertain which of them are absent, when less than the maximum number is found.

The full number of dorsal papillae is seven pairs. Pairs Nos. 1, 2, 4, and 6 are in all the specimens well developed, measuring 2–4 cm. Nos. 3 and 5 are reduced or absent, while No. 7 is reduced, although present in all the specimens.

The fact that the reduced pairs of papillae are always the same and that the reduction always applies to both papillae of a pair, is very remarkable. A further peculiarity in the arrangement of the dorsal papillae is common to all the specimens: The left papilla of pair No. 4, and to some degree of No. 6, is in all the specimens placed more posteriorly than the corresponding right one. In some specimens this applied also to the second pair of papillae.

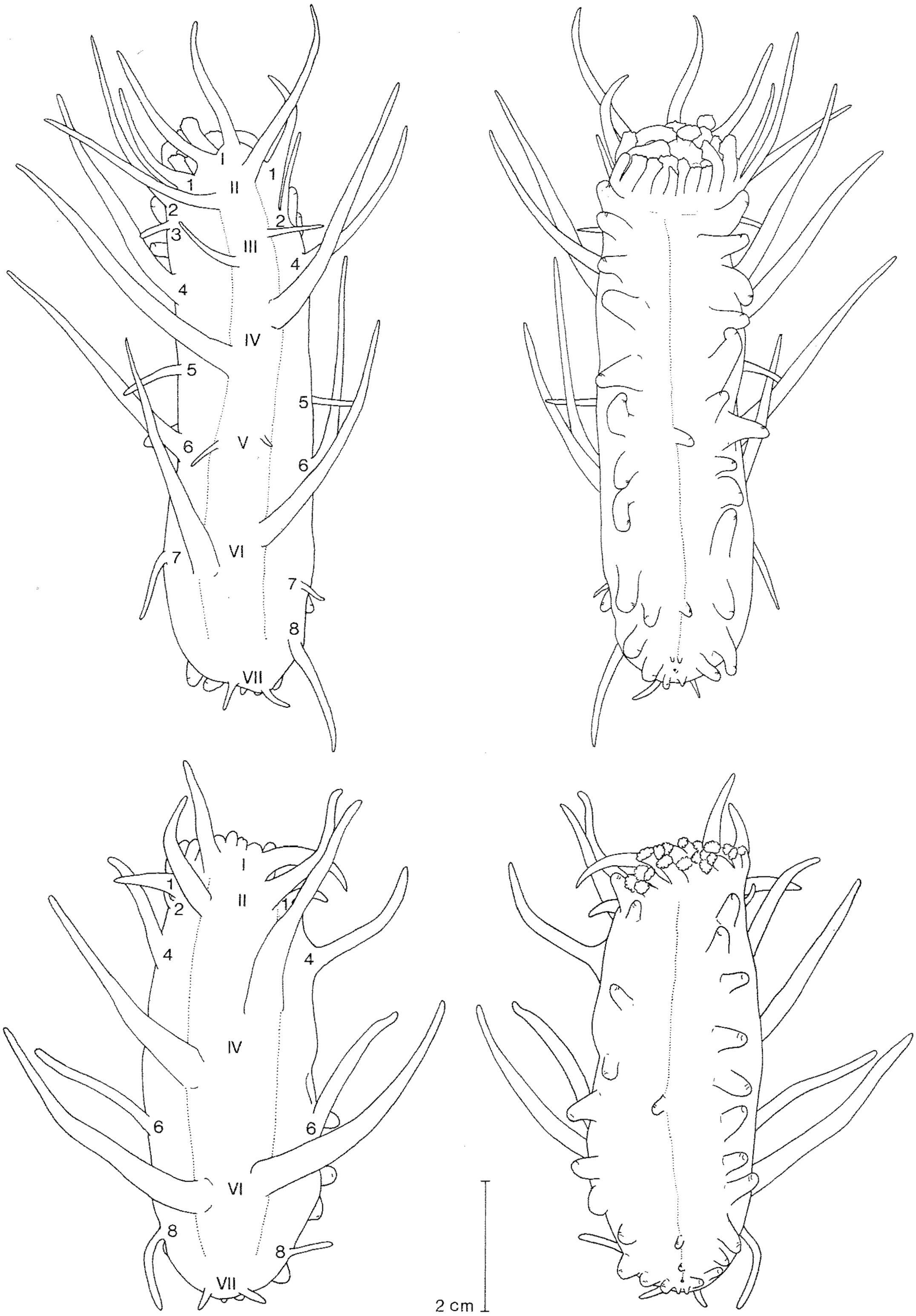


Fig. 3. *Oneirophanta mutabilis mutabilis*. St. 654.
Two specimens in dorsal and ventral view. (Above, specimen No. 14; below, specimen No. 10).
I–VII, dorsal papillae; 1–8, ventrolateral papillae.

The ventrolateral papillae show, apart from the rather irregularly reduced first two pairs, a similar regularity in the reduction. Here, the starting-point for the reduction is a specimen with eight pairs of papillae. The first two pairs are placed near each other on the head, while the remaining pairs are placed at a more or less equal distance down the body.

Pairs Nos. 3, 5, and 7 are more or less reduced, or absent, in all the specimens. Pairs 4 and 6 are always long. Pair 8 is, like the hindmost pair of dorsal papillae, usually rather short.

Only in specimen No. 14 (Fig. 3, above) all eight pairs of ventrolateral papillae are represented. The specimen lacks only the right papilla of pair 3 and the left one of pair 8 (the right one of the latter pair is 2 cm long). While the absent No. 3 belongs to a pair which is always reduced, the absence of the left No. 8 is an exceptional case of asymmetrical reduction.

The ventrolateral papillae are generally somewhat shorter than the dorsal ones, although they may reach 3.5 cm.

The left ventrolateral papillae are often posteriorly displaced compared to the corresponding right ones – a peculiarity similar to the conditions found in the dorsal papillae.

Midventral tubefeet are present on the posterior half of the body in all the specimens. They show in their arrangement a uniformity as remarkable as that of the papillae. The four midventral tubefeet present in most of the specimens consist of a rudimentary pre-anal pair and two larger, unpaired ones – one placed a little in front of the anus, the other near the middle of the ventrum. In the three specimens with three midventral tubefeet, one of the rudimentary pre-anal ones is absent, while the two unpaired ones are present at the usual place. The specimen with two midventral tubefeet lacks one of the pre-anal and the posterior of the unpaired tubefeet.

Deposits (Fig. 4) greatly varying; usually, numerous irregular developmental stages are present in the preparations.

The degree of development of the deposits is not correlated with the size of the specimens. Two of the smallest specimens, 3.5 and 4.0 cm long, have almost without exception the deposits developed as large, perforated plates, while one of the largest specimens has incompletely developed plates with open ramifications. Similarly, in some specimens the deposits are nearly all at the same stage of development, while in others

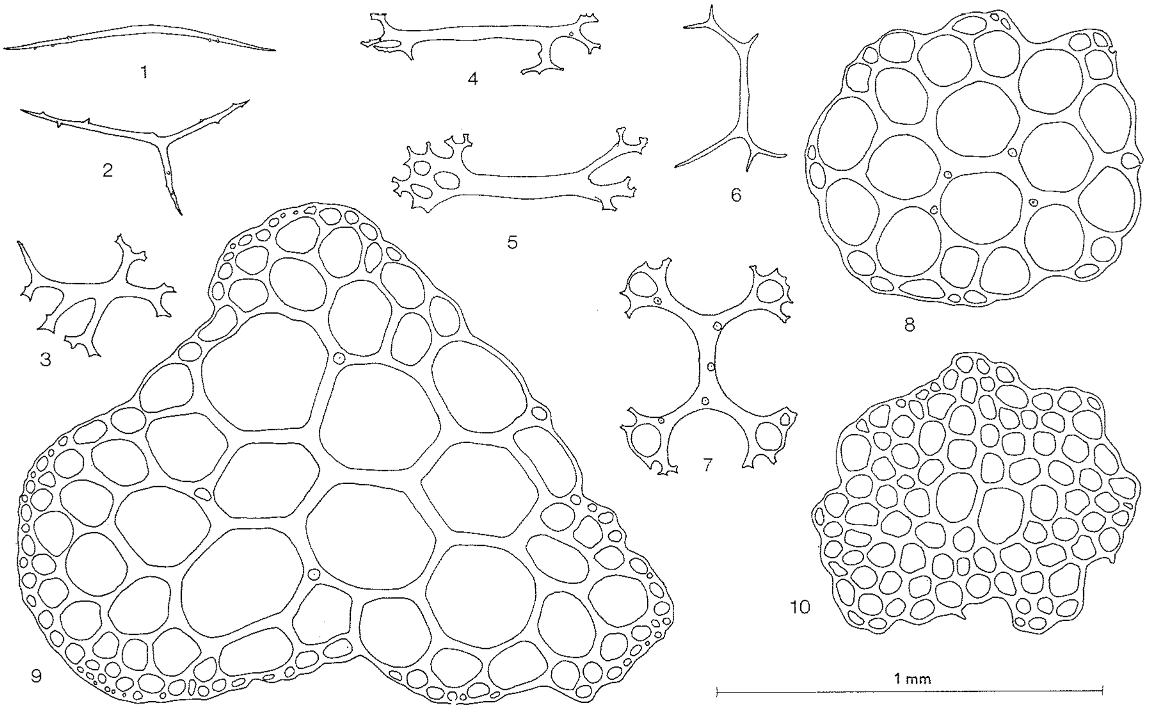


Fig. 4. *Oneirophanta mutabilis mutabilis.* Deposits. St. 654. 1–5, irregular deposits; 6–7, developmental stages towards large-holed plates; 8–9, large-holed plates; 10, small-holed plate.

the deposits belong to very different developmental stages.

Often the incompletely developed deposits are so irregular (3–5) that they cannot be regarded merely as developmental stages of plates.

Fully developed plates with closed holes round the whole periphery (8–9) are rare in all the preparations. They are up to 1.8 mm in diameter both in large and small specimens. Usually, the central holes are large and the peripheral ones small; however, another type (10) is also found in which the holes are all small. In some specimens the separation between the two types is very clear, but in others intermediary forms occur. The small-holed plates have a more irregular outline than the large-holed ones, although they both attain the same size. Some of the small-holed plates are derived from the large-holed type by a secondary division of the large holes.

The ventral deposits usually vary more and are less well developed and less irregular than the dorsal ones.

In some papillae spatulated rods prevail from base to tip, while in others the deposits are almost exclusively plates, only with a few spatulated rods at the tip.

Tentacles and tubefeet have sturdy rods with open, terminal ramifications, very different from the long and slender spatulated rods of the papillae.

St. 663. – The single specimen is 5.5 cm long.

Tentacles with marginal knobs on the discs.

Ventrolateral tubefeet 17 pairs.

Midventral tubefeet one pair, rudimentary, pre-anal.

Dorsal papillae 5 left and 6 right. In their arrangement they agree with those of the specimens from St. 654. Compared with specimens possessing the full number of 7 pairs, the specimen lacks both papillae of pair No. 5, and the left one of pair 4 – the right one of the latter pair being as long as 2.5 cm. While pair 5 was also absent or reduced in the specimens from St. 654, the absence of the left No. 4 represents a case of asymmetrical reduction which was unknown in the latter specimens.

Ventrolateral papillae 7 pairs, 2–15 mm long. Their reduction is often asymmetrical, for example, the first pair consists of a two and a 15 mm long papilla, representing the minimum and the maximum size of the papillae in the specimen.

Thus, the papillae of the specimen agree in number and position with those of the specimens from St. 654 but differ in their less symmetrical reduction. Moreover, they are characteristic by their shape, being often of the same width from the base to the rounded end – a shape rarely approached in the specimens from St. 654.

Deposit similar to those at St. 664 (q. v.).

St. 664. – The five poorly preserved specimens are 5.0–7.5 cm long.

Tentacles with marginal knobs.

Ventrolateral tubefeet 17–20 on each side.

Midventral tubefeet completely absent in the smallest specimen. The largest specimen, and possibly some of the others, has four midventral tubefeet, placed as in the specimens from St. 654.

Dorsal papillae. The smallest and most complete specimen has two pairs on the head, an unpaired right, 2.5 cm long, at the middle of the body, and a somewhat shorter unpaired left one posteriorly; the dorsal skin is so intact that it is doubtful whether more papillae could have been present. According to their placing the papillae belong to those pairs which are unreduced in the St. 654 specimens. However, the asymmetrical reduction is a notable difference.

In the other specimens the numbers of dorsal papillae probably fall within the variation at St. 654. It could not be ascertained, however, whether they were reduced in the same way.

Ventrolateral papillae. The numbers fall within the variation at St. 654; but the type of reduction could not be made out.

Deposits (Fig. 5) very different from those at St. 654. They are more sturdy and of a characteristically rounded appearance. The holes are more circular and more regularly distributed, with the large holes in the centre gradually passing into the small peripheral ones. The peripheral holes are closed, and the margin of the plates smooth. The special type of small-holed plate found in the St. 654 specimens is here completely absent.

In the corners between the large plates much smaller plates (2) are present. Their central holes are of the same size as those in the large plates, but they are immediately surrounded by the small peripheral holes.

Found among the normal deposits are, in some preparations, sparsely scattered spatulated rods

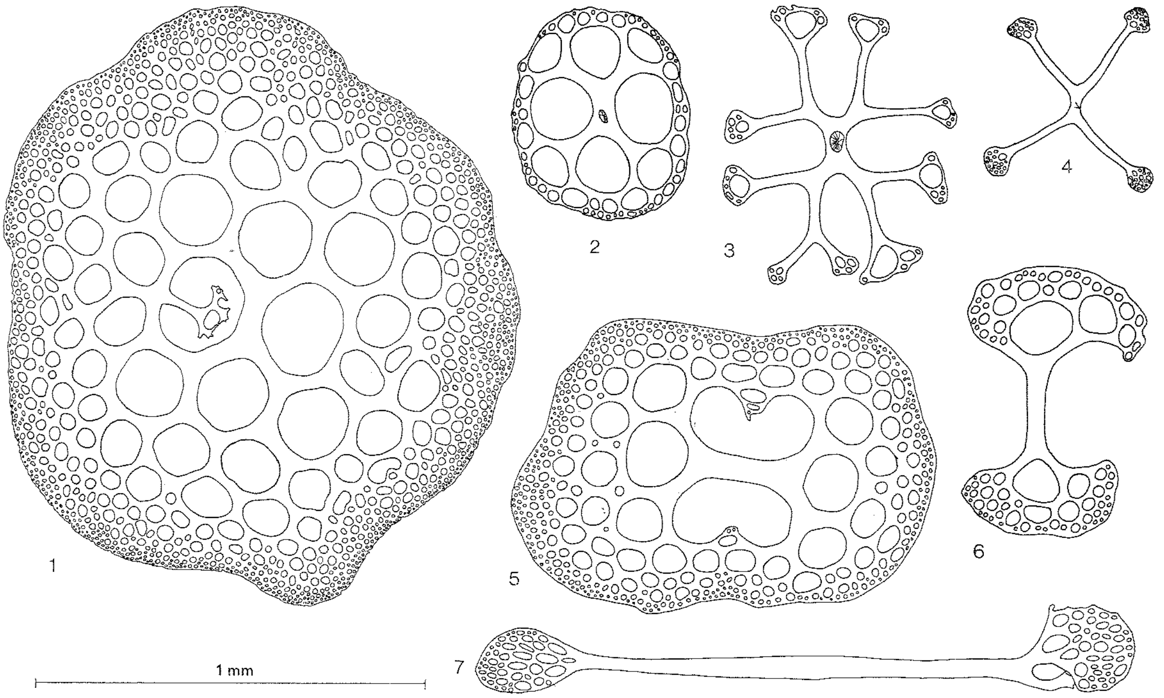


Fig. 5. *Oneirophanta mutabilis mutabilis.* Deposits. St. 664. 1, large plate; 2, small plate from interspace between large plates; 3–4, spatulated crosses; 5, plate with prolonged primary rod; 6, spatulated rod from body wall; 7, spatulated rod from papilla.

(6), spatulated crosses (4) which cannot be distinguished from those of *Oneirophanta setigera* and *Orphnurgus protectus,* and spatulated crosses with the arms twice divided (3). Sometimes the terminal plates of the shorter spatulated crosses meet, forming a perforated plate with a prolonged primary rod (5).

Papillae with perforated plates even at the tip. Some spatulated rods (7) are present under the layer of plates.

Tentacles and tubefeet with sturdy spatulated rods.

The deposits of the specimens from Sts. 663 and 664 show practically no overlapping in shape with those from St. 654. In the few specimens from St. 654, in which the deposits consist of imbricating, perforated plates only, these are less regularly built and lack the broad margin of small peripheral holes. The rods and crosses of the specimens from Sts. 663 and 664 are likewise, with their regular shape and spatulated ends, very different from the unfinished, abnormal deposits with open ramifications found in the St. 654 specimens. The deposits of the St. 654 specimens usually carry some small vertical spines. These are absent in all the specimens from Sts. 663 and 664.

Review and re-examination of previously described material:

In addition to the 24 specimens taken by the *Galathea,* 42 specimens from previous expeditions were re-examined.

Oneirophanta mutabilis Théel was first taken by the *Challenger.* Théel (1882) gave a thorough description and specified the number of ambulacral appendages in 32 specimens. The shape of the deposits were described collectively, except for the statement that the specimens from the Antarctic St. 157 (53°55'S, 108°35'E) had plates of an extremely firm construction with comparatively small holes and quite destitute of spines.

Théel emphasized the great variation shown by the species; however, his specimens were rather uniform considering the variation later revealed.

A total of 25 *Challenger* specimens were re-examined, comprising specimens from all the eight stations where this species was taken (21 specimens in BM, 2 in ZMA, 1 in ZMUC, and 1 in MNHN).

The following comments on Théel's description may be made: The tentacle discs possess 6–8 marginal knobs; the knobs may be contracted or concealed in the furrows of the rather soft skin of the discs, but never absent as in *O. m. affinis.*

The papillae were single-rowed in all the specimens. There was no regularity in the reduction of the papillae, as found in the specimens from *Galathea* St. 654 (and in Grieg's North Atlantic specimens of *O. mutabilis).* Nor showed any of the specimens an extreme and irregular reduction of the papillae as found in the *Galathea* specimens from the western Indian Ocean.

The skin, according to Théel, was "sometimes pliable, sometimes very hard, brittle, transparent, and clear like glass". Such a difference is no longer apparent in the preserved *Challenger* specimens. Similarly, the statement that the colour of the specimens from *Challenger* St. 157 was darker or lighter violet was confirmed only for the largest specimen, while the two smaller specimens had now lost their pigment altogether.

The deposits showed remarkably little variation compared to that found in the *Galathea* specimens. Even a slight prolongation of the primary rod was rare, and a prolongation approaching that found in the plates of the subspecies *O. m. affinis* was not found in any of the specimens. The plates of the specimens from *Challenger* St. 157 which, according to Théel, were robust, smooth, and small-holed, appeared on re-examination to be much more similar to the normal type than to the robust plates characteristic of the subspecies *affinis.* Similarly, specimens in which unfinished plates with open ramifications predominate (as in the specimens from *Galathea* St. 654) were not present in the *Challenger* material.

Spatulated rods were rare in the papillae, even at the tip. In one specimen from *Challenger* St. 146 long, spatulated rods predominated in the distal half of some of the papillae, while other papillae (among which also very slender papillae) had plates throughout their length and no spatulated rods at all. This is as found in the specimens from *Galathea* St. 654: The presence in the papillae of rods versus plates is of no taxonomic importance.

R. Perrier (1902) described 11 specimens from six *Talisman* stations in the region between the Bay of Biscay and the Azores. Eight specimens were referred to *O. mutabilis,* two to *O. alternata* and one to *O. alternata* var. *talismani.* (During re-examination of the species in MNHN a disagreement was found between the labelling of the *mutabilis* specimens and the information given in the report: The report lists 3 specimens from St. 133, 4 from St. 138, and one from St. 139, but the collection contained one specimen from St. 138, 7 from St. 139, but none from St. 133).

The tentacles and the deposits in all the specimens are of the normal *mutabilis* type; the differences mentioned by Perrier are individual variations only.

O. alternata was characterized first of all by the alternating reduction of the papillae pairs, as shown in the figure of the specimen from St. 137 (Perrier 1902, pl. XIV: 4). The external features of this specimen could be verified during re-examination, while the specimen from St. 134 no longer permitted a re-examination of the papillae. Perrier's figure of the specimen of *O. alternata* var. *talismani* (ibid., text-fig. 6) shows every second pair of papillae reduced to a small knob, but the re-examination revealed the presence of additional reduced papillae. In this specimen the reduction can scarcely be said to comprise alternating pairs of papillae.

Grieg (1921) described 10 specimens of *O. mutabilis* from the Bay of Biscay. The specimens showed a regularity in the reduction of the dorsal papillae somewhat reminiscent of the specimens from *Galathea* St. 654 in the Kermadec Trench: 5–8 pairs of dorsal papillae were present; pair No. 5 was smaller in all the specimens and in two specimens also pair No. 3 was smaller.

Hérouard (1923) reported *O. mutabilis* from the Monaco stations 1450 and 2986, without stating the number of specimens. Re-examination of the material in MOM revealed the presence of one specimen from St. 1450 and three from St. 2986. The specimens agreed both in tentacle type and in deposits (not preserved in the specimen from St. 1450) with the usual type in *O. mutabilis.*

Clark (1913) reported one specimen of *O. mutabilis* from off Baja California. A re-examination of the specimen (in USNM) showed that tentacles as well as deposits were as typical of *O. mutabilis mutabilis.* This is notable in view of the rather close proximity to the distributional region of *O. m. affinis.* The papillae could not be counted in the specimen.

Ekman (1927) with some doubt referred an Antarctic specimen to *O. mutabilis.* The doubt was caused by the presence of numerous spatulated rods in the papillae, which is now known to be taxonomically unimportant.

Agatep (1967b) reported 36 specimens from

15 Antarctic stations of the *Eltanin*. Body length (3.5–17.0 cm) and number of tubefeet and papillae were specified for each specimen, but the dorsal and ventrolateral papillae were not counted separately. Tubefeet 9–36 on each side, few specimens having less than 20. Papillae (dorsal + ventrolateral) 8–32 (37) on each side, and placed in single rows. Tentacles 20, usually with 8 marginal digits. Deposits perforated plates of the usual type in *O. m. mutabilis*.

Variation:
Although the variation in the taxonomic features within this widely distributed subspecies may partly be geographic, a further subdivision of the species seems inadvisable on the basis of our present knowledge. A review of the variation in the different features may be of interest for a comparison with future materials.

Tentacles. As in subspecies *affinis* the normal number is 20, with numbers of 18 and 19 occurring occasionally. The discs are soft, with few spicules, and always with marginal digits. The digits vary in number from 6 to 8 at practically all the stations; the total variation is 5–10. No geographic variation is found in the number of digits.

Ventrolateral tubefeet 8–36 on each side. The 36 Antarctic specimens taken by the *Eltanin* comprised practically the whole variation in the species (9–36 on each side), and also the eight specimens from the North Pacific *Challenger* stations 241 and 244 showed a large variation (12–27 on each side).

Midventral tubefeet few, but always present.

Dorsal papillae 4–19 on each side (usually less than 13). The range of variation may be rather narrow in some regions (Kermadec Trench: 5–7 pairs), while in other regions it may be large, although far from as large as in the subspecies *affinis*. The specimens from the western Indian Ocean comprised almost the whole variation in number within the subspecies *mutabilis*.

Ventrolateral papillae 4–17 on each side, but usually not more than 10.

A large-scale geographic pattern in the variation in number of tubefeet and papillae is not apparent from the available data.

Deposits. In the specimens from *Galathea* St. 654 the deposits differ from those of all other examined specimens by the predominance of irregularly formed plates with open ramifications.

In sturdiness the plates in none of the specimens of *O. m. mutabilis* exceeded that found in the specimens from *Galathea* Sts. 663 and 664.

Spatulated rods may predominate in the distal half of the papillae, while they may be completely absent in other, equally slender papillae. Both types of papillae may be present in the same specimen.

Conclusion. A *geographic variation* within the subspecies *O. m. mutabilis* is indicated by the pronounced and irregular reduction of the papillae in the *Galathea* specimens from the western Indian Ocean.

A *local variation* is shown by the specimens from *Galathea* St. 654 in the Kermadec Trench. The 14 specimens from this station had very peculiar features in common in the arrangement and reduction of the papillae, as well as in the type of deposits. No such features were found in the specimens from the two other stations in the Kermadec Trench. The fact that the specimens from St. 654 ranged in size from 3.5 to 9.5 cm indicates that the striking similarity between them is not due to the specimens being derived from a single batch of young. The presence of such a narrow local variation indicates that the possibilities of dispersal are very limited in the species. This again suggests that brood protection in the species is not restricted to the eastern Pacific region (p. 201).

The *individual variation* is usually narrow at each station. There is no example of a variation comparable to that shown by the numbers of dorsal papillae in the specimens of subspecies *affinis* from *Galathea* St. 716.

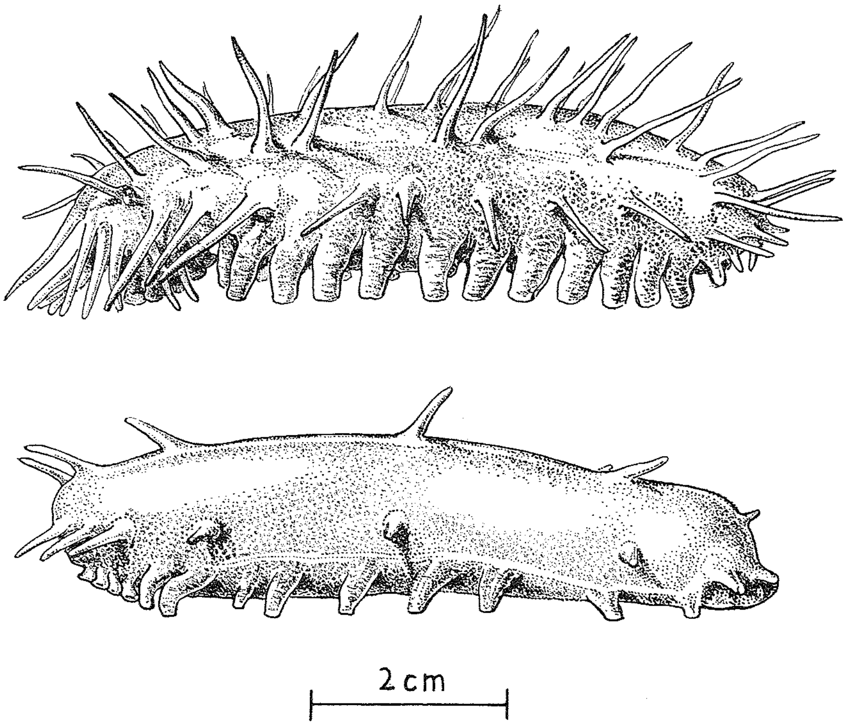
An *age variation* is shown by the increase in the average number of papillae and tubefeet with the size of the specimens, as indicated by the exclusive presence of low numbers in the smallest specimens. The larger specimens show a great variation in number of papillae and tubefeet, including specimens with very low numbers.

Oneirophanta mutabilis affinis Ludwig, 1894

Oneirophanta affinis Ludwig, 1894, pp. 72–74, pls. VII: 7–13, VIII: 1–4.

Oneirophanta mutabilis Théel, Ludwig 1894, pp. 70–72, pl. VII: 6; Clark 1920 (partim), pp. 136–137.

Fig. 6. *Oneirophanta mutabilis affinis*. St. 716. Two specimens. JT.



Oneirophanta mutabilis affinis Ludwig, Hansen 1967, pp. 485–488, figs. 2–4.

Diagnosis: Tentacle discs with a smooth or incised edge, and lacking marginal knobs. Each body side with 15–20 (44) ventrolateral tubefeet, 5–35 dorsal papillae (in single or double rows), and 5–11 ventrolateral papillae. Deposits robust and rather small plates, often irregularly shaped due to elongation of the primary rod; clusters of rod-shaped spicules in tentacle discs.

Material:

St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – 30 specimens.

St. 726, Gulf of Panama (5°49'N, 78°52'W), 3270–3670 m. – 1 specimen.

Description:

St. 716. – The 30 specimens (Fig. 6) measure 4.0–9.5 cm.

Tentacles (Pl. VIII: 3) 18–20. The broad, flat or slightly vaulted discs are completely devoid of knobs on the edge.

Ventrolateral tubefeet 17–20 on each side, except for one specimen with 15 on each side.

Midventral tubefeet 3–9.

Dorsal papillae 5–25 on each side, slender and not exceeding 15 mm in length. When less than ten pairs of dorsal papillae are present, these are usually placed in a single row medial to each dorsal radius. In specimens with a larger number of dorsal papillae most of them are likewise placed medial to the dorsal radii, but in addition, some papillae are found lateral to them. The ratio between the medially and laterally placed dorsal papillae varies a great deal. In some specimens only a single pair, or a single unpaired one, is placed lateral to the radius, while in other specimens the ratio is more equal. In specimens

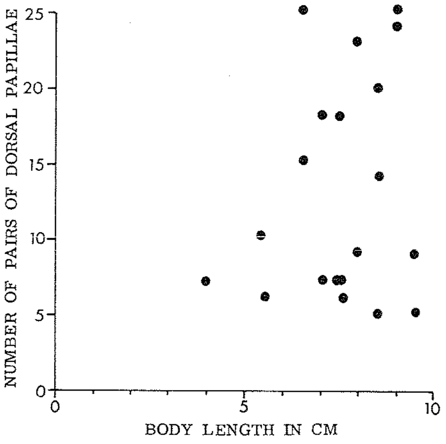


Fig. 7. *Oneirophanta mutabilis affinis*. St. 716. Number of pairs of dorsal papillae in relation to body length.

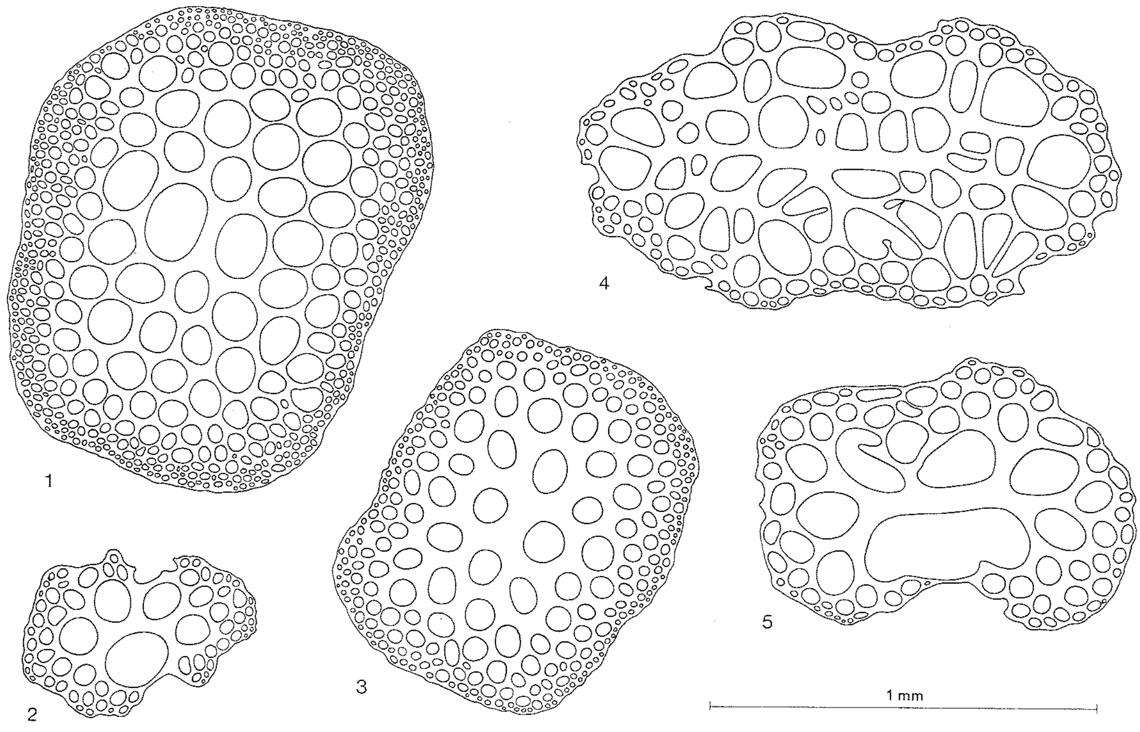


Fig. 8. *Oneirophanta mutabilis affinis.* St. 716. Deposits from dorsum. 1, large-holed plate of delicate structure; 2, small plate from interspace between large plates; 3, robust plate typical of the subspecies; 4, irregularly perforated plate developed round a long primary rod; 5, stage towards an irregularly perforated plate.

with a large number of dorsal papillae four to six pairs are usually placed lateral to the radii. Even the largest specimens may have a low number of papillae (Fig. 7).

The dorsal papillae vary irregularly in size. The number and position of the dorsal papillae may be very different in the left and right side of the specimen.

Ventrolateral papillae 7–11 on each side, similar to the dorsal ones in size, shape, and irregular reduction.

Deposits (Fig. 8) sturdy, perforated plates (3); only in two specimens were they more delicately built (1). The diameter of the fully developed plates is usually 0.8–1.1 mm, the variation being 0.5–1.4 mm.

In all the specimens a number of peculiar, irregularly perforated plates (4) are present amongst the normal ones. They are developed from spatulated rods through an extension and merging of the perforated ends, together with an outgrowth of transversal beams on the rod (5).

The deposits of the papillae vary a great deal. In some papillae only plates are present, while in others the deposits consist, throughout almost the entire length of small, sturdy, spatulated rods.

Tentacles with sturdy, spatulated rods. Discs with numerous rods which are often placed in somewhat radially arranged clusters.

Tubefeet with sturdy spatulated rods.

St. 726. – The single specimen is 13 cm long.

Tentacles 20, with broad, flattened or slightly concave discs without peripheral knobs.

Ventrolateral tubefeet 20 pairs.

Midventral tubefeet 6, consisting of a pre-anal pair and 4 unpaired ones, the foremost one placed less than 2 cm from the anus.

Dorsal papillae 10 pairs, in single rows, all less than 2 cm long and only 2–3 mm broad at the base.

Ventrolateral papillae 9 pairs, similar to the dorsal ones.

Deposits falling within the variation at St. 716. Dorsally the plates are more delicate than is usual in the St. 716 specimens, but in the ventrum they are just as heavy as the latter. Irregular plates developed from a long primary rod are present both in the dorsum and ventrum. The plates are small as in the St. 716 specimens; the dorsal ones attain 1.4 mm in diameter, although they are generally less than 1.1 mm; the ventral plates do not exceed 1.1 mm.

Papillae with plates from base to tip; in addition, some spatulated rods are present under the plates.

Tentacles and tubefeet with sturdy, spatulated rods similar to those from St. 716.

Remarks:

The re-examined *Albatross* specimens belong to six stations and comprise the six specimens described by Ludwig and eight of the 16 specimens described by Clark. Only one of Clark's specimens, taken at the *Albatross* St. 4732 in the Central Pacific, did probably belong to *O. m. mutabilis,* being taken outside the established geographic range of the subspecies *affinis.* (The specimen seems lost).

The specimens from the five stations situated closest to the coast (Fig. 9: 1–5) represent the subspecies *affinis* in its typical form, while the specimens from the three stations lying farther from the coast (Fig. 9: 6–8) show a transition to the *mutabilis* type. The subspecies *affinis* apparently occupies a narrow region along the coast. The northern and southern limits of distribution cannot yet be determined. However, the specimen which Clark (1913) reported from off Baja California and the *Challenger* specimens taken off Valparaiso proved on re-examination to agree with the subspecies *mutabilis,* both in external features and deposits.

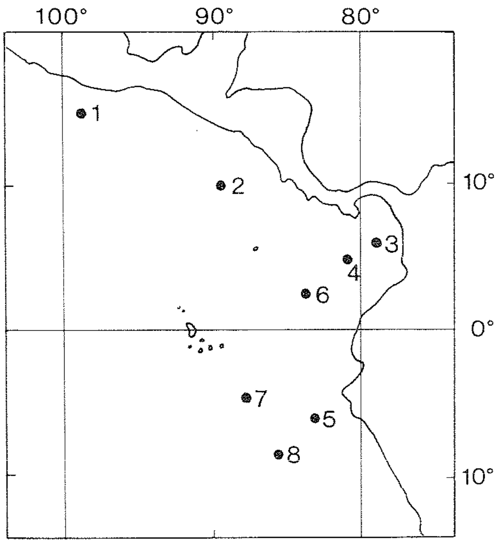


Fig. 9. *Oneirophanta mutabilis affinis.* Stations of the *Galathea* and the *Albatross* from which specimens have been examined or re-examined. 1, *Albatross* St. 3415; 2, *Galathea* St. 716; 3, *Galathea* St. 726; 4, *Albatross* St. 3381; 5, *Albatross* St. 4651; 6, *Albatross* St. 3374; 7, *Albatross* St. 4647; 8, *Albatross* St. 4658.

The taxonomic features are thus distributed on the stations:

Tentacles normally 20, but occasionally 18 or 19. The complete absence of marginal digits on the tentacle discs in all the specimens from the *Galathea* Sts. 716 and 726 is very remarkable in view of the fact that such digits were present on the tentacles of all specimens examined of the subspecies *mutabilis.*

The tentacle discs of the re-examined *Albatross* specimens vary in shape from the *mutabilis* type to the smooth-edged *affinis* type found in the specimens from *Galathea* Sts. 716 and 726. Intermediate stages were represented by discs with a number of incisions on the margin – the incisions being probably derived from interspaces between digits.

The specimen from *Albatross* St. 3415 (1) lacked, as the *Galathea* specimens (2, 3), both digits and incisions on the margin of the discs. The two specimens from Sts. 3381 (4) and 4651 (5) had incisions, but no digits.

Of the four specimens from St. 3374 (6) one had marginal digits, and one had marginal incisions on the discs. The two other specimens had tentacles of an intermediate type, with the interspaces between the digits being reminiscent of incisions.

Of the six specimens from St. 4647 (7) only two had the tentacles preserved. One had discs with a smooth margin, the other had 5–12 (usually 8) digits. (The variation in number of digits is a deviation from the true *mutabilis* type).

The specimens from St. 4658 (8) had normal *mutabilis* tentacles, with about 8 marginal digits.

A geographic pattern seems to be present in the distribution of the tentacle types. Discs lacking both digits and incisions are found in the specimens from the three stations off the coast of Central America. The specimens from the five more southerly stations showed transitions to the *mutabilis* type, most pronouncedly on the stations situated farthest from the coast.

Tentacles lacking marginal digits have not been found in any specimens of the subspecies *mutabilis.*

Deposits. Preparations of the dorsal and ventral skin were made from all the re-examined *Albatross* specimens, except the specimen from St. 3415 which had lost the deposits altogether.

The specimen from *Albatross* St. 4651 (5) possessed, as the specimens from *Galathea* Sts. 716 (2) and 726 (3), small and robust plates, interspersed with irregularly perforated plates developed round an elongated primary rod. At the other *Albatross* stations the irregularly perforated plates were absent or represented by their initial stage only.

Rounded and robust plates are, apart from the specimens from the three above-mentioned stations, characteristic of the two specimens on which Ludwig described *O. affinis.* A re-examination proved that in the specimen from St. 3374 (6) both the dorsal and ventral deposits belonged to this type, while in the specimens from St. 3381 (4) this applied to the ventral deposits only.

The three specimens from St. 3374 (6) which Ludwig referred to *O. mutabilis* had more slenderly built plates than the one described as *O. affinis.* The plates are, as in the specimens from Sts. 4647 (7) and 4658 (8), intermediate in shape between the *affinis* and the *mutabilis* type.

The distribution of the types of plate shows a geographic pattern corresponding to that found in the shape of the tentacle discs. The deposits which are farthest from the *mutabilis* type were found at *Galathea* Sts. 716 (2) and 726 (3), and at *Albatross* St. 4651 (5), while the specimens from the remaining stations are nearer to the *mutabilis* type.

The plates of all the eastern Pacific specimens are remarkable for their small size. The dorsal plates do not exceed 1.5 mm across, and the ventral plates are even smaller. The plates of the robust type are usually small; thus, in Ludwig's two original specimens of *O. affinis* all the plates were smaller than 1.0 mm. All intermediates are found between specimens with small and specimens with large plates.

The plates of the eastern Pacific specimens almost completely lack vertical spines.

Numerous rods are usually present in the tentacle discs, a further difference from the subspecies *mutabilis.*

Dorsal papillae 5–35 on each side. This highly varying number of dorsal papillae characterizes the eastern Pacific *Galathea* specimens, as well as the specimens described by Ludwig. The presence of numerous papillae was in both cases combined with an arrangement in double rows. (The number of papillae is unknown in Clark's specimens).

Ventrolateral papillae 5–11 on each side.

Ventrolateral tubefeet 15–20 on each side in both *Galathea*'s and Ludwig's specimens. Clark did not state the number; but the tubefeet have been counted in two of his specimens. One had 18–20 on each side. In the other specimen (from *Albatross* St. 4647) 44 tubefeet could be counted on one side of the body, by far the highest number found in any specimen of the species.

Midventral tubefeet present in all examined specimens.

No subspecific differences are found in the number of ventrolateral papillae, ventrolateral tubefeet, or midventral tubefeet.

Biology:
Developmental stages of young up to 30 mm long were present in the ovarian sacs in six females from St. 716 (Pl. XI: 4–8). This singular case of brood protection in deep-sea holothurians is considered elsewhere (pp. 199–201).

Oneirophanta conservata Koehler & Vaney, 1905

Koehler & Vaney 1905, pp. 57–59, pls. VI: 3, XI: 16–19.

Diagnostic features: The single known specimen had on each side 33–34 ventrolateral tubefeet, about 30 dorsal papillae (in double rows), and 13 ventrolateral papillae. Deposits perforated plates.

Record: Indian Ocean, southwest of Ceylon, 1315 m. One specimen.

Remarks: The species is of uncertain relationship. Koehler & Vaney stated that the tentacle discs possessed about ten marginal lobes; however, the lobes may represent contracted ramifications, in which case the species should be transferred to the genus *Orphnurgus.*

Oneirophanta setigera (Ludwig, 1894)
Fig. 10, 94: 1

Scotodeima setigerum Ludwig, 1894, pp. 74–79, pls. VI: 6–12, VII: 1–5; Clark 1920, p. 138.

Diagnosis: Tentacles 15–20; discs with about 8 marginal knobs. Each body side with 16–30 ventrolateral tubefeet (in alternating double rows), 12–32 dorsal papillae (in irregular double rows), and 9–17 ventrolateral papillae. Midventral tubefeet 0–6. Deposits spatulated crosses, measuring 1.1–3.0 mm across in the dorsum and 0.2–2.3 mm in the ventrum; spatulated rods densely packed in the slender and rigid papillae.

Material:

St. 664, Kermadec Trench (36°34'S, 178°57'W), 4540 m. – 1 specimen.

St. 726, Gulf of Panama (5°49'N, 78°52'W), 3270–3670 m. – 1 specimen.

Description:

St. 664. – Length 5.0 cm.

Skin whitish, transparent, and due to the densely crowded spicules, quite hard.

Tentacles 20, the discs with about 8 rounded knobs on the edge.

Ventrolateral tubefeet, about 20–22 on each side, in alternating double rows.

Midventral tubefeet one, 8 mm in front of the anus.

Dorsal papillae about 15 on each side, placed in irregular double rows.

Ventrolateral papillae about 11–12 on each side.

Both dorsal and ventrolateral papillae consist almost exclusively of a bristle-like cluster of long, spatulated rods. The papillae are of equal slenderness from base to tip, and leave only little trace when torn off. The numbers of papillae given may therefore be a little too low.

Deposits (Fig. 10: 1–3, 6–7) spatulated crosses (1) – dorsally 1.5–3.0 mm across, ventrally 1.2–1.8 mm. Tentacles and tubefeet (6) with smooth, spindle-shaped, transversally placed rods, sometimes with rudiments of terminal ramifications. Papillae (2–3) with 5–6 mm long, spatulated rods. Gonads (7) with numerous slender rods, often with a small enlargement in the middle; occasionally with a single ramification.

St. 726. – Length 5.3 cm.

Skin as in the Kermadec specimen.

Tentacles 19, the discs with about 8 rounded knobs on the edge.

Ventrolateral tubefeet 16–18 on each side, in alternating double rows.

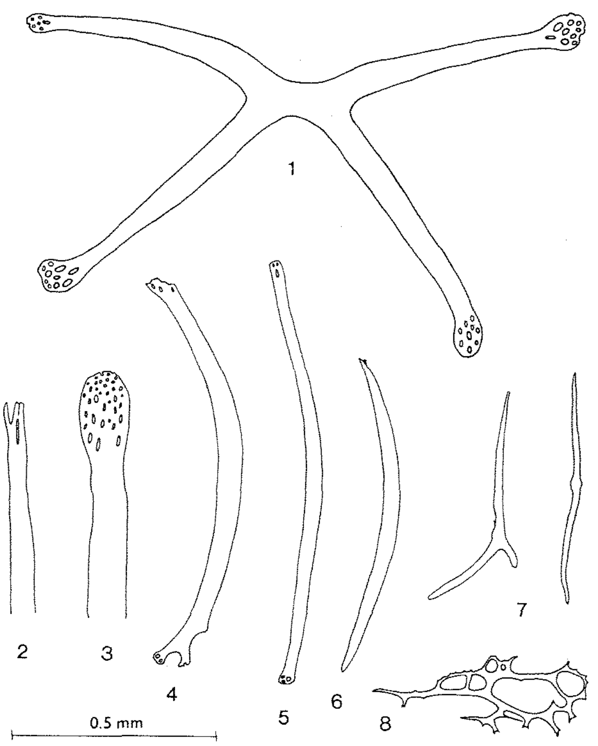


Fig. 10. *Oneirophanta setigera.* Deposits. 1, St. 664, ventrum; 2–3, St. 664, papilla; 4, St. 726, tentacle; 5, St. 726, tubefoot; 6, St. 664, tubefoot; 7, St. 664, gonad; 8, St. 726, gonad.

Midventral tubefeet 2, immediately in front of the anus.

Papillae consisting of a bristle-like cluster of spatulated rods. Their number could not be established.

Deposits (Fig. 10: 4–5, 8) spatulated crosses, measuring both in dorsum and ventrum 1.5–2.3 mm across. Tentacles and tubefeet (4–5) with spindle-shaped rods which, particularly in the tentacles, show distinct rudiments of terminal ramifications. Spatulated rods of papillae exceeding 4 mm in length. Gonads (8) with irregularly ramified spicules, very different from those of the Kermadec specimen.

Remarks: The agreement between the *Galathea* specimens and the two specimens described by Ludwig from the Gulf of Panama (both in USNM) is good, although some differences were found in the numbers of tubefeet and papillae, and in the size of the deposits. Ludwig's specimens had 20 tentacles with 8 knobs on the discs, 28–30 ventrolateral tubefeet on each side, 6 midventral tubefeet, 30–32 dorsal, and 17 ventrolateral papillae on each side; the spatulated crosses measured 1.1–1.4 mm across in the dorsum, 0.2–0.7 mm in the ventrum, and the spatulated rods of the papillae were 1.4–1.7 mm long.

The 17 specimens reported by Clark, likewise from the Gulf of Panama, were all re-examined (4 specimens in MCZ and 13 in USNM). They had 15–20 tentacles (one specimen had only 12), each with about 8 marginal knobs, 0–2 midventral tubefeet, and on each side 17–22 ventrolateral tubefeet, 12–25 dorsal papillae and 9–14 ventrolateral papillae. Deposits examined in eight specimens. The dorsal crosses measured 1.5–2.2 mm across, the ventral crosses 1.2–1.6 mm, occasionally up to 2.0 mm.

Distribution: Gulf of Panama and vicinity, 2104–4064 m. Kermadec Trench, 4540 m.

Genus *Orphnurgus* Théel, 1879
Fig. 111

Orphnurgus Théel, 1879, p. 8; Théel 1882, p. 82. – Type species: *Orphnurgus asper* Théel, 1879, by monotypy.
Scotodeima Ludwig, 1894, pp. 74–75, partim.
Amphideima Koehler & Vaney, 1905, p. 59.

Diagnosis: Tentacles 15–20, unretractile; discs with ramified processes. Circum-oral papillae absent. Deposits spatulated crosses and/or rods of greatly varying shape.

Key to the species of *Orphnurgus*

1. Deposits of body wall exclusively spatulated crosses. Papillae always rigid from the densely crowded cluster of spatulated rods .... *protectus* (p. 47)
1. Deposits of body wall differently developed, but spatulated crosses always rare. Papillae usually flexible 2
2. Deposits of body wall small spinous rods .... *asper* (p. 38)
2. Deposits of body wall varying greatly, but never small, spinous rods 3
3. Deposits dorsally slender, spatulated rods, ventrally small rods with a few dichotomous ramifications .... *vitreus* (p. 46)
3. Deposits varying from spatulated rods and rods with open ramifications at the end, to robust bodies, the latter being especially common in the ventrum. Some specimens have spatulated rods exclusively both in dorsum and ventrum.. *glaber* (p. 39)

Orphnurgus asper Théel, 1879
Fig. 11

Théel 1879, p. 8, fig. 7; Théel 1882, pp. 82–84, pls. XV, XXXIV: 15–16, XXXVIII: 10, XLI: 3, XLIV: 3; Théel 1886b, p. 2; Deichmann 1930, p. 117, pl. XI: 4–8; Deichmann 1940, pp. 199–200.

Diagnosis: Tentacles 20, discs with irregular ramifications on the margin; underside of disc and ramifications crowded with deposits. Ventrolateral tubefeet about 23 on each side, partly projecting horizontally from the body, placed in single rows. Midventral tubefeet absent. Dorsal papillae about 75 on each side, in irregular double rows. Ventrolateral papillae about 25 on each side, in single rows. Deposits small and rod-shaped, with spines throughout their length.

Records: Several stations off the West Indian Islands, 818–1171 m.

Remarks: The species in external appearance is similar to *O. glaber*, but the deposits consist exclusively of small rods with spines throughout their length, a type never found in *O. glaber*.

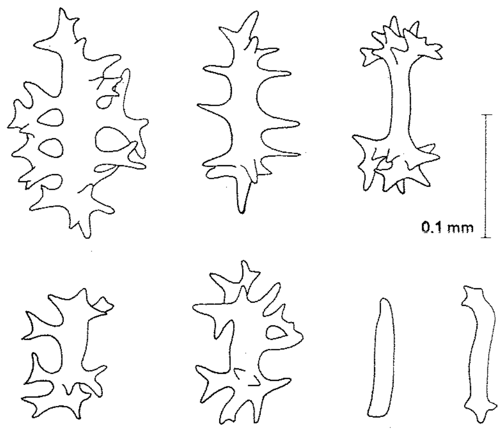


Fig. 11. *Orphnurgus asper*. *Challenger* St. 23. Deposits from the type specimen. (Redrawn after Théel).

The tentacle discs are large and provided with conspicuous and irregular ramifications. Re-examination of the type specimen (in BM) showed that the underside of the discs and their ramifications contained densely crowded deposits, which apparently make the ramifications less retractile than in *O. glaber*.

Type: BM, the only specimen taken by the *Challenger*.

Type locality: *Challenger* St. 23 (off Sombrero Island).

Orphnurgus glaber Walsh, 1891
Figs. 12–13, pl. VIII: 5–7

Orphnurgus asper Théel var. *glaber* Walsh, 1891, p. 198.

Orphnurgus glaber Walsh, Koehler & Vaney 1905, pp. 60–62, pls. VIII: 3, XII: 1–3; Hansen 1967, pp. 491–493, figs. 9–10.

Orphnurgus invalidus Koehler & Vaney, 1905, pp. 62–64, pl. XII: 9.

Orphnurgus insignis Fisher, 1907, pp. 702–706, pls. LXXIII: 1, LXXVII: 1–3; Ohshima 1915, p. 234; Ohshima 1916–1919, with three figures.

Orphnurgus rigidus Ohshima, 1915, pp. 234–235; Ohshima 1916–1919, with one figure.

Amphideima investigatoris Koehler & Vaney, 1905, pp. 59–60, pls. IV: 6, XII: 8.

Diagnosis: Tentacles (15–)20, with ramified discs. Ventrolateral tubefeet 15–60 on each side, partly projecting horizontally from the body, placed in single, double, or triple rows. Midventral tubefeet occasionally present. Dorsal papillae 12–125 on each side, in single to double rows, or scattered over the dorsum. Ventrolateral papillae

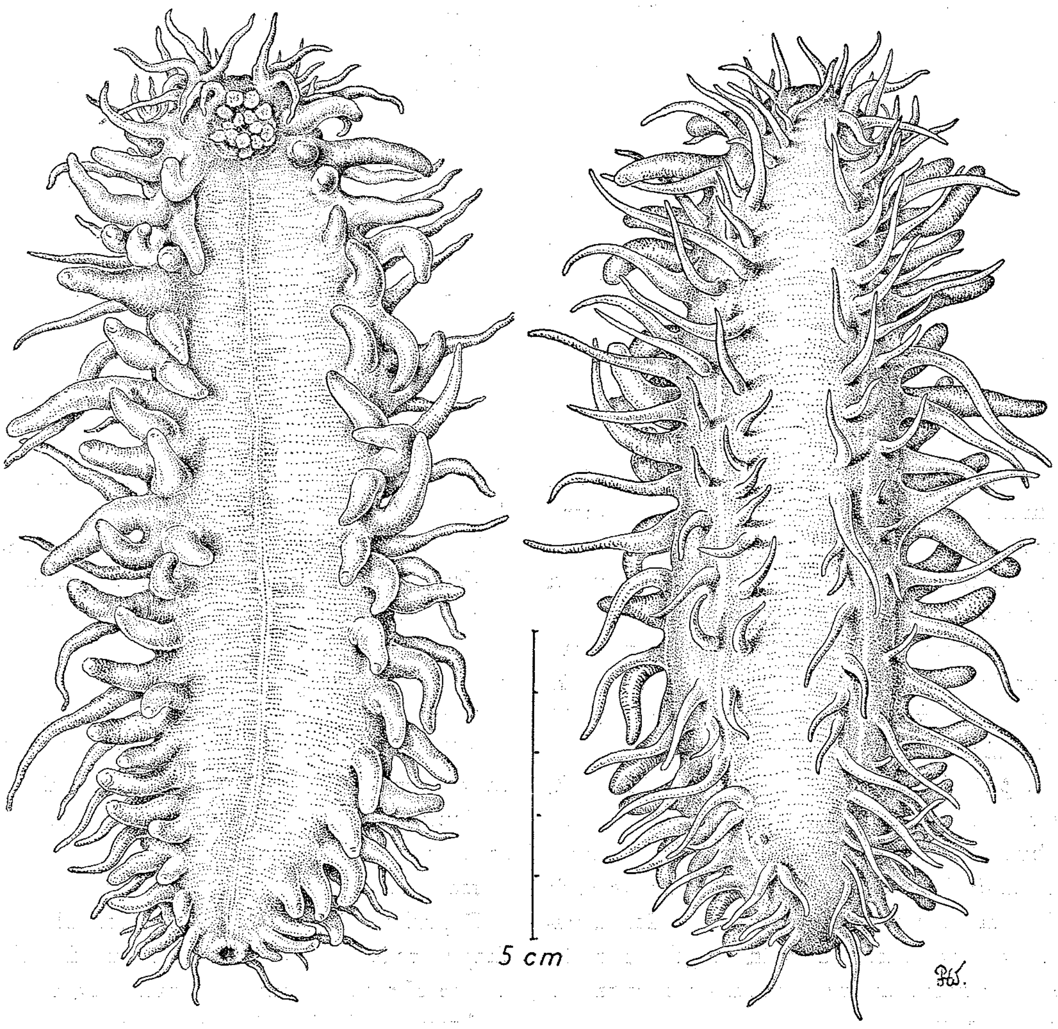


Fig. 12. *Orphnurgus glaber*. Kei Exp. St. 52. Ventral and dorsal view. PHW.

0–30 on each side, usually larger than the dorsal ones; placed in single rows, sometimes with a number of additional, rudimentary ones placed dorsal to this row. Deposits spatulated rods, especially in the ventrum often reduced and deformed into spindle-shaped, ellipsoid, and amorphous bodies. A few spatulated primary crosses sometimes present. Papillae usually almost completely devoid of spicules and quite soft, although in some specimens they may be rigid proximally due to the presence of numerous spatulated rods.

Material:

Galathea St. 490, Bali Sea (5°25'S, 117°03'E), 545–570 m. – 3 specimens and 2 fragments.

Dr. Th. Mortensen's Pacific Exp., 27.III.1914, 15 miles W. 1/2 S. of Jolo (Philippines), 458 m. – 3 specimens.

Dr. Th. Mortensen's Kei Exp., Kei Islands:
St. 41 (5°29'S, 132°28'E), 245 m. – 1 specimen.
St. 51 (5°46'S, 132°51'E), 348 m. – 1 specimen.
St. 52 (5°46'S, 132°50'E), 352 m. – 1 specimen.
St. 56 (5°31'S, 132°51'E), 345 m. – 1 specimen.

Description:

The specimens show pronounced differences in the taxonomic characters, particularly in the deposits. The decision to refer them all, besides five previously described species, to one and the same species, *Orphnurgus glaber,* is due to the presence of many intergradations.

Galathea St. 490. – The largest of the three specimens measures 7.5×1.5 cm.

Tentacles (Pl. VIII: 5–6) 20, fully extended, with 4 mm long stalks and ramified discs covered with small, subglobular papillae.

Ventrolateral tubefeet 18 pairs, placed in an irregular row along each side, usually projecting horizontally from the body. They are cylindrical, with rounded ends provided with a small sucking-disc. Length varying irregularly from 3 to 11 mm, dependent on the state of contraction.

Dorsal papillae about 125 on each side, soft, mostly about 10 mm long, double-rowed posteriorly, but otherwise scattered over the dorsum.

Ventrolateral papillae, usually one above each ventrolateral tubefoot. Contrary to the dorsal papillae they vary considerably in length, from 15 mm to quite rudimentary. The larger ones rather rigid proximally.

Skin thin, hard, and whitish-transparent.

Deposits (Fig. 13: 1–6), densely crowded, 0.8–1.3 mm long spatulated rods, dorsally slender (1), ventrally slightly more sturdy. A few small, spatulated crosses (2) were present in the preparations.

Stalks of tentacles (4) with sturdy, transversally or obliquely placed rods. Tentacle discs (3) with numerous small, curved rods, framing the bases of the ramifications.

Tubefeet (6) proximally with irregularly placed spatulated rods. Distally, the rods are smaller and transversally placed; end-plates absent. Dorsal papillae almost devoid of spicules. The largest of the ventrolateral papillae with spatulated rods similar to those of the skin.

Gonads with rods which may be spatulated or ramified at the ends.

The two other specimens from St. 490 are 3.1 and 3.8 cm long, and less well preserved.

Tentacles 20 in both specimens. Discs with somewhat contracted ramifications.

Papillae could not be counted.

Deposits similar to those of the large specimen.

Kei Exp. St. 41. – The specimen measures 7×1.5 cm.

Tentacles 15, the discs with contracted ramifications.

Ventrolateral tubefeet about 35 on each side, in double or triple rows.

Papillae could not be counted.

Deposits resembling those from Kei Exp. St. 51.

Kei Exp. St. 51. – The specimen measures 7.5×3 cm.

Tentacle discs with contracted ramifications.

Ventrolateral tubefeet about 60 on each side, in double or triple rows.

Dorsal papillae about 75 on each side, soft, reaching 15 mm, placed in two bands, each being 2–4 papillae broad. Here and there the dorsal papillae extend so far down the body side that they intermingle with the ventrolateral papillae.

Ventrolateral papillae 25–30 on each side, soft, reaching 15 mm, usually more sturdy than the dorsal ones.

Deposits (Fig. 13: 12–14) dorsally spindle-shaped rods (13); ventrally varying from a prevalence of similar spindles, anteriorly, to ellipsoid and rounded bodies (14), posteriorly.

Tubefeet (12) with rather sturdy spindles. Dor-

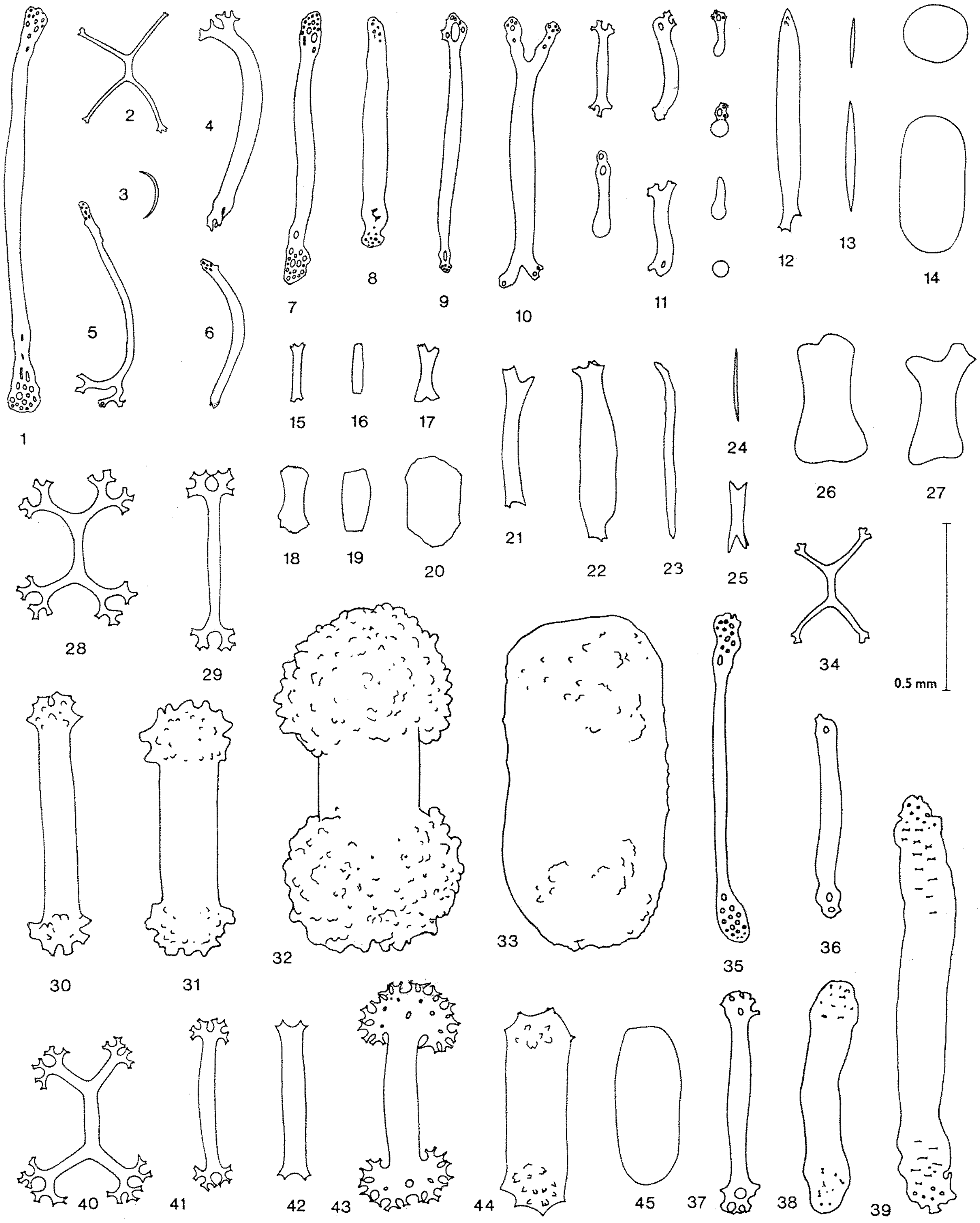


Fig. 13. *Orphnurgus glaber*. Deposits. 1–6, *Galathea* St. 490 (1, dorsum; 2, ventrum; 3, tentacle disc; 4, tentacle stalk; 5, gonad; 6, tubefoot); 7–11, Kei Exp. St. 52 (7–10, the dominant type both in dorsum and ventrum; 11, eight reduced rods of types occurring sporadically both in dorsum and ventrum); 12–14, Kei Exp. St. 51(12, base of a tubefoot; 13, dorsum; 14, posterior part of ventrum); 15–20, Kei Exp. St. 56 (15–16, dorsum; 17–19, middle part of ventrum; 20, posterior part of ventrum); 21–27, Pacific Exp., off Jolo Islands (21–24, dorsum; 25–27, posterior part of ventrum); 28–33, Japan, *O. insignis* (redrawn after Ohshima); 34–39, Japan, *O. rigidus* (redrawn after Ohshima); 40–45, Hawaii, *O. insignis* (40–43, dorsum; 44–45, ventrum).

sal and ventrolateral papillae with a few slender spindles. The spindles of both tubefeet and papillae sometimes show rudiments of terminal ramifications.

Kei Exp. St. 52. – The specimen (Fig. 12), the largest in the collection, measures 15×3.5 cm.

Tentacles (Pl. VIII: 7) 20, with contracted ramifications on the discs.

Ventrolateral tubefeet 32 left, 34 right.

Dorsal papillae about 40 on each side, soft, in irregular double rows.

Ventrolateral papillae 22–23 on each side, proximally rather rigid.

Both dorsal and ventrolateral papillae vary in length from 25 mm to quite rudimentary; the ventrolateral papillae are usually larger and more robust than the dorsal ones.

Deposits (Fig. 13: 7–11) 0.5–0.8 mm long spatulated rods, usually with fewer holes than those of the *Galathea* specimens. Small, spherical bodies and intermediary stages between these and spatulated rods occur sporadically in both dorsum and ventrum. The spatulated rods may be forked, but true spatulated crosses were not found. The rods are shortest, most sturdy, and most crowded in the posterior part of the ventrum.

Through the simultaneous presence of spherical bodies and reduced, spatulated rods the specimen is intermediate between the *Galathea* specimens and those from the Kei and Jolo Islands possessing only spindle-shaped, ellipsoid, spherical, and amorphous bodies. The thus proven derivation of these deposits from spatulated rods is noteworthy.

Tubefeet with extremely crowded spatulated rods. Dorsal papillae and the smaller ventrolateral papillae almost devoid of deposits. Larger ventrolateral papillae with irregularly placed, spatulated rods, proximally numerous and reaching 0.9 mm in length, distally rather few and not exceeding 0.5 mm.

Kei Exp. St. 56. – The specimen measures 9×4.5 cm.

Tentacles 20, the discs with contracted ramifications.

Ventrolateral tubefeet 50–60 on each side, in double or triple rows.

Dorsal papillae about 75 on each side, soft, in rather regular double rows.

Ventrolateral papillae about 30–40 on each side, soft, in single to double rows.

Deposits (Fig. 13: 15–20) dorsally rather slender rods (15–16); ventrally varying from slender and thick rods (17–19) to ellipsoid and spherical bodies – the most sturdy ones (20) prevailing posteriorly. Both slender and thick rods nearly always with some blunt, terminal ramifications, but never with spatulated ends. The total absence of spindle-shaped rods is remarkable.

Tubefeet with blunt rods with rudiments of terminal ramifications. Dorsal and ventrolateral papillae lacking deposits, except for a few small, distal rods.

Pacific Exp., off Jolo. – The three specimens are 2, 3, and 4 cm long. The smallest specimen is so defective that tentacles, tubefeet, and papillae cannot be counted.

Tentacles 20 and 19 in the 3 and 4 cm long specimens, respectively. Discs slightly contracted, but distinctly ramified.

Ventrolateral tubefeet in double to triple rows, each side with 30–35 papillae in the 3 cm long specimen, and 40–45 in the 4 cm long one.

Dorsal papillae in irregular double rows, soft, each side with 30–35 papillae in the 3 cm long specimen, and 45–50 in the 4 cm long one.

Ventrolateral papillae in single rows, soft, with a few rudimentary ones placed above the main row; the total number on each side is about 15 in the 3 cm long specimen, and 20 in the 4 cm long one.

Deposits (Fig. 13: 21–27) rods and spindles, the larger ones often forked or with rudimentary distal ramifications; ellipsoid and rounded bodies rare. The ventral deposits (25–27), in particular those posteriorly, are more robust than the dorsal ones (21–24).

Tubefeet with both slender and sturdy rods. Dorsal and ventrolateral papillae with extremely slender rods.

Synonymy:
The here recorded specimens together with the synonyms proposed extend the distribution of *Orphnurgus glaber* from the Bay of Bengal to the Hawaiian Islands. In addition to a large individual variation a geographic variation appears to be present in the deposits, as well as in the numbers of tubefeet and papillae.

In order to motivate the proposed synonymies and to make possible an analysis of the variation in the species, a short description of the synonymous species is given below, arranged according to locality.

Bay of Bengal. Three species described by Koehler & Vaney (1905):

Orphnurgus glaber Walsh. One specimen from 1026 m. Length 15 cm. Tentacles 20, discs composed of "about 15 lobes". Tubefeet 23–25 on each side, in single rows. Dorsal papillae about 100 on each side, in double rows. Ventrolateral papillae one above each tubefoot. Deposits, long rods with small terminal ramifications; the ramifications may be reduced almost into a simple bifurcation, or developed as a cluster of spines. The specimen was originally described by Walsh (1891) as a variety of *O. asper* Théel.

Orphnurgus invalidus Koehler & Vaney. One specimen from 548 m. Length 5 cm. Tentacles 15, with "enlarged terminal discs". Tubefeet about 15 on each side. Dorsal papillae about 60 on each side, in double rows. Ventrolateral papillae apparently one above each tubefoot. Deposits spatulated rods and rods with small terminal ramifications.

The number of 15 tentacles, the chief distinguishing character of the species, falls within the variation in the here described specimens of *O. glaber.*

Amphideima investigatoris Koehler & Vaney. One specimen from 457 m. Length 6 cm. Tentacles 18, with "lobated" discs. Tubefeet 21–22 on each side, in double rows. Dorsal papillae in single rows (except posteriorly), with 17 pairs medial to the radius and a few posterior ones lateral to it. Ventrolateral papillae absent. Deposits spatulated rods.

The specimen falls within the variation of *O. glaber,* except in the absence of ventrolateral papillae which was considered of generic importance by Koehler & Vaney. However, in view of the extensive variation in number and degree of reduction of the papillae in *O. glaber,* a specimen with all the ventrolateral papillae reduced is not an improbable variant.

Japan. Ohshima (1915 and 1916–1919) recorded two species from five stations. On two of the stations both species occurred.

Orphnurgus insignis Fisher. 12 specimens from 3 stations at 741–1057 m. Length of largest specimen 8.5 cm. Tentacles, tubefeet, and ventrolateral papillae not described. Dorsal papillae in single to double rows, with 15–27 medial, and 0–17 lateral to each dorsal radius. Deposits (Fig. 13: 28–33) resembling those of the Hawaiian specimens.

Orphnurgus rigidus Ohshima. 6 specimens from 4 stations at 741–1210 m. Length stated to be 4.3 cm (probably applying to the largest specimen only). Tentacles 20, discs not described. Tubefeet 16–25 on each side, in single or zigzag rows. Dorsal papillae in double rows, with 12–29 medial, and 6–17 lateral to each dorsal radius. Lateral papillae 13–17 on each side. Basal part of papillae conical and rigid, distal part soft and slender. Deposits (Fig. 13: 34–39) spatulated rods, slender in the dorsum, sturdy in the ventrum – in particular posteriorly; a few spatulated crosses present in dorsum.

Hawaii. Of the two species described by Fisher (1907), *O. insignis* is here regarded as a synonym of *O. glaber,* whereas *O. vitreus* is retained as a separate species.

Orphnurgus insignis Fisher. 123 specimens from 20 stations at 462–765 m. The specimens (most of them in USNM, a few in MCZ) were re-examined (11 specimens by means of spicule preparations).

Length of largest specimen 16 cm. Tentacles 17–20, the discs with "about ten branched divisions ending in small subglobular papillae". Tubefeet in single rows, about 17 on each side in "medium-sized" specimens, and 19–22 in large ones. Dorsal papillae 12–36 on each side, in single rows. Ventrolateral papillae 11–18 on each side. Deposits (Fig. 13: 40–45) comprising crosses and rods with dichotomously ramified ends, small rods with rudimentary ramifications, robust rods with enlarged ends, and large ellipsoid to rounded bodies. All intermediates are present between these types. The ends of the robust rods and of most of the ellipsoid and rounded bodies are covered with small spines which represent the pointed ends of otherwise fused ramifications. There is usually a pronounced difference between the dorsal and ventral deposits, the robust types of deposit being prevalent in the ventrum, and especially in the posterior part of it. Spatulated crosses and rods seem to be altogether absent.

Two specimens were mentioned by Fisher as "aberrant". One (5 cm long) had 10 small, midventral tubefeet, and on each side about 30 double-rowed ventrolateral tubefeet and 30 double-rowed dorsal papillae. The other specimen (7.2 cm long) had 26 rudimentary, midventral tubefeet, about 24 pairs of single-rowed ventrolateral tubefeet, and "numerous" double-rowed dorsal papillae.

Variation:

The extensive variation found in *Orphnurgus glaber* can to some degree be separated into a geographic variation, an age variation, and an individual variation. Due partly to lack of a sufficiently large material, partly to the small weight laid upon the individual variation in the descriptions of the species, the following analysis of the variation is to some degree tentative. Examination of additional material might considerably alter the outline given here. However, the importance of working up future materials with regard to such an analysis should be emphasized.

Tentacles normally 20, but as few as 15 may be present. The variation in number is apparently an individual one only, without correlation to locality or to size of specimens.

The tentacle discs are when fully extended pronouncedly ramified – as in the large *Galathea* specimen and in the Hawaiian specimens referred to *O. insignis*. In the more or less contracted state the ramifications appear only as irregular lobes on the edge of the discs. Such tentacles were reported from most of the synonymous species, and were likewise found in most of the specimens examined here. In the Indonesian specimens the discs showed all intermediates in shape, proving that the variation is due to different states of contraction.

Ventrolateral tubefeet. A geographic variation was found in the number and arrangement of the ventrolateral tubefeet. While the specimens from the Kei and Jolo Islands had 30–60 tubefeet on each side placed in double or triple rows, the specimens from all other regions had about 15–25, only two Hawaiian specimens with 30–34 on each side providing an exception. The tubefeet were, outside the Kei and Jolo Islands, nearly always placed in single rows.

A correlation between the number of tubefeet and the size of the specimens is often demonstrable, although remarkable individual variations are found. In the specimens from the Bay of Bengal and the Bali Sea, as well as in those from the Kei and Jolo Islands the tubefeet number, in the main, increased with the size of the specimens. (The large specimen from the Kei Exp. St. 52 had an unusually low tubefeet number for this region). Similarly, Fisher reported a general increase in the number of tubefeet with the size of the specimens in his Hawaiian material, although again the highest numbers were found in three rather small specimens.

Midventral tubefeet recorded only from the two "aberrant" Hawaiian specimens of *O. insignis*.

Dorsal papillae showed a rather regular cline, decreasing in number and changing from double-rowed (or partly scattered) to single-rowed from the Bay of Bengal and the Bali Sea, over the Kei and Jolo Islands to Japan and Hawaii. In addition, the dorsal papillae, like the ventrolateral tubefeet, increase in the main with the size of the specimens, with some remarkable individual variants.

The specimens from the Bay of Bengal and the Bali Sea had 60–125 dorsal papillae on each side, placed in double rows, or partly scattered. The specimen of *Amphideima investigatoris*, with its sparse and almost exclusively single-rowed papillae, provided an exception. No correlation between the number of dorsal papillae and the size of the specimens was apparent in the material from this region.

At the Kei and Jolo Islands the variation was 30–75 on each side, broadly increasing with the size of the specimens, although the largest specimen had remarkably few papillae for this area. The papillae were, as in the specimens from the Bay of Bengal and the Bali Sea, placed in double rows or scattered over the dorsum.

In the Japanese specimens the papillae formed an outer and inner row along each dorsal radius. The outer papillae were only about half as numerous as the inner ones; thus, the papillae approached an arrangement in single rows, although specimens with purely single-rowed papillae were rare. Ohshima, who described all known Japanese specimens, specified the numbers of outer and inner papillae, but did not state the total number of papillae. Probably, the numbers varied from about 15–45 pairs – a number remarkably smaller than that found in the specimens from the Bay of Bengal and Indonesia. The numbers of papillae in the outer rows were said to increase with the size of the specimens.

At Hawaii the dorsal papillae were placed in single rows in 121 of the 123 specimens described by Fisher. Correspondingly, the number was even smaller than in Japanese specimens, amounting to only 12–36 on each side.

The dorsal papillae are usually soft and almost without spicules, although the basal part may be rather rigid due to the presence of spatulated rods.

Ventrolateral papillae in single rows, except possibly for a few, small ones placed above the main row. Some of the ventrolateral papillae, like some of those dorsally, often reduced; the specimen described as *Amphideima investigatoris* lacked ventrolateral papillae. The ventrolateral papillae are usually more sturdy than the dorsal ones, and usually contain more spicules. The numbers of ventrolateral papillae, as well as their contents of spicules, showed no correlation to the locality or size of the specimens.

A correlation exists between the number of the different types of ambulacral appendages in the deviating specimens. Thus, the specimen of *A. investigatoris* from the Bay of Bengal lacked the ventrolateral papillae and had an unusually low number of dorsal ones. The large specimen from Kei Exp. St. 52 had an unusually low number of both ventrolateral tubefeet and dorsal papillae for a specimen of that size and from that region. Similarly, the two "aberrant" Hawaiian specimens of *O. insignis* had an exceptionally high number of both dorsal papillae and ventrolateral tubefeet, and were, besides, the only specimens known (of all the synonymized species) possessing midventral tubefeet.

It is noteworthy that this correlation applies only to the individual variation in the species – not to the geographic variation. In the specimens from the Bay of Bengal and the Bali Sea a low number of tubefeet was combined with a high number of dorsal papillae, while in Hawaiian specimens the number was low in both tubefeet and papillae. The specimens from the Kei and Jolo Islands had numerous tubefeet, but rather few dorsal papillae. Thus, there is an independent geographic variation in the numbers of tubefeet and papillae.

Anus terminal, or slightly dorsal or ventral.

Deposits. In the single individual, the deposits may consist of spatulated rods only, or of spindle-shaped, ellipsoid, and spherical bodies. In the specimen from Kei Exp. St. 52 spatulated rods occurred together with spherical bodies – the latter proving to be reduced spatulated rods. In the Hawaiian specimens referred to *O. insignis* an enormous variation was found in the single individuals – the deposits varying from dichotomously branched primary crosses to large, ellipsoid bodies.

The ventral deposits are more robust than the dorsal ones, and usually increase in sturdiness posteriorly. Similarly, the deformed deposits, if present, prevail in the ventrum, and are largest and most crowded posteriorly.

The individual variation is likewise extensive. Of the four specimens from the Kei Islands, that from St. 52 had spatulated rods almost exclusively, while these were absent in the specimens from Sts. 41, 51, and 56.

A similar individual variation was found in Japanese material where specimens with exclusively spatulated rods and crosses occurred together with specimens in which reduced and deformed deposits predominated.

An age variation in the shape of the deposits is not present. Reduced and deformed deposits occur in small as well as in large specimens.

A geographic variation is shown by differences in the type of transformation of the deposits. The basic type of spicule in the species is probably the slender spatulated rod found in the specimens from the Bali Sea and in the two specimens from the Bay of Bengal referred to *Orphnurgus invalidus* and *Amphideima investigatoris.*

The Kei and Jolo specimens show all transitions from spatulated rods to various types of reduced deposit. Although spatulated rods were present only in the specimen from Kei Exp. St. 52, it seems unjustified to separate this specimen taxonomically from the other specimens from the region.

At Japan also there are specimens with spatulated rods *(O. rigidus)*, as well as specimens in which all the deposits are transformed into robust bodies *(O. insignis)*. The spatulated rods resemble those of the specimens from Kei Exp. St. 52, being slender in the dorsum and robust in the ventrum, especially in the posterior part. The transformed deposits of the *insignis* specimens, on the other hand, resemble those of the Kei-Jolo specimens, although their ends are usually enlarged and covered with spines. Intermediate stages are present between these deposits and the slender rods with open ramifications at the ends, showing that the spines represent the ends of otherwise fused ramifications.

Although a re-examination of the Japanese specimens could not be made, there seems little doubt that the Japanese *rigidus* and *insignis* specimens belong to one and the same species. Slender rods with open ramifications – the starting-point for the transformation of the deposits in the *insignis* specimens – did also occur in *O. rigidus*. Furthermore, it is noteworthy that the transformation of the deposits in both of the Japanese species does not involve a reduction of their ends, while this is always the case in the specimens from the Kei-Jolo Islands.

The Hawaiian specimens resemble the Japanese *insignis* specimens, all intermediates being present between slender rods with open ramifications and rounded and ellipsoid, robust bodies. These bodies are usually covered with small spines at their ends, although specimens were found during re-examination in which practically all the round and ellipsoid deposits were smooth. The smooth bodies are indistinguishable from those found in the Kei-Jolo specimens although of a somewhat different derivation, having passed through a spinous stage.

Spatulated rods seem to be completely absent in Hawaiian specimens (unless the species *Orphnurgus vitreus* is considered a synonym of *O. glaber*).

The type specimen of *Orphnurgus glaber*, from the Bay of Bengal, had deposits reminiscent of the Japanese and Hawaiian *insignis* specimens. Rods with a few ramifications at the ends and rather sturdy rods with spinous, enlarged ends were present, but spatulated rods were absent. Thus, the type specimen of *O. glaber* showed the same type of transformation of the deposits as the Japanese and Hawaiian specimens, although the transformation had not proceeded as far as in the latter.

Thus, the species shows an all-over tendency of a transformation of the rods into robust bodies. At the Kei and Jolo Islands the transformation involves a reduction of the ends of the rods, while in the Bay of Bengal, at Japan, and at Hawaii the ends of the spicules are preserved. The ends are usually covered with spines due to the derivation of the bodies from rods with open ramifications.

A geographic variation is indicated by the pronounced transformation of the deposits at the Kei and Jolo Islands on one hand, and Japan and Hawaii on the other, and by the fact that the process of transformation is different in the two regions.

Conclusion. An analysis revealed the following types of variation in the species:

An *individual variation* is present in the number of tentacles, tubefeet, and papillae, as well as in the shape of the deposits. In the single individual, the variation in the deposits may be wide or narrow.

An *age variation* is generally present in the number of tubefeet and papillae, although with notable exceptions. The deposits show no variation with age.

A *geographic variation* is present in the number and arrangement of the ventrolateral tubefeet and dorsal papillae, and in the shape of the deposits. The geographic variation in the number of tubefeet and papillae is mutually independent.

Distribution: Bay of Bengal, 457–1026 m. Indonesia, 245–545 m. Japan, 741–1210 m. Hawaiian Islands, 462–765 m.

Orphnurgus vitreus (Fisher, 1907)
Fig. 14

Scotodeima vitreum Fisher, 1907, pp. 697–701, pls. LXXIV: 2–2a, LXXV: 1–4, LXXVI: 1–2.

Diagnosis: Tentacles 17; discs with ramified processes on the margin. Ventrolateral tubefeet about 34 on each side, in double rows. Midventral tubefeet 6 or 7. Dorsal papillae in double rows, with about 30 medial and 17–18 lateral to each dorsal radius. Ventrolateral papillae 23–29 on each side. Deposits, dorsally slender spatulated rods and occasional spatulated crosses; ventrally, rods with a few dichotomous ramifications at the ends; in papillae, crowded spatulated rods.

Record: Off the Hawaiian Islands, 406–707 m. One specimen.

Remarks: The specimen (in USNM) was reexamined and compared with the numerous specimens of the other Hawaiian species, *O. insignis* which in the present paper is considered a synonym of *O. glaber*. The fact that the variation of the deposits in *O. glaber* includes spatulated rods

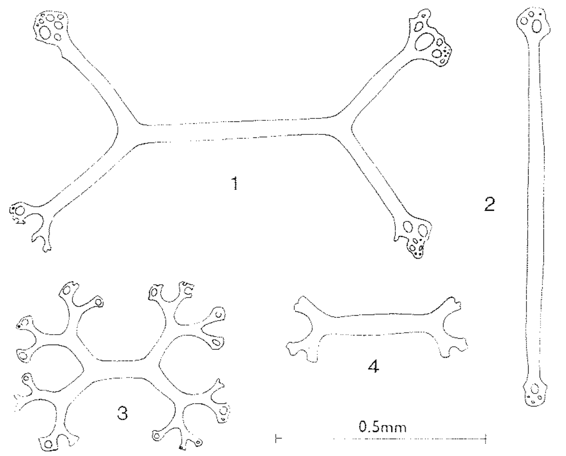


Fig. 14. *Orphnurgus vitreus*. *Albatross* St. 3979. Deposits from the type specimen. 1–2, dorsum; 3–4, ventrum.

similar to the dorsal deposits of *O. vitreus* suggests that also this species might be identical with *O. glaber*. However, as the re-examination of Fisher's material of *O. insignis* failed to reveal the presence of spatulated rods, or derivatives of these, it was preferred to retain *O. vitreus* as separate. (The deposits of all the specimens could be referred to type without making preparations).

Orphnurgus protectus (Sluiter, 1901)

Scotodeima protectum Sluiter, 1901a, pp. 20–21; Sluiter 1901b, pp. 61–62, pls. II: 7, IX: 4.

Diagnosis: Tentacles 15; discs with irregular ramifications on the margin. Ventrolateral tubefeet 24 pairs. Midventral tubefeet few and rudimentary. Dorsal papillae 22 pairs, in irregular double rows. Ventrolateral papillae 21 pairs. Spatulated crosses of the body wall measuring 0.7 mm across. Spatulated rods densely packed in the slender and rigid papillae.

Record: Celebes Strait, 1301 m. One specimen.

Remarks: The species agrees with *Oneirophanta setigera* in the exclusive presence of spatulated crosses in the body wall and of spatulated rods in the papillae. Re-examination of the specimen revealed that the tentacle discs had ramified processes on the margin. For this reason, the species is referred to *Orphnurgus* – the similarity to *Oneirophanta setigera* being supposed due to convergence. Only 13 tentacles could be counted during re-examination.

Family **LAETMOGONIDAE** Ekman, 1926

Diagnosis: Deposits wheel-shaped. In addition, only scattered rods or (in *Laetmogone violacea*) spinous crosses occur. Gonads with numerous slender and branched tubules, usually arranged in several clusters.

Taxonomy: The taxonomic position of the family is considered elsewhere (p. 206). The family is here divided into four genera, characterized as follows:

Benthogone has a circum-oral ring of papillae, simply shaped wheels, small-sized dorsal papillae, and 15–20 tentacles. (None of the species have a constant number of 15 tentacles).

Apodogaster has a brim of fused ventrolateral papillae above the tubefeet – a unique feature in the Elasipoda.

Pannychia differs from all other laetmogonids by the type of wheel.

Laetmogone is characterized primarily by negative features. The number of tentacles is 15, except in *L. theeli* (20) and *L. interjacens* (15–17). The latter species has several features in common with *Benthogone*, but lacks circum-oral papillae.

Differences are found in the shape of the tentacle discs within the family, although the disc

Key to the genera of *Laetmogonidae*

1. Circum-oral papillae present . . . . *Benthogone* (p. 48)
1. Circum-oral papillae absent 2
2. Brim of fused ventrolateral papillae present above the ventrolateral tubefeet . . . .
. . . . *Apodogaster* (p. 75)
2. Brim, if present, composed of fused ventrolateral tubefeet 3
3. Wheels having marginal teeth. Papillae of dorsum belonging to dorsal as well as ventrolateral radii. Midventral tubefeet present . . . . *Pannychia* (p. 72)
3. Wheels lacking marginal teeth. Papillae of dorsum belonging to dorsal radii only. Midventral tubefeet absent . . . . *Laetmogone* (p. 52)

types are not as clearly separated as in the Deimatidae (p. 191).

The variation found in the external morphology of the gonads (p. 194) is of little value in the taxonomy of the family.

Genus **Benthogone** Koehler, 1896
Fig. 112

Benthogone Koehler, 1896, pp. 113–114. – Type species: *Benthogone rosea* Koehler, 1896, by monotypi.
Benthophyces Koehler & Vaney, 1905, p. 64.
Ilyodaemon Théel, 1879, p. 11 (partim).

Diagnosis: Circum-oral papillae present. Mid-ventral tubefeet absent. Dorsal papillae small, in single rows, double rows, or bands. Ventrolateral papillae absent. Wheels lacking marginal teeth.

Remarks: *Benthogone* differs from the other genera of the family by the presence of a ring of circum-oral papillae. Koehler stressed that the dorsal papillae and the tubefeet were retractile, but this is here discarded as a generic character. The papillae and tubefeet may be retractile also in species of *Laetmogone*, while they are unretractile in *Benthogone (Ilyodaemon) abstrusa*.

Key to the species of *Benthogone*

1. Tubefeet projecting horizontally from the flattened body side, and continuing in transversal ridges on the ventrum. Papillae in narrow double rows .... *abstrusa* (p. 51)
1. Tubefeet ventrally directed 2
2. Papillae in single or double rows .... *rosea* (p. 48)
2. Papillae in bands .... *fragilis* (p. 49)

Benthogone rosea Koehler, 1896
Fig. 15

Benthogone rosea Koehler, 1896, pp. 114–117, figs. 2, 3, 36, 46; R. Perrier 1902, pp. 399–405, pls. XIV: 1–2, XIX: 8–14; Grieg 1921, pp. 5–6; Hérouard 1923, pp. 38–39; Heding 1940, p. 369; Madsen 1947, pp. 15–16; Pawson 1965a, pp. 219–221, pl. 5.
Benthogone rosea var. *cylindrica* R. Perrier, 1896, p. 900.
Benthogone rosea var. *4-lineata* R. Perrier, 1896, p. 900.
Benthogone quadrilineata R. Perrier, Heding 1940, p. 369; Heding 1942, p. 15.
Non *Benthogone quatrolineata* Augustin, 1908 (= *Laetmogone ijimai*).

Diagnosis: Tentacles 15–20. Tubefeet retractile, 13–24 on each side. Papillae small and retractile, placed in a single or double row along each dorsal radius. Wheels of a single type, 0.06–0.16 mm in diameter; spokes 8–14, without correlation to the size of the wheels; central rays 4, occasionally 5; nave somewhat narrowed by a calcareous membrane.

Material:
St. 241, off Kenya (4°00'S, 41°27'E), 1510 m. – 1 specimen.

Description: The specimen, which is rather defective, was probably about 7 cm long.

Colour in the preserved state light reddish-violet, the papillae dark violet.

Tentacles 17; discs similar in shape to those of *Benthogone fragilis* (Pl. VIII: 11).

Tubefeet 12 pairs, partly retracted.

Papillae about 25 on each side, minute, single-rowed.

Wheels (Fig. 15: 4) 0.06–0.13 mm in diameter, with a central primary cross, and the nave somewhat narrowed by a calcareous membrane. Spokes 8–12, without clear prevalence of any single number (Table 3).

Rods present in tentacles and tubefeet, but absent from papillae.

End-plate present in tubefeet.

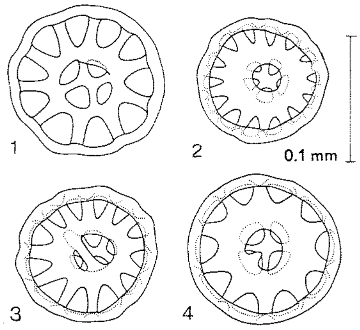


Fig. 15. *Benthogone rosea*. Deposits. 1–3, *Skagerak* Exp. (Atlantic off Gibraltar); 4, *Galathea* St. 241.

Table 3. *Benthogone rosea, B. fragilis,* and *B. abstrusa.*
Number of spokes in 100 wheels from five specimens.

Number of spokes	8	9	10	11	12	13	14	15	16	17	18	19
Benthogone rosea (Galathea St. 241)	4	12	32	39	13	–	–	–	–	–	–	–
– – (off Gibraltar)	–	5	14	32	43	4	2	–	–	–	–	–
– *fragilis (Galathea* St. 324)	13	28	30	18	11	–	–	–	–	–	–	–
– *abstrusa (Siboga* St. 314)	3	23	20	29	18	5	2	–	–	–	–	–
– – (– – –)	–	1	3	5	24	22	20	14	8	1	–	2

Remarks: The specimen was taken near the locality of one of the *Valdivia* specimens. Re-examination of the latter confirmed Heding's statement that it is indistinguishable from the Atlantic ones. It is 8 cm long, has 17 pairs of retracted tubefeet, 30–35 minute, single-rowed papillae on each side, and a conspicuous ring of circum-oral papillae. (The circum-oral papillae were not seen in the more defective *Galathea* specimen). The tentacles were all retracted.

The covering membrane of the nave of the wheels, found in the *Galathea* specimen, has not previously been described for *B. rosea.* In the preparation from an Atlantic specimen taken by the *Skagerak* off Gibraltar (Madsen 1947) it was, however, similarly present. As in the *Galathea* specimen, no particular spoke number prevailed (Table 3). The variation in the shape of the wheels appears from Fig. 15: 1–3. The tentacle discs were in none of the re-examined Atlantic specimens as well expanded as in the *Galathea* specimen. Probably, they did not differ in type.

Two specimens were described by Pawson (1965a and c) from north of New Zealand. They had 15 tentacles, approximately 13 pairs of retractile tubefeet, about 40 short, retractile dorsal papillae on each side, arranged in a single, sometimes double, row. Wheels similar to those otherwise found in the species (a calcareous membrane covering the nave was not mentioned), with 7–12 (most often 11) spokes. Circum-oral papillae not mentioned. In the shape, number, and arrangement of the dorsal papillae the New Zealand specimens agree with the other known specimens.

Synonymy: R. Perrier (1896), in his preliminary report on the holothurians from the *Travailleur* and the *Talisman,* erected the variety *4-lineata* of *Benthogone rosea* for a single specimen with four instead of two rows of papillae. In his final report, however, he rejected the variety, as all intermediates between specimens with two and four rows of papillae had been found.

Heding (1940, 1942), on the other hand, maintained the taxonomic significance of two versus four rows of papillae, and raised the variety of Perrier to the rank of a species, *Benthogone quadrilineata.* A re-examination, however, of a number of specimens of *B. rosea* and of Heding's *B. quadrilineata* (all in ZMUC) confirmed that all intermediates are present.

Relationships: Closest related to *B. fragilis* (q. v.).

Distribution: Eastern Atlantic from Ireland to the Cape Verde Islands, 1103–2480 m. East Africa, 1510 and 1668 m. North of New Zealand, 1170 m.

A record of the species from Monaco St. 2290 in the western Mediterranean (Hérouard 1923) is due to a misprint. The specimen actually came from St. 2990 in the eastern North Atlantic.

Benthogone fragilis (Koehler & Vaney, 1905)

Figs. 16–17, Pl. VIII: 11

Benthophyces fragilis Koehler & Vaney, 1905, p. 65, pls. VIII: 6–7, XII: 4–7.

Diagnosis: Tentacles 16–20. Tubefeet 17–20 on each side. Papillae small, numerous, and placed in a band along each dorsal radius. Wheels similar to those of *B. rosea.*

Material:
St. 324, Strait of Malacca (6°38'N, 96°00'E), 1140 m. – 1 specimen.

Description: The specimen (Fig. 16) is 9 cm long, 2.5 cm broad, and slightly more than 1 cm high.

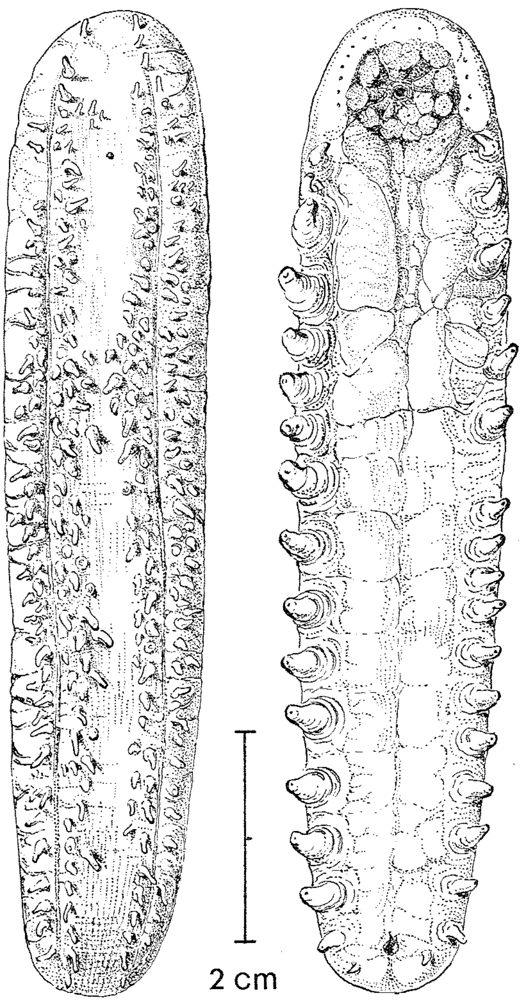


Fig. 16. *Benthogone fragilis.* St. 324. Dorsal and ventral view. JT.

Colour of preserved specimen light reddish-violet.

Tentacles 16; discs (Pl. VIII: 11) with conspicuous papillae in radially arranged fields which continue into marginal processes.

Circum-oral papillae visible in places.

Tubefeet unretracted, conical with a small sucking-disc. 18 left and 17 right are present, placed without bilateral symmetry, and sometimes with irregular intervals.

Papillae broad, conical, 2–3 mm long, placed in two bands containing about 125 in each. Only here and there does the arrangement approach a double row.

Wheels (Fig. 17) 0.10–0.14 mm in diameter, similar to those of *B. rosea.* They have 8–12 spokes; as in *B. rosea* no particular spoke number prevails (Table 3).

Rods present in tentacles, tubefeet, and papillae. The rods of the papillae and tubefeet are transversally placed.

End-plate present in tubefeet.

Anus ventral.

Remarks: *Benthophyces fragilis,* known from one specimen taken in the Arabian Sea, agrees with the *Galathea* specimen in the following respects:

A "collerette péribuccale", apparently identical with a ring of circum-oral papillae, was mentioned in the diagnosis of *Benthophyces,* though not shown in the drawing of the specimen.

The small elevations of the dorsal skin, on which the papillae were placed, are probably identical with the enlarged bases found in many of the papillae in the *Galathea* specimen. Likewise, the papillae were as in this latter specimen, numerous and irregularly placed, approximately forming two dorsal bands.

The tubefeet numbered about 20 on each side and were ventrally placed, which agrees well with the *Galathea* specimen. Judging from the drawing they were somewhat retracted, as is usually found in specimens of *B. rosea.* This retraction might have been responsible for the low elevations of the ventral skin, which together with the enlarged bases of the dorsal papillae formed the generic characters of *Benthophyces.*

The tentacle number was stated to be 18 or 20.

The wheels probably fall within the variation of *B. rosea.* The small, rounded knobs mentioned by Koehler & Vaney from the distal ends of the central rays seem to be insignificant aberrations in the overall pattern of rather irregular wheels.

Relationships: *B. fragilis* is closest related *B. rosea* from which it differs by the papillae being more numerous and placed in bands. Further knowledge of the species may prove it to be a geographic form – possibly a subspecies – of *B. rosea.*

Distribution: Arabian Sea, 1345 m. Strait of Malacca, 1140 m.

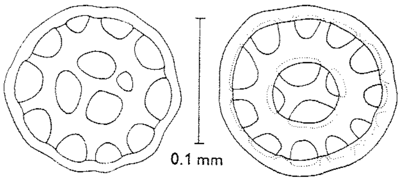


Fig. 17. *Benthogone fragilis.* St. 324. Deposits.

Benthogone abstrusa (Sluiter, 1901)

Fig. 18

Ilyodaemon abstrusus Sluiter, 1901a, pp. 24–25; Sluiter 1901b, pp. 69–71, pls. IV: 1–3, IX: 9. Non Pawson 1965c, pp. 20–22, fig. 5.

Diagnosis: Tentacles 18. Tubefeet large, projecting more or less horizontally from the flattened body side, and continuing in transversal ridges on the ventrum. Papillae short, conical, placed without intervals in a narrow double row along each dorsal radius. Wheels of a single type, 0.05–0.16 mm in diameter, usually more or less irregular in shape; spokes 8–14, without correlation to the size of the wheels; centre formed as a primary cross which is sometimes irregularly developed; nave usually covered by a perforated calcareous membrane. Sturdy, unbranched, or slightly branched rods present in tubefeet, papillae, and ventrum.

Re-examination of the *Siboga* specimens: *Benthogone abstrusa* is known from 33 specimens, taken at five Indonesian stations of the *Siboga*. Spicule preparations were made from eight specimens.

External characters. In external appearance the species is very characteristic and cannot be mistaken for any other species.

The large tubefeet and the conical dorsal papillae placed in two very narrow double rows are in all the specimens, including the smallest ones measuring 6 cm, exactly as illustrated by Sluiter. The tubefeet project more or less horizontally from the lateral edge of the body; on the ventral sole they often continue in transversal elevations which may reach the ventral midline of the body.

The tentacles numbered 18, except in one specimen with 17.

Deposits. While Sluiter found that the wheels were regular in shape and possessed a remarkably constant number of 11 spokes, the wheels in the eight specimens re-examined showed a large variation in shape (Fig. 18) as well as in spoke number (Table 3). The spoke number illustrated for the two specimens represents the total variations in the eight specimens examined. No correlation was found between number of spokes and diameter of wheels.

The outline of the wheels is usually strikingly irregular, though in the preparations from two of the specimens most wheels were as regular as shown in Fig. 18: 4. The length and thickness of the spokes likewise vary greatly, and in addition they are often irregularly shaped.

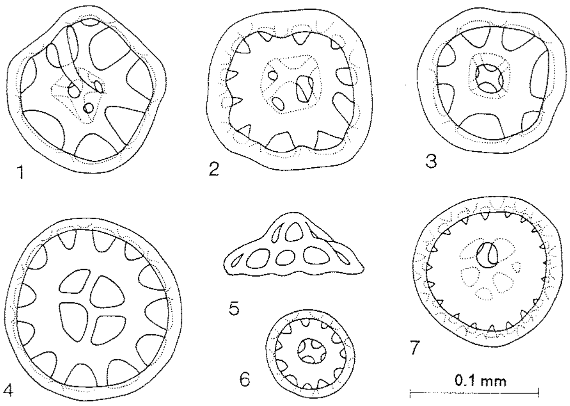


Fig. 18. *Benthogone abstrusa.* Deposits. 1–5, *Siboga* St. 45; 6–7, *Siboga* St. 314.

The centre of the wheels is usually a regular primary cross, but sometimes this develops into a more or less irregular 3-, 5-, or 6-rayed structure. The nave is, in most wheels, covered by a thin calcareous membrane, perforated by one or more holes. A few wheels possessed calcareous bridges from the covering membrane to the rim of the wheel.

The diameter of the wheels is 0.05–0.16 mm. In some preparations practically all the wheels were smaller than 0.10 mm, in others most wheels exceeded 0.10 mm, and in others again a large variation was found within a single preparation.

The tubefeet, papillae, and ventrum contained in all the specimens examined sturdy, often slightly ramified rods, as mentioned by Sluiter. A small end-plate is usually present in the tubefeet.

Remarks: The specimens reported by Pawson (1965c) differ in some essential points from the *Siboga* specimens, and probably represent a new species of *Laetmogone.* The wheel-shaped deposits belonged to two distinct types: Large wheels measuring 0.08–0.13 mm, with 9–11 spokes and 6 central rays, and small wheels about 0.04 mm in diameter and typically with 12 spokes and 4 central rays. These wheel types are very different from those found in the *Siboga* specimens, in which all the wheels are of the same type and all (typically) have four central rays.

The ring of circum-oral papillae, which is very conspicuous in the *Siboga* specimens, was not mentioned by Pawson. The tentacle number could not be determined, but the number was supposed to exceed 15.

The specimens seem to be closest to *Laetmogone maculata.*

Relationships: While *Benthogone rosea* and *B. fragilis* are closely interrelated, the species *B. abstrusa* stands somewhat apart in the genus. It differs from the other two species by the flattened body form.

Distribution: Indonesia, 694–959 m.

Genus *Laetmogone* Théel, 1879
Figs. 113–114

Laetmogone Théel, 1879, pp. 9–10; Théel 1882, p. 73. – Type species, designated by Fisher (1907): *Laetmogone wyvillethomsoni* Théel, 1879.
Cryodora Théel, 1879, p. 9.
Ilyodaemon Théel, 1879, p. 11; Théel 1882, p. 84.
Laetmenoecus Clark, 1913, p. 230.
Bathygone Pawson, 1965b, p. 77.

Diagnosis: Circum-oral papillae absent. Midventral tubefeet absent. Dorsal papillae in single rows, double rows, or bands. Ventrolateral papillae absent. Wheels lacking marginal teeth.

Synonymy: *Ilyodaemon* was regarded as being distinct from *Laetmogone* on account of its double-rowed papillae, contrary to the single-rowed ones in *Laetmogone.* The validity of the genus was doubted by Sluiter (1901b), but nevertheless it has been retained until now.

In *L. fimbriata, L. biserialis,* and *L. maculata* the arrangement of the papillae changes from single rows to double rows (or even to an arrangement in bands) with the age of the specimens. The distinction between *Ilyodaemon* and *Laetmogone* thus cannot be upheld.

Bathygone, with the species *B. papillatum,* was distinguished by the presence of small heaps of aggregated calcareous deposits, a feature claimed to be unique in the family. However, similar aggregations of deposits occur in most specimens of *Laetmogone maculata.* They seem to be of little taxonomic significance. Here the species *B. papillatum* is regarded as a synonym of *Laetmogone fimbriata.*

Laetmenoecus, with the single species *L. scotoeides,* was distinguished from *Laetmogone* by the supposed absence of dorsal papillae. Reexamination of a specimen showed that small papillae were indeed present.

Taxonomic characters: *Deposits.* The wheel-shaped deposits exhibit species differences in the shape and in the varying degree of separation into two types.

In *L. interjacens* the wheels all possess a central primary cross, a similarity to the wheels in the genus *Benthogone.* The wheels measure 0.08–0.14 mm in diameter and have 9–12 spokes. The nave of the wheels is sometimes covered by a calcareous membrane which grows inwards from the edge of the nave, a similarity to the wheels in the genus *Benthogone* and in *L. theeli, L. wyvillethomsoni,* and *L. violacea.*

In *L. theeli* almost all the wheels possess a central primary cross, and wheels smaller than 0.08 mm are rare. The total variation in diameter is 0.05–0.19 mm, and 10–16 spokes are present; the highest spoke numbers are generally found in the small wheels.

In *L. wyvillethomsoni* and *L. violacea* the wheels possess 4–6 central rays and 8–16 spokes. The highest spoke numbers are generally found in the smaller wheels, but there is no abrupt change in spoke number at any size. The wheels are 0.04–0.18 mm in diameter; wheels about 0.05 mm in diameter are especially numerous.

In *L. scotoeides* the wheels are to some degree differentiated into two types. The small type (0.04–0.08 mm) has 4 central rays, while the large type (0.06–0.30 mm) has 5 (occasionally 6) central rays. The number of spokes varies from 10 to 18 with a prevalence of 12 spokes both in large and small wheels.

In *L. maculata, L. ijimai, L. fimbriata,* and *L. biserialis* the wheels are of two very distinct types, small ones 0.04–0.05 mm in diameter, with a central primary cross and (10–)12 spokes, and larger ones 0.06–0.30 mm in diameter, with 6 central rays and 9 or 12 spokes.

L. maculata differs from all other laetmogonids by the presence of rosette-shaped spicules, derivatives of the small type of wheel. A transformation of a somewhat similar kind is sometimes found in *L. fimbriata,* where the small wheels may change into small reticulated plates.

Tentacle number 15, with the exception of *L. theeli* (20) and *L. interjacens* (15–17).

Tubefeet. L. fimbriata and *L. biserialis* differ from the other species of the genus by their slender, almost threadlike, tubefeet. The specimens which Hérouard (1902) referred to *L. wyvillethomsoni* had similar tubefeet. These specimens probably represent a new species of *Laetmogone.*

In *L. interjacens* the tubefeet are placed on the edge of a brim which surrounds the whole body, a unique feature in the family.

Key to the species of *Laetmogone*

1\. Tubefeet placed on the edge of a brim which surrounds the whole body. Tentacles 15–17. Wheels belonging to a single type, with a lower size limit of 0.08 mm; central rays 4 (occasionally 5); spokes 8–12 (15) . . . . *interjacens* (p. 53)
1\. Brim absent. Tentacles 15 (in one species 20). Wheels belonging to one or two types; lower size limit 0.04–0.05 mm 2
2\. Papillae extremely small. Wheels indistinctly differentiated into two types, one with a central primary cross and measuring 0.05–0.08 mm, the other with 5 (occasionally 6 or 7) central rays and measuring 0.08–0.30 mm . . . . *scotoeides* (p. 61)
2\. Papillae conspicuous. Wheels belonging to one or two types 3
3\. Wheels belonging to two distinct types, one with a central primary cross and rarely exceeding 0.05 mm in diameter, the other with 6 central rays, and always larger than 0.05 mm 4
3\. Wheels not belonging to two distinct types. Central rays 4–5; spokes 8–15 (20), in the main inversely correlated to the size of the wheels 7
4\. Tubefeet bulky, narrowing towards the tip 5
4\. Tubefeet crowded, very slender from base to tip, the diameter of the sucking-discs equal to that of the tubefeet 6
5\. Rosette-shaped deposits present. Some of the wheels of the large type with a triangular superstructure. Papillae varying in size, some being rather large *maculata* (p. 63)
5\. Rosette-shaped deposits absent. Triangular superstructure absent in large wheels. Dorsal papillae small and uniform in size . . . . *ijimai* (p. 67)
6\. Large type of wheel with about 9 spokes . . . . *fimbriata* (p. 67)
6\. Large type of wheel with about 12 spokes . . . . *biserialis* (p. 70)
7\. Cross-shaped deposits present . . . . *violacea* (p. 58)
7\. Cross-shaped deposits absent 8
8\. Tentacles 15. Tubefeet 15–33 pairs . . . . *wyvillethomsoni* (p. 54)
8\. Tentacles 20. Tubefeet 45–53 pairs . . . . *theeli* (p. 57)

Laetmogone interjacens Sluiter, 1901

Fig. 19

Laetmogone interjacens Sluiter, 1901a, pp. 21–22, Sluiter 1901b, pp. 64–65, pl. IX: 6.

Laetmogone wyvillethomsoni Théel, Sluiter 1901b, p. 63 (partim).

Diagnosis: Tentacles 15–17. Body, including the head, surrounded by a continuous brim, on the edge of which tubefeet with small sucking-discs are placed. Papillae minute, in single rows. Wheels of a single type, 0.08–0.14 mm in diameter; central rays 4; spokes 9–12; nave often covered by a perforated calcareous membrane.

Re-examination of the *Siboga* specimens: The species was erected on two specimens, 3.5 and 5.0 cm long, from *Siboga* St. 45 (south of Celebes). A re-examination gave additional information on the two specimens, and further revealed that a specimen reported as *L. wyvillethomsoni* from *Siboga* St. 170 (west of New Guinea) in actual fact belongs to *L. interjacens.*

Colour (in alcohol) dark violet in the specimens from St. 45, and light violet in the specimen from St. 170.

Brim. The presence of a broad, lateral brim was stressed by Sluiter as being especially characteristic of the species. On re-examination the brim was seen to continue round the anterior

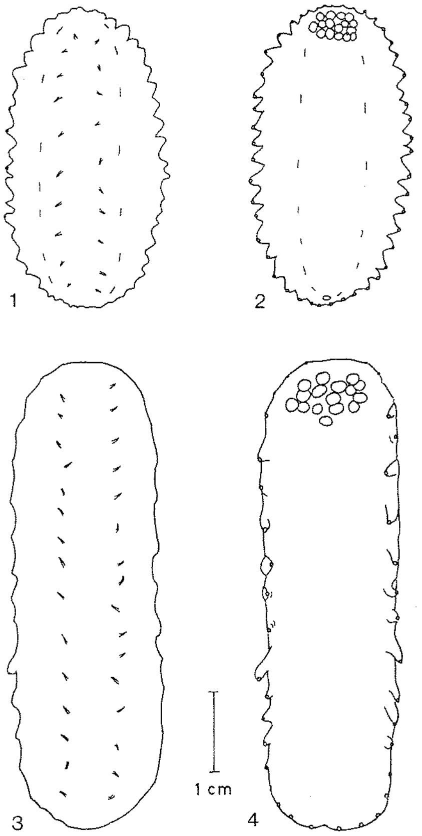


Fig. 19. *Laetmogone interjacens.* Two specimens in dorsal and ventral view. 1–2, *Siboga* St. 45; 3–4, *Siboga* St. 170.

and posterior end of the body, a unique feature in the genus.

In the small specimen from St. 45 (Fig. 19: 1–2) the brim is very broad and clearly distinguishable from the body, whereas in the specimen from St. 170 (Fig. 19: 3–4) it is more narrow and less distinct from the body proper. The difference may be due to a different state of contraction. In the large specimen from St. 45 the brim is defective.

Tubefeet present along the whole edge of the brim. In the small specimen from St. 45 about 25 are present on each side. The specimen from St. 170, in which the brim is not quite intact, probably had about the same number. Some tubefeet are completely retracted into the brim. A small, but conspicuous sucking-disc is present on all the tubefeet, even on the minute ones of the anterior margin.

Papillae small and single-rowed. According to Sluiter about 14 pairs were present. On re-examination the small specimen from St. 45 was found to have about 10 pairs of minute papillae, but more might have been present. The large specimen from St. 45 has 18 and 25 papillae along the right and left radius, respectively. The specimen from St. 170 has about 15 pairs.

Tentacles. Sluiter counted 17 tentacles in both the specimens from St. 45. This number was confirmed as regards the small specimen, while only 15 could be counted in the large one, and 16 in the specimen from St. 170.

Table 4. *Laetmogone interjacens.* Number of spokes and diameter of 100 wheels in the dorsum of the specimen from *Siboga* St. 170.

Diam. mm	Spokes					
	8	9	10	11	12	8–12
0.08	–	1	7	1	–	9
0.09	–	2	3	5	4	14
0.10	1	4	6	2	9	22
0.11	–	2	8	4	1	15
0.12	–	3	12	10	7	32
0.13	–	1	4	–	2	7
0.14	–	–	–	–	1	1
0.08–0.14	1	13	40	22	24	100

Wheels similar in shape to those of *Benthogone rosea* and *B. fragilis.* Table 4 shows the diameter and spoke number of 100 wheels from the specimen from *Siboga* St. 170. The other two specimens showed similar features. Sluiter found that the spoke number was very regularly 11, but that a few large wheels (0.16 mm in diameter) had 15 spokes. These large wheels may be alien bodies, possibly wheels of *Pannychia.* (A *Pannychia* wheel was present in one of the preparations made during re-examination).

Central rays 4 (only one out of a hundred wheels had 5 rays). Nave in some wheels covered by a perforated calcareous membrane.

Relationships: *L. interjacens* differs from all other species of the genus by the brim which surrounds the whole body. The high tentacle number suggests a relationship to the genus *Benthogone* (p. 47).

Distribution: Indonesia, 794 and 924 m.

Laetmogone wyvillethomsoni Théel, 1879
Fig. 20

Théel 1879, p. 10, figs. 12–13; Théel 1882, pp. 73–78, pls. XI, XII, XXXI: 14–16, XXXIV: 1,

XXXVI: 3, XXXVII: 5, 7, 11, XXXVIII: 9, XXXIX: 4, XLII: 1, 7, XLIII: 4, XLIV: 14, XLVI: 2–3; Agatep 1967b, p. 63, pls. VIII: 1–11, IX: 1–10.

Diagnosis: Tentacles 15. Tubefeet 15–33 on each side, rather cylindrical with conspicuous sucking-discs. Papillae 5–18 on each side, slender and single-rowed. Wheels of a single type, 0.04–0.16 mm in diameter, those of about 0.05 mm being especially numerous; number of spokes increasing from 8–10 in the large wheels to 11–14 in the small ones; central rays 4–5, rarely more; nave covered by a calcareous membrane, usually with a few minute perforations. Numerous sturdy rods with blunt or rounded ends usually present in ventrum, rarely in dorsum. Spinous crosses absent.

Material:
St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 1 specimen.

Description: The specimen is 5.5 cm long, 1.3 cm broad, and light violet in colour.

Tentacles 15; discs similar to those of *L. violacea* (Pl. VIII: 8).

Tubefeet 17 pairs, single-rowed, rather cylindrical, with conspicuous sucking-discs.

Papillae 10 pairs, single-rowed, all about 15 mm long, slender from base to tip.

Wheels (Fig. 20: 1–2) 0.04–0.14 mm in diameter, with 8–13 spokes. The wheels are further described in connection with the re-examination of the *Challenger* specimens.

Rods (Fig. 20: 3–4) crowded in ventrum, but absent in dorsum. They are rather sturdy, usually smooth, with blunt or rounded ends, and often more or less ellipsoid. Similar rods in the distal parts of the tubefeet. Papillae practically devoid of rods.

End-plate present in tubefeet.

Re-examination: *L. wyvillethomsoni* was previously known from three *Challenger* stations in the southern Indo-Pacific (depth 2514–3296 m) and three *Eltanin* stations in the Antarctic Ocean (depth 3020–3678 m). Probably all bathyal records were based on erroneous identifications.

(1) The *Challenger* specimens. Re-examination was made of eight specimens from St. 300, two from St. 147, and one from St. 158. (Two of the specimens from St. 300 are kept in ZMA, all the remaining are in BM. Deposits examined in all the BM specimens).

Body 2–17 cm long, 3–4 times as long as broad. (Théel stated that the specimens were up to 24 cm long). Tubefeet 15–29 on each side; as in the *Galathea* specimen, they are rather cylindrical. Papillae 5–17 on each side (almost the whole variation is comprised in the specimens from *Challenger* St. 300). The papillae vary greatly in length, even in one and the same specimen; the longest papillae are as long as the body.

The spokes were counted and the diameter measured in a hundred wheels from the *Galathea* specimen and from three specimens from *Challenger* St. 300 (Tables 5–8).

The wheels are all of the same type. The highest spoke numbers are found in the smallest wheels, but there is no abrupt change in spoke number at any size. The centre of the wheels is similar in small and large wheels, with 4–6 (usually 5) rays. The relative abundance of wheels with 4 rays differs from specimen to specimen. No correlation was evident between ray number and size of wheels. A thin calcareous membrane, usually perforated by a few tiny holes, covers the nave of the wheels in all the preparations. The membrane is probably present in all the wheels, but is difficult to demonstrate in the small ones.

The size distribution shows a prevalence of wheels of 0.05 mm in diameter, while wheels of

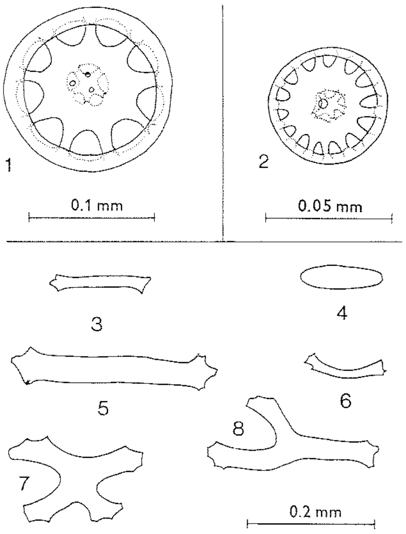


Fig. 20. *Laetmogone wyvillethomsoni*. Deposits. 1–4, *Galathea* St. 663, two wheels and two rods from ventrum; 5–8, *Challenger* St. 300, rods from tubefeet.

Tables 5–8. *Laetmogone wyvillethomsoni.* Number of spokes and diameter of 100 wheels in the *Galathea* specimen (5) and in three specimens from *Challenger* St. 300 (6–8).

Table 5. *Galathea.*

Diam. mm	Spokes						
	8	9	10	11	12	13	8–13
0.04	–	–	1	1	3	1	6
0.05	–	1	5	9	8	4	27
0.06	–	2	–	3	–	–	5
0.07	7	2	8	3	–	–	20
0.08	4	8	4	–	–	–	16
0.09	3	3	1	1	–	–	8
0.10	2	–	1	–	–	–	3
0.11	–	5	–	–	–	–	5
0.12	–	–	2	1	–	–	3
0.13	3	1	1	–	–	–	5
0.14	–	2	–	–	–	–	2
0.04–0.14	19	24	23	18	11	5	100

Table 6. *Challenger.*

Diam. mm	Spokes								
	8	9	10	11	12	13	14	15	8–15
0.04	–	–	–	–	2	4	1	–	7
0.05	–	–	1	8	9	12	10	1	41
0.06	–	–	–	–	–	1	–	–	1
0.07	–	1	–	3	6	1	–	–	11
0.08	–	2	3	3	5	2	–	–	15
0.09	–	1	1	–	–	–	–	–	2
0.10	2	–	3	1	1	–	–	–	7
0.11	2	3	1	1	–	–	–	–	7
0.12	1	2	1	–	–	1	–	–	5
0.13	–	1	1	–	–	–	–	–	2
0.14	–	1	–	–	–	–	–	–	1
0.15	1	–	–	–	–	–	–	–	1
0.04–0.15	6	11	11	16	23	21	11	1	100

Table 7. *Challenger.*

Diam. mm	Spokes								
	8	9	10	11	12	13	14	15	8–15
0.04	–	–	–	1	4	1	–	–	6
0.05	–	–	1	12	25	10	5	1	54
0.06	–	–	–	1	1	1	–	–	3
0.07	–	–	2	2	6	–	2	–	12
0.08	–	1	1	3	3	–	–	–	8
0.09	–	–	4	–	2	–	–	–	6
0.10	1	–	2	2	1	–	–	–	6
0.11	–	1	–	–	–	–	–	–	1
0.12	–	1	1	1	–	–	–	–	3
0.13	–	–	1	–	–	–	–	–	1
0.04–0.13	1	3	12	22	42	12	7	1	100

Table 8. *Challenger.*

Diam. mm	Spokes									
	8	9	10	11	12	13	14	15	16	8–16
0.04	–	–	–	–	–	4	–	–	–	4
0.05	–	–	–	–	9	9	4	–	1	23
0.06	–	–	1	–	1	1	–	–	1	4
0.07	–	–	2	–	2	2	–	–	–	6
0.08	–	–	3	–	1	–	1	–	–	5
0.09	–	–	2	–	1	–	–	–	–	3
0.10	–	–	5	–	–	–	–	–	–	5
0.11	–	–	6	1	–	–	–	–	–	7
0.12	–	–	4	–	–	–	–	–	–	4
0.13	–	4	9	–	–	–	–	–	–	13
0.14	1	1	6	–	–	–	–	–	–	8
0.15	1	–	8	–	–	–	–	–	–	9
0.16	–	–	5	–	–	–	–	–	–	5
0.17	–	–	4	–	–	–	–	–	–	4
0.04–0.17	2	5	55	1	14	16	5	–	2	100

0.04 and 0.06 mm are rare. In the preparations from the *Galathea* specimen and two of the *Challenger* specimens the large wheels were most often 0.07–0.08 mm. In a third specimen from the same *Challenger* station (Table 8) the size distribution shows, however, a maximum at 0.13 mm. The same specimen shows a striking prevalence of the number of exactly 10 spokes in the larger wheels, in contrast to the three other specimens, in which the spoke number varied remarkably in wheels of all sizes. Nevertheless, even in this specimen the wheels cannot be separated into two types; the wheels intermediate in size are also on an average intermediate in spoke number.

A remarkable individual variation may thus be found both in the size distribution and in the distribution of spoke numbers in the wheels of specimens from a single station. All the preparations were from a tubefoot.

Rods (Fig. 20: 5–8) were present in the tubefeet and sometimes in the ventrum, and even dorsum, of the *Challenger* specimens. In none of the specimens were the ventral rods as crowded as in the *Galathea* specimen. In the tubefeet a few intermediate stages between rods and primary crosses were sometimes present.

End-plate of sucking-discs sometimes rudimentary, despite the large size of the discs.

(2) Misidentified specimens. The two specimens reported by Sluiter (1901b) were re-identified as belonging to *L. interjacens* (p. 53) and *L. biserialis* (p. 71).

The specimens reported by Koehler (1896) from various stations in the Bay of Biscay, as well as the North Atlantic specimens recorded by Grieg (1921), probably all belong to *L. violacea* (p. 61).

The six specimens reported by Hérouard (1902) from a depth of 1550 m off the Azores seem to belong to a new species. The specimens (five in MOM and one in MNHN) were re-examined, but only two yielded information on the external features. The wheels are similar (apart from the absence of a covering membrane of the nave) to those of *Laetmogone wyvillethomsoni, L. theeli,* and *L. violacea,* whereas the tubefeet are similar in shape and arrangement to those of *L. fimbriata* and *L. biserialis.* 12 pairs of short and conical dorsal papillae were preserved in one of the specimens in MOM. The specimen in MNHN possessed 15 tentacles with pronouncedly incised discs, a type which is otherwise unknown in the genus *Laetmogone.*

Further material is required to clear up the relationship of these specimens.

A specimen from *Challenger* St. 232 (off Japan, depth 630 m), which Théel with hesitation referred to *L. wyvillethomsoni,* proved on re-examination to have lost the calcareous deposits.

Relationships: *L. wyvillethomsoni* is closest related to *L. theeli.* It has often been confused with *L. violacea.* The relationships of the three species are discussed under *L. violacea.*

Distribution: Southern Ocean, 2514–4410 m.

Laetmogone theeli Ludwig, 1894

Ludwig 1894, pp. 79–85, pl. XI: 14–23.

Diagnosis: Tentacles 20. Tubefeet 45–53 on each side, rather cylindrical, with conspicuous sucking-discs. Papillae 8–15 on each side, slender and single-rowed. Wheels of a single type, 0.05–0.19 mm in diameter, usually larger than 0.9 mm; number of spokes usually 10–12, numbers of 13–16 occurring occasionally, most often in smaller wheels; central rays 4, occasionally 5 or 6; nave covered by a calcareous membrane, usually with a few minute perforations. Rod-shaped spicules sometimes present in the body wall. Spinous crosses absent.

Record: East of the Galapagos Islands, 2417 m. Four specimens.

Re-examination: Length of specimens 9–17 cm. While Ludwig's description refers to the largest specimen, a re-examination was made of a 9 cm long specimen (in MCZ).

Body slender, similar in shape to *Laetmogone wyvillethomsoni.* Tubefeet about 45 on each side in the small specimen, and 53 in the large specimen. The tubefeet are similar in shape to those of *L. wyvillethomsoni,* being rather cylindrical and with conspicuous sucking-discs. In contrast to *L. wyvillethomsoni,* the tubefeet of *L. theeli* are arranged without interspaces, a feature correlated with their higher number. Papillae about 15 pairs (Ludwig found 8–10 pairs in the large specimen). The papillae are as slender as those of *L. wyvillethomsoni.* Tentacles 20, according to Ludwig. (They could not be counted in the re-examined specimen). Tentacle discs similar to those of *L. wyvillethomsoni* and *L. violacea* (Pl. VIII: 8).

Wheels similar in shape to those of *L. wyvillethomsoni* and *L. violacea.* According to Ludwig, the wheels measured 0.05–0.18 mm in diameter and had 4 (occasionally 5 or 6) central rays; the larger wheels had usually 10–12 spokes. The nave of the wheels was covered by a thin calcareous membrane. (A similar membrane was found on re-examination to be present also in the wheels of *L. wyvillethomsoni* and *L. violacea).*

A count of the spokes (Table 9) showed a prevalence of 12 spokes, with 11 spokes coming next in abundance; the total variation was 10–16 spokes. As in *L. wyvillethomsoni* and *L. violacea* the highest spoke numbers are generally found in the smaller wheels, although the absence of wheels smaller than 0.06 mm makes a correlation between spoke number and wheel size less evident in *L. theeli.*

Also apart from the absence of the small wheels, the wheels of *L. theeli* seem to have a higher average size than those of *L. wyvillethomsoni.* Ludwig also supposed that the larger wheels had a higher average number of spokes than those of *L. wyvillethomsoni.* Although this was confirmed by the count of the spokes in the re-

Table 9. *Laetmogone theeli.* Number of spokes and diameter of 100 wheels from the dorsal skin in a specimen from *Albatross* St. 3400. (The ventral wheels show a similar distribution).

Diam. mm	Spokes							
	10	11	12	13	14	15	16	10–16
0.06	–	–	–	–	–	1	–	1
0.07	–	–	–	–	–	–	–	–
0.08	–	–	–	–	3	–	1	4
0.09	–	–	2	1	–	–	–	3
0.10	–	2	6	–	2	–	–	10
0.11	1	6	6	2	–	–	–	15
0.12	–	2	7	–	1	–	–	10
0.13	1	4	8	–	–	–	–	13
0.14	2	2	6	–	1	–	–	11
0.15	–	3	11	–	–	–	1	15
0.16	–	3	5	–	–	–	–	8
0.17	–	1	4	1	–	–	–	6
0.18	–	–	3	–	–	–	–	3
0.19	–	–	1	–	–	–	–	1
0.06–0.19	4	23	59	4	7	1	2	100

examined specimen of *L. theeli,* the differences found in the distribution of spoke numbers in the preparations from the three re-examined *wyvillethomsoni* specimens from *Challenger* St. 300 call for circumspection in lending a taxonomic significance to such differences.

The wheels had 4 central rays, rarely 5 or 6. (The deviations from the number 4 was uncorrelated with the size of the wheels).

The relationships of the species are further discussed under *L. violacea.*

Laetmogone violacea Théel, 1879

Figs. 21–22, pls. VIII: 8, XI: 9–10

Laetmogone violacea, Théel, 1879, p. 11, fig. 14; Théel 1882, pp. 78–80, pls. XIII, XXXVI: 20–24, XLII: 2; Sluiter 1901b, pp. 62–63; R. Perrier 1902, pp. 390–398, pl. XIX: 1–7; Koehler & Vaney 1905, p. 64; Augustin 1908, p. 21; Mitsukuri 1912, pp. 192–198, fig. 36, pl. VI: 52–54; Mortensen 1913, p. 322; Ohshima 1915, p. 237; Ohshima 1916–1919, with one figure; Grieg 1921, p. 5; Hérouard 1923, pp. 37–38; Heding 1942, pp. 14–15, fig. 14; Pawson 1965c, pp. 23–25, fig. 6.

Cryodora spongiosa Théel, 1879, p. 9, figs. 15–16.

Laetmogone spongiosa (Théel), Théel 1882, p. 80, pls. XIV, XXXIX: 5–6.

Laetmogone jourdaini Petit, 1885, pp. 9–11.

Laetmogone brongniarti E. Perrier, 1886, fig. 241.

Laetmogone wyvillethomsoni Théel, Koehler 1896, pp. 117–118; Grieg 1921, p. 5.

Diagnosis: Tentacles 15. Tubefeet 11–18 on each side, usually rather bulky and with small sucking-discs. Papillae 7–28 on each side, in single rows. Wheels of a single type, usually 0.04–0.18 mm in diameter, rarely up to 0.26 mm; wheels of about 0.05 mm especially numerous; number of spokes increasing from 8–10 in the large wheels to 13–18(20) in the small ones; central rays 4–5, rarely more; nave covered by a calcareous membrane, usually with a few minute perforations. Rods with blunt, somewhat spinous or knobbed ends sometimes present in ventrum, rarely in dorsum. Star-shaped spicules with usually 4–5 upwardly-curved, spinous arms always present.

Description: *L. violacea* is not represented in the *Galathea* collections. However, a large number of specimens from previous expeditions have been re-examined in order to clear up the variations in the taxonomic features of the species and its relationship to *L. wyvillethomsoni,* with which it has sometimes been confused.

The re-examination comprised the greater part of the known North Atlantic material of the species (the specimens described by R. Perrier 1902, Mortensen 1913, Hérouard 1923, and Heding 1942), and the two Indonesian specimens taken by the *Siboga* (Sluiter 1901b). The re-examination, combined with information drawn from earlier descriptions, revealed the following variation in the species:

Tentacles 15. Slightly lower numbers have occasionally been found, while higher numbers have not. Discs (Pl. VIII: 8) with a smoth surface, and a straight or feebly indented margin.

Tubefeet 11–18 on each side (Table 10), rather bulky and with a small sucking-disc containing a calcareous end-plate.

Papillae 7–28 on each side (Table 10), in single rows. Heding (1942) reported a variation of c. 20–35 papillae on each side in a collection of 73 North Atlantic specimens. Re-examination of the same specimens revealed that the number did not exceed 24 on each side.

No geographic variation is evident in the number of tubefeet and papillae.

Table 10. *Laetmogone violacea*

Locality	Depth m	Number of specimens	Body length cm	Tubefeet pairs	Papillae pairs
Baffin Bay (Mortensen 1913)	225–490	12	4.5–10	11–14	12–17
N. E. Atlantic (Koehler 1896, Perrier 1902, Grieg 1921, Hérouard 1923, Heding 1942)	256–1804	c. 200	2.3–14	11–18	8–24
W. of Ceylon (Koehler & Vaney 1905)	1316	1	5	13	13–15
Indonesia (Sluiter 1901b)	694–835	2	3	14–15	17–18
S. E. of Australia (Théel 1882)	1738	2	9	11–12	20–23
N. of New Zealand (Pawson 1965c)	481–780	14	5.7–10.2	11–16	19–28
Japan (Mitsukuri 1912)	c. 575–820	21	1.8–11.5	11–16	7–28

The length of the papillae, on the other hand, may exhibit some geographic variation. While the papillae of the North Atlantic specimens only occasionally reached one-fourth of the body length the papillae of Mitsukuri's Japanese specimens were stated to measure 3.6–4.0 cm, which is more than one-third of the body length.

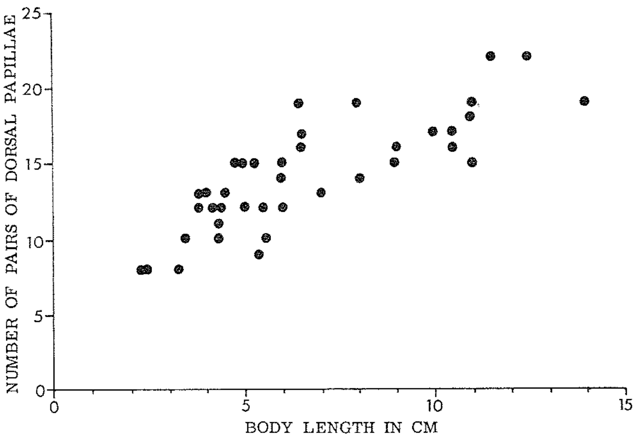


Fig. 21. *Laetmogone violacea.* Number of pairs of dorsal papillae in relation to body length.

The number of papillae generally increases with the length of the specimens, this feature being found both in North Atlantic specimens (Fig. 21) and in Mitsukuri's Japanese specimens. In the tubefeet, with their more narrow variation in number, no such correlation is evident.

Deposits (Fig. 22) consisting of wheels, spinous crosses, and rods.

The wheels range in size from 0.04 to 0.18 mm (occasionally up to 0.26 mm).

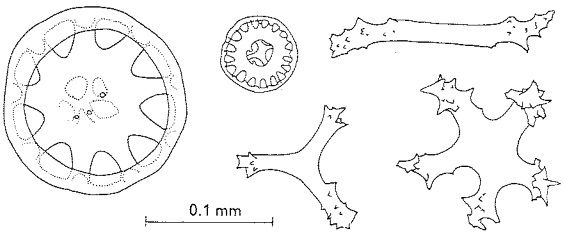


Fig. 22. *Laetmogone violacea.* Deposits. *Michael Sars* St. 76.

Table 11. *Laetmogone violacea.* Number of spokes and central rays, and diameter of 100 wheels in dorsum of a specimen from *Michael Sars* St. 76.

Diam. mm	Central rays			Spokes									
	4	5	6	8	9	10	11	12	13	14	15	16	8–16
0.04	1	6	1	–	–	–	–	1	4	2	1	–	8
0.05	2	15	1	–	–	–	2	5	3	3	5	–	18
0.06	–	2	2	–	–	–	–	–	1	2	–	1	4
0.07	–	4	1	–	–	–	–	2	1	1	1	–	5
0.08	–	6	1	–	1	1	2	1	2	–	–	–	7
0.09	–	8	2	–	1	4	1	4	–	–	–	–	10
0.10	–	7	2	–	–	4	1	2	1	1	–	–	9
0.11	1	5	–	1	–	3	–	1	1	–	–	–	6
0.12	1	6	–	1	–	6	–	–	–	–	–	–	7
0.13	4	2	–	3	1	2	–	–	–	–	–	–	6
0.14	2	1	1	2	–	1	–	1	–	–	–	–	4
0.15	5	–	1	4	–	–	–	2	–	–	–	–	6
0.16	3	2	–	2	–	3	–	–	–	–	–	–	5
0.17	2	2	–	1	1	2	–	–	–	–	–	–	4
0.18	1	–	–	1	–	–	–	–	–	–	–	–	1
0.04–0.18	22	66	12	15	4	26	6	19	13	9	7	1	100

A local variation in the size of the wheels was supposed by Hérouard, who found the wheels in his specimens from west of Gibraltar to reach a diameter of 0.24 mm, while those of the specimens from the Bay of Biscay attained only 0.16 mm. The re-examination of specimens from the whole North Atlantic distributional area confirmed Hérouard's supposition. One of his specimens from west of Gibraltar had wheels as large as 0.26 mm, while the wheels in specimens from all other localities rarely exceeded 0.18 mm in diameter. It is usually stated that the small and large wheels represent different types, the small wheels having 12–13 (occasionally up to 18) spokes, while the large wheels usually have 8–10 spokes. Hérouard even suggested that the small and large wheels might be of a different derivation, as they were separated by a large interval in size.

The question whether the small and large wheels are different types or variations of one single type of spicule is important, as both possibilities are realized in the family.

Table 11 shows the number of spokes and central rays in relation to the diameter of the wheels in a specimen from *Michael Sars* St. 76. The inverse correlation between spoke number and wheel size was found in all the re-examined North Atlantic specimens as well as in the *Siboga* specimens (Table 12). In most of the specimens a number of five central rays prevailed; only in a few North Atlantic specimens were four-rayed

Table 12. *Laetmogone violacea.* Number of spokes and diameter of 100 wheels in a tubefoot of a specimen from *Siboga* St. 314.

Diam. mm	Spokes								
	8	9	10	11	12	13	14	15	16	8–16
0.03	–	–	–	–	–	–	1	–	–	1
0.04	–	–	–	1	4	5	2	3	–	15
0.05	–	–	–	1	1	1	1	1	1	6
0.06	–	–	–	–	2	1	1	–	–	4
0.07	–	–	–	–	4	–	–	–	1	5
0.08	–	–	1	–	1	1	1	–	–	4
0.09	–	1	1	1	2	–	–	–	–	5
0.10	–	–	2	–	–	–	–	–	–	2
0.11	–	–	4	–	–	–	–	–	–	4
0.12	–	–	2	1	1	–	–	–	–	4
0.13	–	–	3	2	1	–	–	–	–	6
0.14	2	1	1	–	1	–	–	–	–	5
0.15	2	1	4	2	–	1	–	–	–	10
0.16	3	1	2	1	–	–	–	–	–	7
0.17	2	3	4	1	–	–	–	–	–	10
0.18	1	1	1	1	–	–	–	–	–	4
0.19	1	1	2	–	–	–	–	–	–	4
0.20	1	1	–	1	–	–	–	–	–	3
0.21	1	–	–	–	–	–	–	–	–	1
0.03–0.21	13	10	27	12	17	9	6	4	2	100

wheels equally abundant. No correlation was evident between ray number and wheel size.

The centre of the wheels is covered by a perforated calcareous membrane similar to that found in *L. wyvillethomsoni* and *L. theeli.*

The characteristic spinous crosses with upwardly curved arms were present in all re-examined specimens recorded in the literature as *Laetmogone violacea.* As their presence has also been stated for Japanese, Australian, and New Zealand specimens (Mitsukuri 1912, Théel 1882, Pawson 1965c), they seem to be invariably present in the species. The crosses may be reduced to spinous tripartite or rod-shaped spicules. Deeper in the skin, more smooth rods were found in some specimens.

The specimens which Koehler (1896) and Grieg (1921) referred to *L. wyvillethomsoni* are here regarded as belonging to *L. violacea.* Four specimens re-examined (two from *Caudan* St. 15, one from *Michael Sars* St. 4, and one from *Michael Sars* St. 24) agreed with *L. violacea* in external features as well as in the presence of spinous crosses.

Relationships: R. Perrier (1902) discussed the relationship between *L. violacea* and *L. wyvillethomsoni* on the basis of a re-examination of a North Atlantic material of *L. violacea.* The result of the present re-examination of numerous specimens in some cases differs from that reached by Perrier and, moreover, indicates that the closest relative of *L. wyvillethomsoni* is not *L. violacea,* but *L. theeli.*

The three species differ in maximum size. *L. violacea* apparently does not exceed 15 cm in length, while *L. wyvillethomsoni* may reach 24 cm. The four specimens known of *L. theeli* were 9–17 cm long.

L. wyvillethomsoni and *L. theeli* generally seem to have a more slender body form than *L. violacea.* However, as this feature varies with the state of contraction and preservation, it is of doubtful value in species distinction.

The tubefeet are usually more bulky, and have smaller sucking-discs than those of *L. wyvillethomsoni* and *L. theeli.* The 11–18 pairs of tubefeet recorded for *L. violacea* are probably an approximate representation of the variation in the species, as the count was based on numerous specimens from widely scattered localities. Therefore, the total of 15–33 pairs of tubefeet in *L. wyvillethomsoni* and of 45–53 in *L. theeli* indicates a significant difference from *L. violacea.*

The papillae of *L. wyvillethomsoni* and *L. theeli* are usually longer and more slender than those of *L. violacea.* However, the intraspecific variation in length is considerable and the feature is, therefore, of little value in species distinction.

Perrier maintained that in *L. wyvillethomsoni* the tubefeet are more numerous than the papillae, while the opposite holds good of *L.violacea.* Although such a strict difference does not exist, it is true that the number of papillae in *L. violacea* (7–28 pairs) exceeds the variation found in *L. wyvillethomsoni* (5–18 pairs) and *L. theeli* (8–15 pairs).

The number of tentacles is 15 in *L. violacea* and *L. wyvillethomsoni,* but 20 in *L. theeli.*

Cross-shaped spicules are always present in *L. violacea,* but even a thorough examination failed to reveal their presence in *L. theeli* and *L. wyvillethomsoni.*

The wheels of *L. violacea* and *L. wyvillethomsoni* have 4–6 (usually 5) central rays, while those of *L. theeli* have 4 (rarely 5 or 6).

Distribution: *L. violacea* is a typical bathyal species, found at depths of 225–1804 m. It has been recorded from the northeastern Atlantic continental slope, the southern slope of the North Atlantic Ridge, and from off the Azores, Indonesia, India, South-East Australia, New Zealand, and Japan.

The distribution may to some degree depend on ocean currents (p. 238).

Laetmogone scotoeides (H. L. Clark, 1913)

Fig. 23

Laetmenoecus scotoeides H. L. Clark, 1913, p. 231.

Diagnosis: Tentacles 15. Tubefeet 15–20 on each side, rather bulky and narrowing towards the tip, although with well-developed sucking-discs. Papillae extremely small. Wheels of two types, with intergradations: A small type (0.04–0.08 mm) with a central primary cross and typically with 12 spokes, and a large type (0.06–0.30 mm) with five central rays and a varying spoke number. Rods numerous in ventrum, but scarce in dorsum.

Record: Off Baja California, 1173 m. Three specimens.

Re-examination: Clark erected a new genus for the species, based on the supposed absence of dorsal papillae. However, re-examination of one of his specimens (in MCZ) revealed the presence of two or three very small, retracted papillae. The full number of papillae could not be made out.

While Clark stated the length of the specimens to be 15–20 cm, the re-examined specimen was only 12 cm long, probably due to later shrinking. Tubefeet 15–20 pairs, narrowing towards the tip, although with well-developed sucking-discs. They were arranged with interspaces of about 4 mm. Tentacles 15.

Clark stated that the wheel-shaped deposits were "similar to those of *Laetmogone*" and therefore needed no detailed description. He only mentioned that the small wheels were up to 0.09 mm in diameter and had 10–13 spokes, while the large wheels measured 0.15–0.20 mm and had commonly 10 spokes.

Re-examination of the deposits (Fig. 23) gave a different result. The wheels measured 0.04–0.30 mm, and all sizes within this interval were represented. Remarkable differences in size distribution between dorsal and ventral wheels were found (Tables 13 and 14). Wheels from the dorsal skin measured 0.05–0.30 mm, with the greatest abundancy at 0.13–0.15 mm, and with very few small-sized deposits. Wheels from the ventral skin, on the contrary, had exclusively wheels measuring 0.04–0.07 mm.

A correlation was found between the number of central rays and the size of the wheels. Wheels with a central primary cross measured 0.04–0.08 mm (only one wheel measured 0.13 mm), whereas wheels with 5 (occasionally 6 or 7) central rays measured 0.06–0.30 mm. The transition from the "small" to the "large" type occurs at 0.06–0.08 mm, where both 4-rayed and 5-rayed wheels are present. The smallest of the 5-rayed wheels appear to be derivatives of 4-rayed wheels, two of the rays usually originating from a bifurcation of one of the four rays of the small type. Otherwise, the wheels of the large type are remarkable for their very regular development of the five central rays. If more than five rays are present, the additional rays are usually somewhat irregularly arranged, developed through bifurcation of one or two of the five regular rays.

The spokes vary in number from 10 to 18, with a prevalence of 12. In contrast to the wheels in *L. wyvillethomsoni, L. violacea,* and *L. theeli* there is no prevalence of high spoke numbers in the smallest wheels.

A covering membrane of the nave is not present.

Rod-shaped spicules are numerous in the ventrum, but scarce in the dorsum.

Relationships: The extremely reduced state of the papillae and the almost constant presence of five rays in the large wheel type distinguish *L. scotoeides* from the other species of the genus.

The separation of the wheels into two types, characterized by different numbers of central rays, is a similarity to *L. maculata, L. fimbriata,* and *L. biserialis. L. scotoeides* differs from *L. fimbriata* and *L. biserialis* by the shape of the tubefeet, and from *L. maculata* by the absence of rosette-shaped spicules.

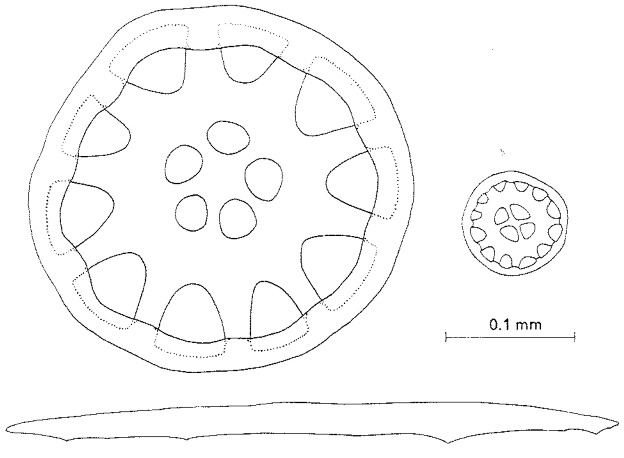


Fig. 23. *Laetmogone scotoeides.* Deposits. *Albatross* St. 5685.

Table 13. *Laetmogone scotoeides*. Number of spokes and central rays, and diameter of 100 wheels in dorsum of the re-examined specimen from *Albatross* St. 5685.

Diam. mm	Central rays				Spokes						
	4	5	6	7	10	11	12	13	14	15	10–15
0.05	1	–	–	–	–	1	–	–	–	–	1
0.06	1	–	–	–	–	1	–	–	–	–	1
0.07	2	–	–	–	–	–	2	–	–	–	2
0.08	2	1	–	–	–	–	3	–	–	–	3
0.09	–	2	–	–	–	–	–	2	–	–	2
0.10	–	4	2	–	–	–	4	–	–	2	6
0.11	–	6	–	–	1	1	2	2	–	–	6
0.12	–	5	1	–	1	1	3	–	1	–	6
0.13	1	8	1	–	–	1	5	3	–	1	10
0.14	–	8	1	–	–	3	2	1	3	–	9
0.15	–	6	1	1	–	1	1	3	3	–	8
0.16	–	4	–	1	–	2	1	–	1	1	5
0.17	–	3	–	–	–	1	1	1	–	–	3
0.18	–	4	–	–	1	1	1	–	–	1	4
0.19	–	2	1	–	–	1	2	–	–	–	3
0.20	–	4	1	–	1	1	3	–	–	–	5
0.21	–	3	1	–	2	–	1	–	1	–	4
0.22	–	4	–	–	1	1	1	1	–	–	4
0.23	–	4	–	–	1	1	1	–	1	–	4
0.24	–	2	1	–	2	–	1	–	–	–	3
0.25	–	4	–	–	1	1	–	–	2	–	4
0.26	–	1	1	–	1	–	1	–	–	–	2
0.27	–	–	1	–	–	–	1	–	–	–	1
0.28	–	2	–	–	2	–	–	–	–	–	2
0.29	–	–	–	–	–	–	–	–	–	–	–
0.30	–	2	–	–	2	–	–	–	–	–	2
0.05–0.30	7	79	12	2	16	18	36	13	12	5	100

Table 14. *Laetmogone scotoeides*. Number of spokes and central rays, and diameter of 30 wheels in ventrum of the re-examined specimen from *Albatross* St. 5685.

Diam. mm	Central rays		Spokes								
	4	5	11	12	13	14	15	16	17	18	11–18
0.04	10	–	2	7	–	–	–	–	1	–	10
0.05	9	–	–	7	1	1	–	–	–	–	9
0.06	4	3	–	3	–	2	–	2	–	–	7
0.07	1	3	–	–	–	1	1	1	–	1	4
0.04–0.07	24	6	2	17	1	4	1	3	1	1	30

Laetmogone maculata (Théel, 1879)

Fig. 24, pls. VIII: 9–10, XI: 11–12

Ilyodaemon maculatus Théel, 1879, p. 12, figs. 9–11; Théel 1882, pp. 84–88, pls. XVI, XXXVI: 12–19, XXXVIII: 6–8, XLII: 3–4, XLIV: 11, XLVI: 1; Sluiter 1901b, pp. 66–67, pl. II: 2; Heding 1940, pp. 369–370, fig. 19.

Ilyodaemon miurense Ohshima, 1915, pp. 239–240, pl. VIII: 9; Ohshima 1916–1919, with one figure.

Laetmogone enisus Sluiter, 1901a, pp. 22–23; Sluiter 1901b, pp. 65–66, pls. II: 5, IX: 7.

Diagnosis: Tentacles 15. Tubefeet rather large, narrowing towards the tip, increasing in number with size of specimens, reaching 29 pairs. Papillae varying in arrangement and number with size of specimens, from few and single-rowed, to about 140 on each side and placed in two dorsal bands. Wheels of two distinct types, a small type, 0.03–0.05 mm in diameter, with a central primary cross and usually 12 spokes, and a large type, 0.06–0.30 mm in diameter (rarely smaller than 0.10 mm), with 6 central rays and 9, occasionally 9–12, spokes; some of the wheels of the large type have the nave covered by a triangular superstructure originating from a central pillar. Rosette-shaped deposits present.

Material:

Dr. Th. Mortensen's Pacific Exp., 2.VII.1914, Sagami Bay, 732 m. – 1 specimen.

- 15.IX.1914, N. E. of Tasmania (39°10'S, 149°55'E), 366–458 m. – 9 specimens.
- 16.IX.1914, N. E. of Tasmania (38°12'S, 149°40'E), 183–293 m. – 1 specimen.

Dr. Th. Mortensen's Kei Exp., St. 41, Kei Islands (5°29'S, 132°28'E), 245 m. – 1 specimen.

- St. 42, Kei Islands (5°35'S, 132°29'E), 225 m. – 1 specimen.

Siboga St. 90, Celebes Sea at the entrance to the Makassar Strait (1°17'N, 118°53'E), 281 m. – 1 specimen (not included in the Siboga Report).

Description:

Tasmania. The ten specimens from Tasmania are remarkably small. They measure 2–4 cm, while the specimens hitherto known are 3.5–13 cm long.

Tubefeet 15 pairs in the two smallest specimens, both 2 cm long. The other specimens have about 20 pairs.

Papillae 10 and 15 pairs, respectively, in the two smallest specimens; 20 pairs in the others.

Deposits of the usual three types in *L. maculata:* Large wheels, small wheels, and rosettes. The wheels of the large type (Fig. 24: 2) are rather small in all the specimens, 0.10–0.15 mm in diameter, usually somewhat larger dorsally than ventrally.

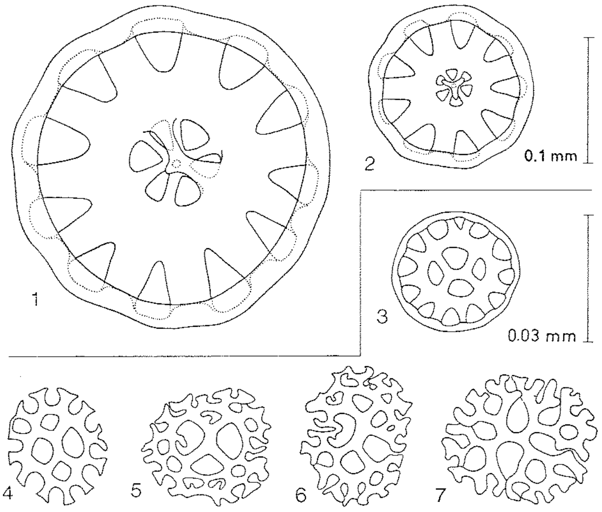


Fig. 24. *Laetmogone maculata.* Deposits. 1, *Challenger* St. 219, large wheel; 2, Pacific Exp., Tasmania, large wheel; 3–7, *Siboga* St. 90, small wheel and rosettes.

Kei Islands. The specimens from the Kei Islands are both 4 cm long.

Tubefeet 15 pairs.

Papillae 50–60 on each side, placed in a double, or in some places in a zigzag row, along each dorsal radius.

Rosettes so densely crowded that the whole area of the skin has become whitish.

Small wheels absent. Though preparations were made from four parts of the skin in both specimens, none were found.

Large wheels absent in the preparations from one of the specimens, and very scarce in those of the other.

Sagami Bay. The specimen is 2.5 cm long, but strongly contracted, with a thick and spongy skin, totally enclosing the papillae and tubefeet. The papillae are red, some with white tips. The tubefeet are large and sparse. (The exact number of papillae and tubefeet could not be ascertained).

Rosette-shaped deposits were sparsely present in the preparations.

Celebes Sea. The specimen (in ZMA) came from *Siboga* St. 90, but was not mentioned in the Siboga Report. It is 3.5 cm long and very contracted. Although it was labelled *Ilyodaemon fimbriatus,* it agreed with *L. maculata* both in external features and deposits. The latter included large wheels, small wheels, and scattered rosettes, plus, remarkably enough, some intermediate stages between the rosettes and the small wheels (Fig. 24: 3–7). Apparently, the rosettes are merely aberrant small wheels, in which the spokes have undergone a few irregular ramifications.

Synonymy:

Laetmogone enisus Sluiter was taken at *Siboga* St. 251 near the Kei Islands, occurring together with *L. maculata.* A re-examination revealed perfect agreement with *L. maculata,* both in external characters and deposits.

The species was primarily defined by having in the papillae a peculiar type of small wheel with minute peripheral holes and rounded lobes at the margin. These wheels proved on re-examination to be wheels of the normal small type, with the exception that the spokes were very thick. The broad insertion of the spokes on the margin might give a false impression of the presence of lobes. These wheels were also present in the body wall and were interconnected with the normal ones through all intermediates. This deviation from the normal wheel is commonly found in *L. maculata.* The large wheels were those typical of *L. maculata,* and rosettes were present.

Ilyodaemon miurense Ohshima, known from five Japanese specimens, possessed deposits of the usual three types in *L. maculata:* Large wheels (with a triangular superstructure growing out from a central pillar), small wheels, and rosettes. Apparently, there were no aggregations of deposits into heaps. Ohshima mentioned as a difference from *L. maculata* that the papillae numbered only 50–60 on each side (the specimens were up to 7.5 cm long). However, the large number of papillae (140–150 on each side) stated by Théel for *L. maculata* applied to the largest specimen (13 cm long). The papillae number in *I. miurense* is well within the range of variation shown by *L. maculata.*

Variation:

The specimens of *L. maculata* here recorded, together with the specimens re-examined from the *Challenger, Valdivia,* and *Siboga* and the descriptions in the literature, make possible an evaluation of the variation.

The specimens known are 2–13 cm long and come from many stations within a wide distributional area.

Tentacles. The discs may have an irregularly lobated margin, but usually the margin is rather smooth. The whole variation in shape was shown by the specimens from *Valdivia* St. 202 (Pl. VIII: 9–10).

Tubefeet large and bulky, narrowing towards the tip. For the most part, their number increases with the size of the specimens, from 15 pairs in the two smallest specimens (both 2 cm long and originating from Tasmania), to 29 pairs in the 13 cm long specimen from the *Challenger.*

Papillae increasing in number with size of specimens. The smallest numbers, 10 and 15 pairs, were again found in the two smallest known specimens, while the largest number, about 140 on each side, was found in the aforementioned 13 cm long *Challenger* specimen.

Concurrently with the increase in number, the papillae change from being strictly single-rowed in the smallest specimens, to zigzag or double rows, and even to an arrangement in two longitudinal bands in the largest specimens.

The papillae show a red, transversal band which sometimes extends down to the base of the papillae, but practically always leaves the tip of the papilla white.

Deposits. Rosettes were present in all the preparations from the specimens examined and re-examined. Their relative abundance varies greatly, from the extreme abundance in the two specimens from the Kei Islands to a very scattered occurrence, as in the specimen from *Siboga* St. 90 in the Celebes Sea and the specimen from the Sagami Bay collected by Dr. Mortensen. Possibly, a local or geographic variation is indicated by these differences.

The rosettes, and less pronouncedly the small wheels, are often aggregated into distinct heaps. This is especially pronounced in many Indonesian specimens, where the aggregations appear as white protuberances on the skin. The aggregations are less pronounced in the specimens from Tasmania, and they seem to be lacking in Japanese specimens.

Small wheels invariably with a central primary cross and about 12 spokes. They are 0.03–0.05 mm in diameter and clearly distinguishable from the wheels of the large type, though all intermediary sizes may be present.

Large wheels remarkably uniform in the species. They are nearly always regularly shaped, have consistently 6 central rays, and usually 9 spokes, though 7–12 or even more spokes may be present. Notable differences in the distribution

Table 15. *Laetmogone maculata.* Distribution of spoke numbers in 100 wheels of the large type from five specimens.

Spoke number	8	9	10	11	12	13	14
Siboga St. 251, near Kei Islands	–	99	1	–	–	–	–
Mortensen's Pacific Exp., Sagami Bay	–	38	22	18	15	5	2
Challenger St. 219, N. of New Guinea	–	41	33	18	7	1	–
Valdivia St. 202, W. of Sumatra	4	94	2	–	–	–	–
Valdivia St. 202, W. of Sumatra	6	50	24	17	3	–	–

of spoke numbers were found, as indicated by the five specimens shown in Table 15.

In the specimens with a varying spoke number no correlation could be demonstrated between spoke number and wheel size.

Common to the specimens examined is the prevalence of 9 spokes. In some specimens practically all the wheels have 9 spokes, while in others the spoke number is more scattered. A geographic variation may be present in the feature.

A consistent number of 9 spokes was found in the seven specimens from *Siboga* St. 251, in the five specimens from *Siboga* St. 302 (near Timor), and in the ten Tasmanian specimens.

A scattered spoke number was found in the two specimens examined from *Challenger* St. 219 and in the specimen from Sagami Bay. The latter may be typical of the Japanese population. Ohshima stated that *L. miurense* (= *L. maculata*) had mostly 9 spokes, but with a variation of 7–12. The closely related *L. ijimai* shows a similar distribution of spoke numbers.

The eight specimens from *Valdivia* St. 202 included some with a rather constant, as well as some with a scattered spoke number. The presence of such individual differences at one and the same station seems to be an exception.

The central concavity of the wheels is often covered by a triangular superstructure growing out from a central, vertical pillar. The superstructure should not be confused with the perforated, calcareous membrane covering the central concavity of the wheels in many other species of *Laetmogone* and in *Pannychia moseleyi;* this membrane always grows out from the margin of the concavity, not from the centre. However, in two of the *Valdivia* specimens some of the wheels had irregular ingrowths originating from the margin of the central concavity, although others had the usual triangular superstructure. The wheels of the two specimens were also otherwise abnormally developed.

The triangular superstructure was present in some wheels in all the preparations made, and thus occurs in the whole distributional area of the species.

The large wheels are usually about 0.18–0.25 mm in diameter, with a variation of 0.06–0.30 mm. (Wheels smaller than 0.10 mm are rare in all the preparations). The remarkably small wheels of the Tasmanian specimens, not exceeding 0.15 mm in diameter, are unlikely to be due to the small size of the specimens; they probably represent a local or geographic feature in the variation of the species. The eight specimens from the *Valdivia* station west of Sumatra had wheels intermediate in size between the Tasmanian and the other specimens. The uniformity in size of wheels from the same station is noteworthy.

The tubefeet contain one or more end-plates surrounded by slender, curved rods. Rods are likewise present in the tentacles, but were never found in the body wall or in the papillae.

Conclusion. The papillae, and to a smaller degree the tubefeet, increase in number with the size of the specimens. However, the small number of papillae in the Tasmanian specimens may be due not only to the small size of the specimens, but also to a geographic variation.

Differences in the relative abundance of the three types of deposit, in the spoke numbers of the large wheels, and in the aggregations of the deposits into heaps, may indicate a local or geographic variation.

At present, an attempt to distinguish between different types of variation has primarily the purpose of pointing out the features which should be examined when further specimens are available.

Relationships: Closest related to *L. ijimai* (q. v.).

Distribution: Japan, 160–732 m. Indonesia, 141–709 m. N. E. of Tasmania, 293–366 m.

Type: BM.
Type locality: *Challenger* St. 192 (5°42'S, 132° 25'E). Although Théel based his description

primarily on the 13 cm long specimen from St. 209, the specimen labelled "Type" was a 5 cm long (and better preserved) specimen from St. 192.

Laetmogone ijimai (Mitsukuri, 1897)

Ilyodaemon ijimai Mitsukuri, 1897b, pp. 133–135; Mitsukuri 1912, pp. 200–207, fig. 37, pl. VI: 55; Ohshima 1915, pp. 238–239; Ohshima 1916–1919, with one figure.
Ilyodaemon fimbriatus var. *magna* Sluiter, 1901a, p. 24; Sluiter 1901b, p. 69.
Benthogone quatrolineata Augustin, 1908, pp. 21–23, fig. 15.

Diagnostic features: *L. ijimai* differs from *L. maculata* by the absence of rosette-shaped deposits, by the absence of a triangular superstructure on the large type of wheel, and by its papillae which are small and conical and lack the red band.

Records: Numerous Japanese stations at depths of 130–900 m. According to Mitsukuri, it is by far the commonest of the holothurians found in the deeper part of the Sagami Sea.

Remarks: The specimen which Sluiter described as *Ilyodaemon fimbriatus* var. *magna* on reexamination proved to agree with Mitsukuri's description of *I. ijimai*. The tubefeet were bulky and narrowing towards the tip as in the two species *L. ijimai* and *L. maculata*, and very different from the slender and thread-like tubefeet characteristic of *L. fimbriata*. In all the three features which distinguish *L. ijimai* from *L. maculata* there was agreement with *L. ijimai*.

Ohshima (1915) is the authority of the synonymy between *Benthogone quatrolineata* Augustin and *L. ijimai*. The former species should not be confused with *B. quadrilineata* Perrier, which is a synonym of *B. rosea*.

The features which distinguish *L. ijimai* from *L. maculata* may represent only local or geographic variations within the latter species. The fact that the rosettes were of scattered occurrence in the specimen of *L. maculata* from the Sagami Bay suggests that the species *L. ijimai* comprises specimens of *L. maculata* in which the rosette-shaped deposits are few or absent.

Laetmogone fimbriata (Sluiter, 1901)

Fig. 25

Ilyodaemon fimbriatus Sluiter, 1901a, pp. 23–24; Sluiter 1901b, pp. 67–68, pl. IX: 8.
Non *Ilyodaemon fimbriatus* var. *magna* Sluiter, 1901a (= *Laetmogone ijimai*).
Laetmogone parva Mitsukuri, 1912, pp. 186–188, fig. 34, pl. V: 46–47; Ohshima 1915, pp. 237–238; Ohshima 1916–1919.
Laetmogone selenkai Mitsukuri, 1912, pp. 189–192, fig. 35, pl. V: 48–51; Ohshima 1915, p. 238; Ohshima 1916–1919, with one figure.
Bathygone papillatum Pawson, 1965b, pp. 77–79, figs. 7–11.

Material:
Dr. Th. Mortensen's Pacific Exp., 10.VI.1914, Sagami Bay, 450 m. – 5 specimens.
– 2.VII.1914, Sagami Bay, 732 m. – 2 specimens.
Dr. Th. Mortensen's Kei Exp. St. 41, Kei Islands (5°29'S, 132°28'E), 245 m. – 1 specimen.
Dr. Th. Mortensen's Java–South Africa Exp.
St. 25, off Durban (29°56'S, 31°19'E), 412 m. – 10 specimens.
Challenger St. 219, N. of New Guinea (1°50'S, 146°42'E), 274 m. – 1 specimen, not included in the Challenger Report.

Diagnosis: Tentacles 15. Tubefeet crowded, slender from base to tip, with the sucking-discs equal in diameter to the tubefeet; number of tubefeet in the main increasing with size of specimens, reaching 60–70 on each side. Papillae varying in arrangement and number with the size of the specimens, from few and single-rowed, to about 40 on each side and placed in double rows. Wheels of two distinct types, a small type, 0.03–0.05 mm in diameter, with a central primary cross and (10–)12 spokes; and a large type, 0.06–0.25 mm in diameter, with 6 central rays and about 9 spokes; aberrant small wheels with additional peripheral holes sometimes present; no triangular superstructure or covering calcareous membrane. Large end-plate and slender, curved rods in tubefeet; rods of a similar type – often likewise curved – sometimes present in ventral and dorsal skin.

Description:
Of the three species synonymized, the specimens particularly agree with Mitsukuri's description and illustrations of *Laetmogone selenkai*. In the

description of the present material only those features related to the variation of the species and to the proposed synonymies are mentioned.

Sagami Bay, 450 m. The five specimens are 9–22 mm long.

Tubefeet 15–35 on each side, all retracted, increasing in number with the size of the specimens.

Papillae 10–17 on each side, red with white tips, increasing in number with the size of the specimens.

Small wheels in all the specimens with central primary cross and mostly 12 spokes. They are particularly crowded in the tips of the papillae. Small wheels with additional peripheral holes absent.

Large wheels usually 0.07–0.09 mm in diameter, with a variation of 0.06–0.16 mm; spokes 8–12, 9 being by far the most common number.

Curved rods, which are slender and pointed, present in tubefeet and often also in dorsal and ventral skin.

Sagami Bay, 732 m. One of the two specimens is 4 cm long, well preserved, and fully extended. The other is 2.5 cm, and strongly contracted. The following description applies to the well-preserved specimen.

Tubefeet 60–70 on each side, placed in single to double rows.

Papillae 20–21 on each side, red with white tips, single-rowed.

Small wheels with central primary cross and mostly 12 spokes. They are densely crowded in the tips of the papillae, where also many irregular wheels with additional peripheral holes are present. Such aberrant wheels are absent from the ventrum and very rare in the dorsum. They hardly exceed the normal small wheels in size, reaching only 0.05 mm in diameter.

Large wheels in the dorsum usually 0.11–0.15 mm in diameter, with a variation of 0.06–0.17 mm. Ventrally, the large wheels are scarce, mostly about 0.08 mm in diameter, with a variation of 0.06–0.09 mm. Number of spokes in the large wheels usually 9, with a variation of 7–10.

Kei Islands. The specimen is about 6 cm long, defective, with only a few groups of tubefeet preserved; these are slender and crowded as is usual in the species. The papillae, about 14 pairs, are red with white tips, and single-rowed.

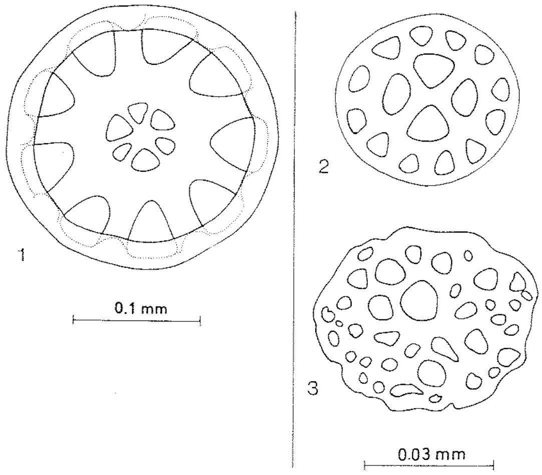


Fig. 25. *Laetmogone fimbriata.* Large wheel, small wheel, and perforated plate of specimen from Kei Exp. St. 41.

Small wheels with central primary cross and generally 12 spokes. An examined papilla contained some small wheels with additional peripheral holes.

Large wheels usually 0.20–0.25 mm in diameter, with a variation of 0.08–0.30 mm. Among 52 wheels from the dorsum and ventrum, 51 had 9 spokes, and one 12 spokes.

Off Durban. The 10 specimens measure 12–35 mm.

Tubefeet about 30–50 on each side, placed in single to double rows, which is probably dependent on the state of contraction of the specimens. No correlation was apparent between the number of tubefeet and the size of the specimens.

Papillae single-rowed, probably about 10–15 pairs; they are white from base to tip, this apparently being the only difference between the South African and the East Asiatic specimens.

Small wheels with central primary cross and nearly always 12 spokes. Wheels with additional peripheral holes absent.

Large wheels usually about 0.12 mm in diameter, in a few specimens about 0.14 mm, with a variation of 0.08–0.16 mm. A count in a hundred wheels gave 95 with 9 spokes, and 5 with 10 spokes.

Curved rods present in tubefeet. In one specimen numerous curved rods were likewise found in the ventral, and to some degree also in the dorsal skin, but in most specimens rods were completely absent from the ventrum and dorsum.

North of New Guinea. The specimen came from *Challenger* St. 219, but was not mentioned in the Challenger Report. It is 4.5 cm long and rather defective.

Tubefeet slender and crowded, but preserved only in places.

Papillae single-rowed, about 12–13 pairs, red, without white tips. The deep layer of skin is red in colour.

Small wheels with central primary cross and usually 12 spokes. Wheels with additional peripheral holes absent.

Large wheels 0.10–0.20 mm in diameter, with a rather even size distribution, and practically all with 9 spokes.

Curved rods present in tubefeet, but absent in the dorsal and ventral skin.

Synonymy:
Ilyodaemon fimbriatus Sluiter was described on a single 8 cm long specimen from the Banda Sea. The specimen was re-examined.

The tubefeet, 51 on each side according to Sluiter, were slender and cylindrical. The "gefranzten Saum" round the posterior end of the body, giving name to the species, was found to consist of the slender, crowded tubefeet, which are separate even at their bases.

The tentacle discs were irregularly lobated at the margin, resembling the discs in some specimens of *L. maculata* (Pl. VIII: 10).

The papillae were counted by Sluiter to be at least 37 on each side, placed in double rows. This placing in double rows, not found in the other species here synonymized, is probably due to the larger size of the specimen. A similar change from single-rowed to double-rowed papillae was found in *Laetmogone biserialis* and *L. maculata*.

The colour of the specimen was light violet, with the discs of the tentacles and tubefeet dark violet.

Sluiter found the small wheels consistently had 10 spokes. Re-examination showed that the small wheels had mostly 12 spokes, though wheels with 11 and 10 spokes were not uncommon.

The large wheels were 0.15–0.20 mm in diameter and had the usual 6-rayed centre without a superstructure; of 28 wheels, 26 had 9, and two 10 spokes.

Rods were absent from the dorsal and ventral skin, but present in the tubefeet.

The specimen of *Ilyodaemon fimbriatus* var. *magna* was re-identified to *L. ijimai.*

L. selenkai Mitsukuri, known from several Japanese stations, was considered a close relative of *L. fimbriata.* A comparison of the type specimen of *L. fimbriata* with the specimens in the present material (which agree well with Mitsukuri's description of *L. selenkai)* showed that the two species can hardly be kept separate. Mitsukuri's specimens exhibited a rather large variation in number of both tubefeet and papillae. (The specimens were 21–47 mm long and had on each side 25–63 tubefeet and 10–34 papillae).

Mitsukuri mentioned as a difference from the type specimen of *L. fimbriata* that the skin was transparent and colourless, and the tentacle discs yellow with crimson spots. However, Mitsukuri's own statement that in the closely related *L. neglecta* (= *L. biserialis)* the tentacle discs were in two specimens dark violet, while in a third one they were yellow, speaks against attributing too much taxonomic significance to colour differences.

L. parva Mitsukuri, known from several Japanese stations, was distinguished from *L. selenkai* by the absence of large wheels, and by the infrequent occurrence of small wheels. The latter had generally 10 spokes and often, through the addition of peripheral holes, they had developed into small reticulated plates.

The scarcity of deposits, or of some types of deposits, seems to be of doubtful value in characterizing a species. Superficially placed deposits, as the large wheels, are rather easily rubbed off, particularly on the ventral side. But also in the frequency of occurrence of the deeper lying deposits noteworthy differences may exist between specimens. While the *parva* specimens of Mitsukuri had the deposits confined to the ambulacral appendages, those of Ohshima possessed deposits also in the dorsal skin.

The prevalence of 10 spokes in the small wheels (both in Mitsukuri's and Ohshima's specimens) would seem to distinguish these wheels from the small wheel type of other laetmogonids, where the number of 12 spokes always prevails.

Bathygone papillatum Pawson, known from three specimens taken north of New Zealand, was characterized primarily by the aggregation of the deposits into distinct heaps, which formed protuberances on the dorsal skin. This feature was considered of generic value. However, *Laet-*

mogone maculata possesses, particularly in Indonesian specimens, similar aggregations of deposits into heaps. Apparently, this feature is of doubtful value even in species distinctions, although it may be indicative of a local or geographic variation within a species.

The specimens of *B. papillatum* almost completely lacked deposits in the ventrum (a feature reminiscent of the Japanese *parva* specimens). Small wheels were absent, being replaced by perforated plates similar to those occurring in specimens from Japan and the Kei Islands. Large wheels, 0.19–0.25 mm in diameter, typically with 6 central rays and 9 spokes. The specimens (holotype 4.2 cm long) had on each side about 50 slender tubefeet and about 10 small, red papillae.

Variation: The specimens known are 0.9–8.0 cm long.

Tentacles. The discs have retractile marginal lobes, and are probably similar in shape to those of *L. maculata.*

Tubefeet, slender from base to tip and with large sucking-discs, are placed without interspaces in a single or double row along each side of the ventrum. Their number broadly increases with the size of the specimens, from 15 to 70 on each side.

Papillae, from 10 to about 40 on each side, small and single-rowed, except in the largest known specimen (the 8 cm long type specimen). In the main, the number increases with the size of the specimens. The papillae are red, except in the South African specimens, which have white papillae. The specimens from the Kei Islands and Japan have red papillae with white tips.

Deposits. The wheels of the large type are regular in shape, with 6 central rays and generally 9 spokes. The only indication of a spoke number higher than 9 in average was apparently found in Mitsukuri's specimens of *L. selenkai,* which were stated to have 9 or 10, rarely 8 spokes. A triangular superstructure or a calcareous membrane covering the nave of the wheel was absent in all the preparations made.

The wheels of the small type have a central primary cross and about 12 spokes. A number of 10 spokes prevailed in some of the Japanese specimens (the specimens described as *L. parva).* The wheels show a tendency to transform into small, perforated plates. These plates are usually present in Japanese specimens, particularly in the papillae, and they were also present in the papillae of the specimens from the Kei Islands. In the New Zealand specimens *(B. papillatum)* the small wheels were all transformed into perforated plates.

The ventral and dorsal skin in South African and Japanese specimens sometimes contains scattered, slender, somewhat curved rods, very similar to those of the tubefeet.

A geographic variation may be present in the colour of the papillae, in the relative abundance of large wheels, small wheels, and perforated plates (each of these types may be completely absent), and in the aggregation of deposits into heaps.

Relationships: Closest related to *Laetmogone biserialis* (q. v.).

Distribution: South-East Africa, 412 m. Indonesia, 242–827 m. Japan, 164–1300 m. New Zealand, 360 m.

Type: ZMA, the only specimen taken by the *Siboga.*
Type locality: *Siboga* St. 145 (0°54'S, 128°39'E).

Laetmogone biserialis Fisher, 1907

Laetmogone biserialis Fisher, 1907, pp. 706–708, pls. LXXV: 5, LXXVIII: 1.
Laetmogone neglecta Mitsukuri, 1912, pp. 183–186, fig. 33, pl. V: 45.
Laetmogone wyvillethomsoni Théel, Sluiter 1901b, p. 63 (partim).

Diagnosis: Tentacles 15. Tubefeet crowded, slender from base to tip, with sucking-discs equal in diameter to the tubefeet; number of tubefeet on an average increasing with size of specimens, reaching about 50 on each side. Papillae small, increasing in number and changing from single to double rows with size of specimens, reaching 60–70 on each side. Wheels of two distinct types, a small type, 0.03–0.05(0.10) mm in diameter, with a central primary cross and about 12 spokes; and a large type, 0.06–0.27 mm in diameter, with 6 central rays and about 12 spokes; no triangular superstructure or covering calcareous membrane. Large end-plate and slender, curved rods in tubefeet. Sturdy, rather straight rods with blunt ends numerous in ventrum.

Synonymy: *Laetmogone biserialis* Fisher was described from two stations off the Hawaiian Islands (number of specimens not stated). One well-preserved specimen from *Albatross* St. 4141 (in USNM), 6.5 cm long, was re-examined. Fisher's thorough description was verified, both as regards the external features and the deposits. The tentacle discs had an irregularly lobated margin.

L. neglecta Mitsukuri is known from three specimens taken in the Sagami Sea (Japan). Mitsukuri compared the species with *L. wyvillethomsoni,* but curiously enough not with *L. biserialis.* In actual fact, *L. neglecta* and *L. biserialis* seem to agree both in external features and deposits, including the number and shape of the tubefeet and papillae, the shape of the tentacle discs, the presence of two types of wheel (both with about 12 spokes), and of rods in the ventral skin.

L. wyvillethomsoni Théel, Sluiter 1901b. Of the two specimens from the *Siboga* material which Sluiter referred to *L. wyvillethomsoni,* one proved on re-examination to belong to *L. interjacens,* the other to *L. biserialis.* The latter specimen came from *Siboga* St. 280 and showed the following features:

Body length 17 mm. Colour rust-red.

Tubefeet about 23–24 on each side, slender from base to tip, densely placed, without any decrease in size posteriorly.

Papillae minute and few, probably single-rowed.

Small wheels with central primary cross and usually 12 spokes. In a preparation of the dorsal skin they were densely crowded in a papilla, but otherwise scarce. They were 0.035–0.050 mm in diameter. A single wheel with additional peripheral holes was present in the papilla, somewhat below the tip.

Ventrally, only few wheels were present. All of them belonged to the small type, although some attained 0.10 mm in diameter. The centre had 4 (the larger wheels occasionally 5) rays.

Large wheels confined to the dorsum and usually about 0.14 mm in diameter, with a variation of 0.09–0.17 mm. The centre invariably had 6 rays and was covered neither by a triangular superstructure nor a calcareous membrane. As shown by a count from a hundred wheels, the spoke number was consistently 12:

Number of spokes	11	12	13
Number of specimens	4	86	10

Rods, slender and straight, numerous in ventrum.

Relationships: *Laetmogone biserialis* is closely related to, and possibly identical with, *L. fimbriata.* The tubefeet are similar in shape and number, and differ from those of all other species of *Laetmogone.* The two species differ in what would appear to be rather insignificant features of the deposits. The large wheels in *L. biserialis* have 12 spokes on average, contrary to the 9 spokes prevailing in all examined specimens of *L. fimbriata.* In addition, straight rods were present in the ventrum in all examined specimens of *L. biserialis;* in *L. fimbriata* these rods, when at all present, were found to be curved.

As no intermediates have actually been found between specimens with 9 and 12 spokes, with the exception of the apparently common occurrence of 10 spokes in Mitsukuri's specimens of *L. selenkai* (= *L. fimbriata),* and as the presence of straight rods in the ventrum was in the known specimens always combined with 12 spokes in the wheels, it is preferred to keep the two species apart. Further material may prove that the differences are invalid.

The absence or scarcity of wheels of the large type in the ventrum of the known specimens of *L. biserialis* is likewise a doubtful difference from *L. fimbriata.* Both in *L. fimbriata* and *L. maculata* the wheels are sometimes few and rather small ventrally, and wheels with a central primary cross or a five-rayed centre may also here attain a larger size than is usual for the small wheels.

The papillae of *L. biserialis* apparently lack the red band which characterizes the papillae in the East Asiatic specimens of *L. fimbriata.*

Distribution: Hawaiian Islands *(L. biserialis),* c. 800 m. Sagami Bay, Japan *(L. neglecta),* 500–700 m. Banda Sea *(L. wyvillethomsoni),* 1224 m.

Type: USNM, Cat. no. 21221.
Type locality: *Albatross* St. 4141 (vicinity of Kauai Island).

Genus *Pannychia* Théel, 1882
Fig. 112

Pannychia Théel, 1882, p. 88. – Type species: *Pannychia moseleyi* Théel, 1882, by monotypy.
Laetmophasma Ludwig, 1894, p. 85.

Diagnosis: Circum-oral papillae absent. Midventral tubefeet present. Papillae of dorsum belonging to dorsal as well as ventrolateral radii. Large wheels with marginal teeth.

Remarks: Three species were previously referred to *Pannychia* and one to *Laetmophasma*. The four species are here merged into one.

Pannychia moseleyi Théel, 1882
Fig. 26

Pannychia moseleyi Théel, 1882, pp. 88–90, pls. XVII, XXXII: 1–13; Sluiter 1901b, pp. 71–72; Edwards 1907, pp. 62–64; Mitsukuri 1912, pp. 207–212, fig. 38; Clark 1913, p. 232; Ohshima 1915, pp. 235–236; Ohshima 1916–1919; D'yakonov, Baranova & Savel'eva 1958, p. 360.
Pannychia moseleyi var. *henrici* Ludwig, 1894, pp. 95–99, X: 1–2.
Pannychia moseleyi virgulifera Ohshima, 1915, p. 236; Ohshima 1916–1919, with three figures.
Pannychia moseleyi mollis Savel'eva, 1933, pp. 38–40, figs. 1–6.
Pannychia multiradiata Sluiter, 1901a, pp. 25–26; Sluiter 1901b, pp. 72–74.
Pannychia pallida Fisher, 1907, pp. 709–711, pl. LXXVIII: 2.
Laetmophasma fecundum Ludwig, 1894, pp. 85–95, pls. X: 3–14, XI: 1–13; Clark 1913, pp. 231–232; Clark 1920, p. 138.

Diagnosis: Tentacles 20. Ventrolateral tubefeet in double rows, with broad, cup-shaped sucking-discs. Midventral tubefeet smaller, but similar in shape to the ventrolateral tubefeet. Papillae (belonging to the dorsal and ventrolateral radii) numerous and small, scattered all over the dorsum, although few in number along the dorsal midline. In addition, a number of longer papillae are usually present along the dorsal radii. Scattered small papillae may be present also in the ventral interradius. Wheels of two types, a small type about 0.05 mm in diameter, with a central primary cross and 10–12 spokes; and a large type, 0.07–0.32 mm in diameter, with a central primary cross or 5–6 central rays, and 11–19 spokes. Large wheels with an inwardly directed tooth or lobe on the rim between each spoke, and with the nave covered by a calcareous membrane, usually perforated, growing inwards from the edge of the nave, and sometimes connected with the centre of the nave by a vertical pillar.

Material:
St. 739, Gulf of Panama (7°22'N, 79°32'W), 915–975 m. – 13 specimens.

Description: Seven specimens are complete, although poorly preserved. One is 20 cm long, the others 10–12 cm. The body is almost cylindrical, and about 1.0–1.5 cm in diameter.

Colour when alive, greyish, one specimen with a yellowish tinge.

Tentacles, all with the discs torn off. Their number could not be ascertained.

Ventrolateral tubefeet 35–45 on each side, single-rowed, about 5 mm long, and provided with broad, cup-shaped sucking-discs.

Midventral tubefeet placed in an alternating double row along the whole ventrum. They are similar in shape, though smaller than the ventrolateral tubefeet. Probably about 40 were present.

Papillae (belonging to the dorsal and ventrolateral radii) numerous and scattered all over the dorsal side, although sparsely scattered in the dorsal midline. The majority of the papillae are very short. However, in all the specimens, about 10–20 papillae, which are slender and range up to 15 mm in length, are interspersed among the small ones along each dorsal radius, often with a bilateral arrangement.

Deposits (Fig. 26). Small wheels about 0.05 mm in diameter, with a central primary cross and 10–12 spokes.

Large wheels 0.08–0.33 mm in diameter, usually larger than 0.25 mm. There are 5–6 central rays, sometimes more; hardly ever is the centre represented as a simple primary cross. Spokes 13–19. Nave covered by a calcareous membrane with small perforations and connected with the centre of the nave by a vertical pillar. No difference in size was found between the dorsal and ventral wheels, and there was no correlation between the size of the wheels and the number of spokes.

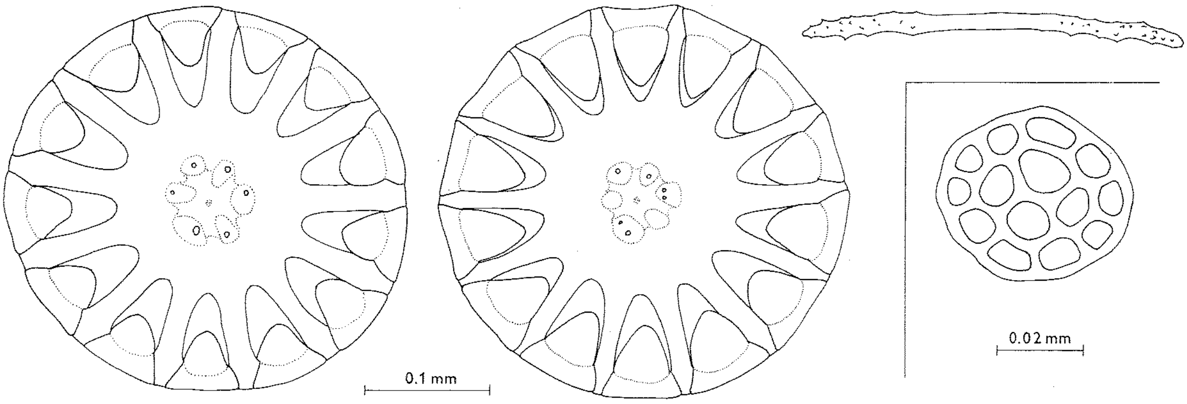


Fig. 26. *Pannychia moseleyi.* St. 739. Dorsal deposits.

Rod-shaped spicules occur in dorsum, ventrum, tubefeet, and papillae. They are usually about 0.30 mm long, slender, with slightly spinous ends.

Numerous small end-plates present in sucking-discs.

Synonymy: *Pannychia moseleyi* was taken in two specimens by the *Challenger,* one well-preserved off southeastern Australia, and one very defective specimen off New Zealand. Both are kept in BM, but only the first one permitted a re-examination.

It agrees well with the *Galathea* specimens. The tubefeet are somewhat larger, but have the same characteristic, cup-shaped sucking-discs. The papillae are less numerous, but likewise with a number of long, radial papillae interspersed amongst the smaller ones.

The dorsal, lobe-like appendage mentioned by Théel proved on re-examination to be an incidental fold of the skin.

The large wheels measure 0.24 mm in diameter and have 11–13 spokes. They were remarkable by the presence of a central primary cross in nearly all of them; only very few had 5 central rays. The nave was covered by a membrane, usually with a single, somewhat eccentric perforation. A central pillar was at the most feebly indicated.

The New Zealand specimen had large wheels with "up to 15 spokes" and 5–6 central rays. The nave was covered by a calcareous membrane with several perforations and connected with the centre of the nave by a vertical pillar.

The different structure of the centre of the wheels in the two *Challenger* specimens is of doubtful taxonomic significance. A re-examination of the Indonesian *Siboga* specimen of *P. moseleyi* revealed a centre intermediate in type between those of the two *Challenger* specimens. Most wheels had a central primary cross, but wheels with 5, or even 6, central rays were also common. A covering membrane with one or more holes, but without a central pillar, was present in all the wheels of the *Siboga* specimen.

P. moseleyi var. *henrici* Ludwig came from the eastern Pacific, partly from the same area as the *Galathea* specimens. The variety was motivated primarily by the low number of midventral tubefeet, a feature of doubtful taxonomic value. In the number of midventral tubefeet the *Galathea* specimens agreed with the *Challenger* specimens.

P. moseleyi virgulifera Ohshima was erected on the presence of numerous rod-shaped spicules in the ventrum. To this subspecies were referred the specimens recorded by Ohshima from northern Japan and the Aleutian Islands, as well as a specimen described by Edwards (1907) from off northwestern North America. Rods were also found in the ventrum of some of the *Galathea* specimens, but were not recorded by Ludwig. Some geographic variation may be present in the relative abundance of rod-shaped spicules.

P. moseleyi mollis Savel'eva was erected for one, poorly preserved specimen taken at 212 m in the Japanese Sea. The subspecies was distinguished by the absence of deposits in the body wall outside the ambulacral appendages, by the colour (white, with the papillae and tips of the tentacles and tubefeet violet) and by the presence of only 16 or 18 tentacles. This low number and the absence of deposits from the body wall proper may be due to insufficient preservation of the specimen, and the colour is so varying in the species that it can hardly be used for taxonomic conclusions.

P. multiradiata Sluiter, known from two Indonesian specimens, was characterized by its deposits. Small wheels were present only in papillae and tubefeet. The large wheels differed from those of the *Challenger* specimens of *P. moseleyi* by their large size (mostly about 0.30 mm in diameter) and high spoke number (16–18). However, in both features the wheels fall within the variation found in the *Galathea* specimens. The absence of small wheels from the ventrum and dorsum does not seem to be significant, as they may be rare also in specimens of *P. moseleyi.*

P. pallida Fisher, from Hawaii, was characterized by its grey colour with the red sucking-discs, the "well-defined" calcareous ring, and the presence of only 12–16 midventral tubefeet. In view of the extensive variation in colour found in *P. moseleyi,* the colour of *P. pallida* probably has no taxonomic significance. A well-defined calcareous ring was also found in the *Galathea* specimens. In the low number of midventral tubefeet *P. pallida* was similar to *P. moseleyi* var. *henrici,* here considered identical with the typical *P. moseleyi.*

Laetmophasma fecundum Ludwig was taken at one station in the eastern Pacific, occurring together with *P. moseleyi.* It differed from *P. moseleyi* only in having small papillae in the ventral interradii. Interradial papillae were not seen in the *Galathea* specimens, but as the ventral skin was defective their absence could not be concluded.

Variation: *Pannychia moseleyi* shows a considerable individual and local variation in several respects. It is not yet possible to demonstrate geographic features in the variation.

The large wheels are often very sparse in the ventrum. In the *Galathea* specimens they comprise the whole variation in size found in the species.

A local variation is indicated in the number of spokes. The variation in the two *Siboga* specimens of *P. multiradiata* taken south of Timor was found to be 14–19, being thus practically identical with the variation of 13–19 in the *Galathea* specimens. On the other hand, the *Siboga* specimen of *P. moseleyi* from the Moluccas and the *Challenger* specimen from south-eastern Australia had 7–13 and 11–13 spokes, respectively. The Hawaiian specimens had 10–14 spokes.

Nave of the large wheels always covered by a perforated calcareous membrane, similar to that found in most species of *Laetmogone.* A central pillar connecting the membrane with the centre of the nave is present in some specimens, but absent in others. The membrane develops from the edge of the nave and not from the central pillar as in *Laetmogone maculata.* The pillar is in *P. moseleyi* a secondary formation; this may explain its frequent absence.

The small wheels are of the usual type in the family, with a central primary cross and about 12 spokes. Through the addition of peripheral holes the wheels may change into small perforated plates. These are particularly common in the tips of the papillae. Their presence was mentioned by Théel, Ludwig, Edwards, and Fisher, and they were also present in the *Galathea* specimens. Small wheels were completely absent from the dorsal and ventral skin in the two specimens of *P. multiradiata* from south of Timor.

Spinous rod-shaped or slightly branched spicules occur in abundance in the ventrum in North Pacific specimens, and less commonly in East Pacific specimens. Otherwise they seem to be present only in papillae and tubefeet. This suggests a geographic variation, as already noted by Ohshima (1915) who erected the subspecies *P. m. virgulifera* for his North Pacific specimens.

The sucking-discs of the tubefeet seem always to possess several small end-plates.

Midventral tubefeet always present. Their variation in number is extensive even in specimens from the same area.

Ventral interradial papillae were found only in specimens from the eastern Pacific.

The colour of the specimens possibly exhibits local or geographic features. Ohshima stated that his specimens of the subspecies *P. m. virgulifera* from the northern Japan and the Aleutians were "pearly white with a bluish tint, papillae whitish purple", whereas the specimens of *P. pallida* from Hawaii were, as mentioned, remarkable for the red sucking-discs on the tubefeet. The variation within a single geographic region may, however, be extensive. The eastern Pacific specimens referred to *P. m.* var. *henrici* were violet, while the specimens referred to *Laetmophasma fecundum* were whitish as were the *Galathea* specimens.

Distribution: Found along the coasts of the Pacific from Australia and New Zealand to Peru, and off the Hawaiian Islands. Depth 212–2598 m.

Genus *Apodogaster* Walsh, 1891

Walsh 1891, p. 202; Koehler & Vaney 1905, p. 66. – Type species: *Apodogaster alcocki* Walsh, 1891, by monotypy.

Diagnosis: Circum-oral papillae absent. Ventrolateral papillae fused into a continuous brim round the body. Ventrolateral tubefeet slender and numerous, placed in a single or alternating double row beneath the brim. Midventral tubefeet absent. Dorsal papillae small and single-rowed. Wheels simple and with a central primary cross.

Remarks: Only one species, *Apodogaster alcocki,* has been described.

Benthodytes salivosus Sluiter, 1901 (a, b), taken by the *Siboga* in one specimen at 521 m in the Flores Sea proved on re-examination to represent an unidentifiable species of *Apodogaster*. The skin with all its spicules had completely worn off.

Apodogaster alcocki Walsh, 1891

Walsh 1891, p. 202; Koehler & Vaney 1905, pp. 66–67, pls. V: 2–3, XII: 13–14; Ekman 1927, pp. 366–368, fig. 3.

Known from two specimens taken in the Bay of Bengal (depth 1026 m) and one specimen taken off the Antarcic coast south of the Indian Ocean (depth 385 m).

Apodogaster sp.

Fragments of a number of specimens of *Apodogaster* (unidentifiable to species) were taken in the Kermadec Trench (Sts. 650, 654, 663, and 664) at 4410–6620 m, and one fragment in the Gulf of Panama (St. 724) at 2950–3190 m. These are the first abyssal and hadal records of the genus. The specimens have an extremely soft skin, which has almost entirely worn off in all the specimens, leaving little more than the muscular coat behind.

Suborder Psychropotina nov. subordo

Diagnosis: Deposits, when present, primary crosses with arrested development of dichotomous divisions, and reductional stages from these.

Remarks: The suborder comprises three families. Of these, the Pelagothuriidae are pelagic and are omitted from the present study.

The taxonomic foundations of the suborder, as well as the mutual relationship of the families, are considered elsewhere (pp. 206–207).

Key to the families

1\. Midventral tubefeet present. Body surrounded by a brim of fused tubefeet. Calcareous ring feebly developed or absent, never consisting of five star-shaped pieces .... Psychropotidae (p. 75)
1\. Midventral tubefeet absent. Body not surrounded by a brim of fused tubefeet. Calcareous ring, when present, consisting of five star-shaped pieces 2
2\. Anterior brim of fused tubefeet present. Tentacles 20. Deposits and calcareous ring absent .... Pelagothuriidae
2\. Anterior brim of fused tubefeet absent (except in *Psychrelpidia*). Tentacles 10-12. Deposits and calcareous ring usually present .... Elpidiidae (p. 127)

Family **PSYCHROPOTIDAE** Théel, 1882

Diagnosis: Tentacles 10-18. Brim of tubefeet surrounding the body. Midventral tubefeet present. Deposits cross-shaped or rod-shaped. Calcareous ring absent or consisting of a diffuse network.

Taxonomy: The taxonomic position of the family is considered elsewhere (p. 207). The family is here divided into three genera, distinguished by the presence or absence of an unpaired dorsal appendage, the position of the anus, the presence or absence of circum-oral (or post-oral) papillae (pp. 190–191), and the number and shape of the tentacles (pp. 191–192).

The shape of the ovaries exhibits some differences of taxonomic significance (p. 194).

Key to the genera of Psychropotidae

1. Anus dorsal. Circum-oral (or post-oral) papillae present (not demonstrated in *B. superba*). Tentacle discs soft and pliable .... *Benthodytes* (p. 76)
1. Anus ventral. Circum-oral (and post-oral) papillae absent. Tentacle discs of a fixed shape, rounded in outline, and with marginal knobs 2
2. Unpaired dorsal appendage present .... *Psychropotes* (p. 99)
2. Unpaired dorsal appendage absent .... *Psycheotrephes* (p. 96)

Genus ***Benthodytes*** Théel, 1882
Figs. 115–116

Théel, 1882, p. 102. – Type species: *Benthodytes typica* Théel, 1882.

Diagnosis: Anus dorsal. Unpaired dorsal appendage absent. Circum-oral (or post-oral) papillae present. Tentacles soft, pliable, and retractile.

Remarks: While the genus is well defined, in particular on account of its circum-oral papillae, the species are difficult to evaluate taxonomically. Some of the species intergrade in external appearance, and the deposits show only few differences.

Differences in the shape of the tentacles and in the external morphology of the gonads are to some degree taxonomically significant.

The species here referred to *Benthodytes* fall into two distinct groups of relationship (only *B. superba* falls somewhat outside):

B. incerta, B. lingua, B. valdiviae, B. sibogae, and *B. plana* have regular cross-shaped deposits with a large bipartite central apophysis, and 15 tentacles (a smaller number may be present, apparently due to failure to regenerate lost tentacles).

B. typica and *B. sanguinolenta* have strongly reduced, rod-shaped deposits, and a high tentacle number (15-20 in *B. typica,* and 18 in *B. sanguinolenta).*

B. superba has cross-shaped deposits as the first group, but the crosses are somewhat irregularly formed, and apparently lack bipartite apophyses. The tentacle number is unknown.

A number of species cannot be definitely placed taxonomically, because their deposits were dissolved or insufficiently preserved. This applied to four of the species from the *Challenger (B. abyssicola* Théel, 1882; *B. sordida* Théel, 1882; *B. mamillifera* Théel, 1882; and *B. selenkiana* Théel, 1882), to *B. janthina* von Marenzeller, 1893a, and *B. spuma* Vaney, 1908.

Benthodytes gigantea Verrill, 1884, was by Deichmann (1930) shown to belong to the genus *Paelopatides* (order Aspidochirota).

Three more species are in the present work removed from the genus *Benthodytes:*

Benthodytes browni Vaney, 1908, known from one Antarctic specimen, was characterized by the ventrolateral tubefeet and the dorsal papillae being placed on elevated parts of the skin. Vaney's illustration shows that the tubefeet are discrete, strictly ventral in position, and cylindrical (except for their enlarged, proximal part). These features refer the species to the Laetmogonidae rather than the Psychropotidae. The specimen lacked deposits and cannot, therefore, be determined to species.

Benthodytes salivosus Sluiter, 1901 (a,b). The single specimen known was re-examined and found to belong to the laetmogonid genus *Apodogaster* (p. 75).

Benthodytes recta Koehler & Vaney, 1905, is here transferred to the genus *Psycheotrephes.*

Three of the specimens taken by the *Galathea,* each probably representing a new species, are left undescribed due to the absence or fragmentary state of the deposits (p. 96).

Key to the species of *Benthodytes*

1.	Deposits cross-shaped. Dorsal papillae usually well developed	2	
1.	Deposits rod-shaped or absent. Dorsal papillae minute	7	
2.	Crosses irregularly shaped, with undivided central apophysis. Tubefeet of brim free in the greater part of their length	*superba*	(p. 89)
2.	Crosses regularly shaped, with a large, bipartite central apophysis. Tubefeet of brim fused throughout their length	3	
3.	Crosses of two types, both with a bipartite apophysis; in the large type the apophysis is bipartite in at least half the length, and the two branches are covered with small spines; in the small type the apophysis is high and smooth, and ends in two small, horizontal branches with downwardly directed spines round their margin	*incerta*	(p. 77)
3.	Crosses of one type only, resembling the large type in *B. incerta*	4	
4.	Brim narrow, often completely enclosed in the body wall	*lingua*	(p. 80)
4.	Brim broad, its margin forming the edge of the rather flattened body	5	
5.	Skin hard from the densely crowded deposits. Body uniformly dark violet	*sibogae*	(p. 84)
5.	Skin rather soft, with less crowded deposits. Body light violet, at least dorsally	6	
6.	Anterior and posterior ends of body regularly rounded; tentacular crown placed a considerable distance from anterior edge of body, leaving ample space for the well-developed circum-oral ring of papillae	*plana*	(p. 87)
6.	Anterior and posterior ends of body somewhat tapered; tentacular crown adjoining the anterior edge of the body, leaving only a narrow space for circum-oral papillae	*valdiviae*	(p. 82)
7.	Dorsal papillae numerous, arranged in two bands. Tentacles 18. Post-oral papillae present	*sanguinolenta*	(p. 94)
7.	Dorsal papillae few, arranged in two single rows. Tentacles 15-20. Circum-oral papillae present	*typica*	(p. 89)

Benthodytes incerta Ludwig, 1894

Figs. 27–28, pls. IX: 1–2, XII: 1

Benthodytes incerta Ludwig, 1894, pp. 60–62, pl. II: 1–4.

Benthodytes gotoi Ohshima, 1915, pp. 246–247, pl. IX: 12; Ohshima 1915–1919, with two figures.

?*Benthodytes regularis* H. L. Clark, 1920, pp. 141–142, pl. II: 2.

Diagnosis: Body semi-circular in cross-section. Skin firm and rather thin. Tentacles (9–)15. Brim narrow, delimiting a well-defined ventral sole. Dorsal papillae filiform or conical, in single rows. Dorsal skin covered with warts, which each contains a large cross-shaped deposit always with a regular bipartite apophysis. Small crosses of a peculiar type, sparsely occurring in the dorsum, with distal arm spines and a high, smooth apophysis which ends in two horizontal branches, each with downwardly directed marginal spines. Ventral deposits usually reduced; apophyses, when present, undivided.

Material:

St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – 16 specimens.

Description: The specimens are 4.5–22.0 cm long and of a rather uniform appearance. Breadth $^{1}/_{7}$–$^{1}/_{5}$ length of the body. The smallest specimens are the most slender.

Skin firm and rather thin. The dorsal skin is covered with warts, which each contains a cross-shaped deposit. Ventral skin smooth.

Colour light violet, but remnants of a dark violet superficial layer are present on the ventral sole, and in some specimens, also dorsally.

Tentacles (Pl. IX: 1–2). The smaller specimens have 15 tentacles, whereas the larger specimens usually have a lower number. Apparently, lost tentacles are not regenerated, the gaps being covered by the growth of adjoining tentacles.

In the small specimens the discs are usually regularly rounded and have about 12 marginal knobs. In the large specimens the tentacles are large and soft, and shaped after each other. The

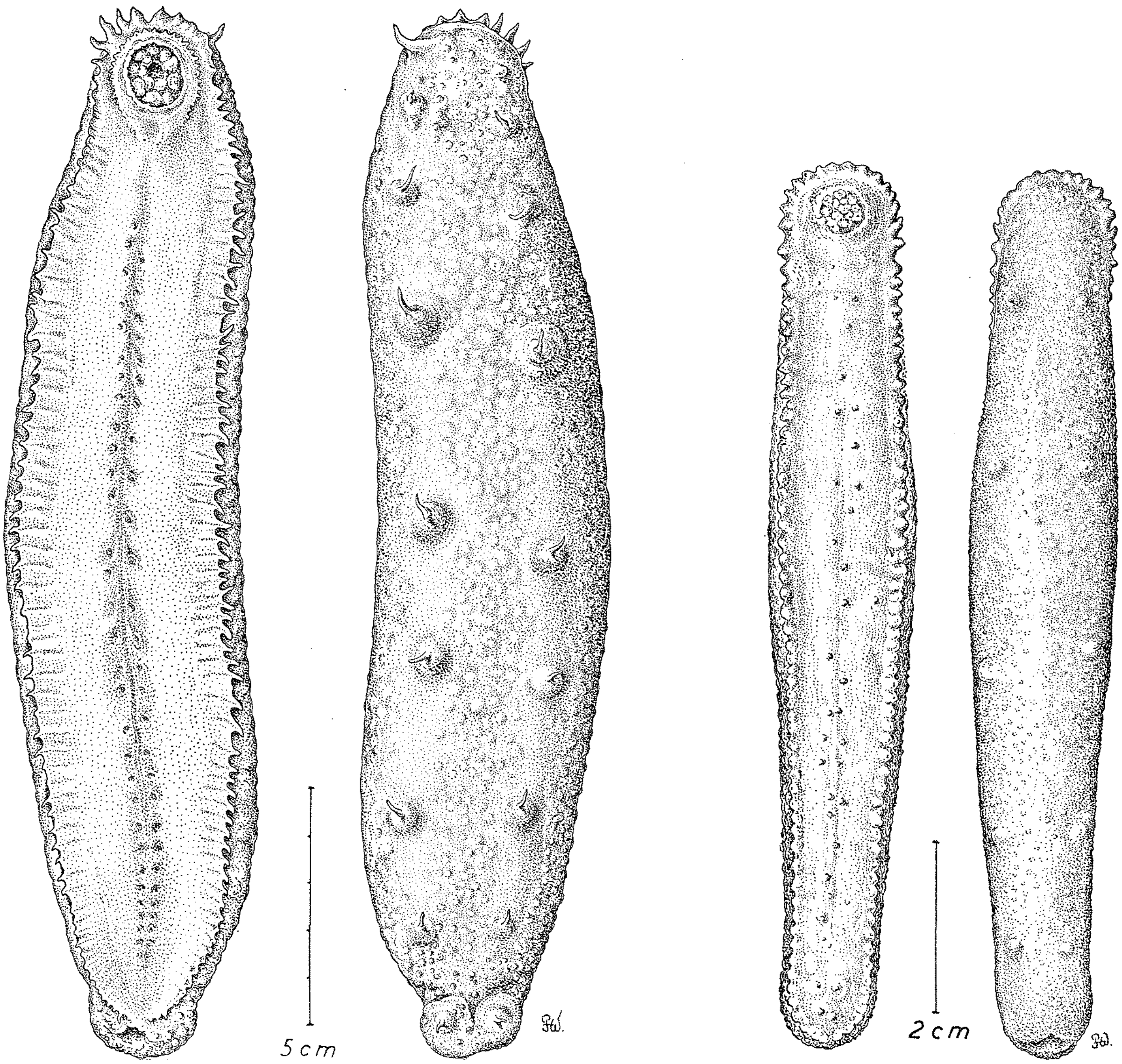


Fig. 27. *Benthodytes incerta.* St. 716. A large and a small specimen in ventral and dorsal view. PHW.

marginal knobs are wholly or partly retracted. In addition, the discs are retractile into the tentacle stalk.

Circum-oral papillae present, but often difficult to discern. When fully extended the papillae are seen to be merged at their bases. A contractile, oral membrane is seen in some of the specimens (cf. the large specimen illustrated).

Brim narrow, in some specimens partly retracted, with only the tips of the tubefeet visible. The brim clearly delimits the flat ventral sole from the vaulted dorsum. The water-vascular canals of the tubefeet are usually visible laterally on the ventral sole.

Midventral tubefeet forming an irregular double row. They are often absent anteriorly.

Dorsal papillae 6–9 along each radius. They are usually equal in number and symmetrically arranged in the two radii. The largest number of papillae is found in the two largest specimens (measuring 22 and 18 cm). The 22 cm long specimen (Fig. 27, left) possesses 9 pairs of papillae while the 18 cm long specimen possesses 9 right and 8 left papillae. The papillae are conical and usually end in a small whiplash. They attain a length of 7 mm in the larger specimens. The smaller specimens have relatively smaller papillae. which are often difficult to distinguish from the numerous warts which cover the dorsal side.

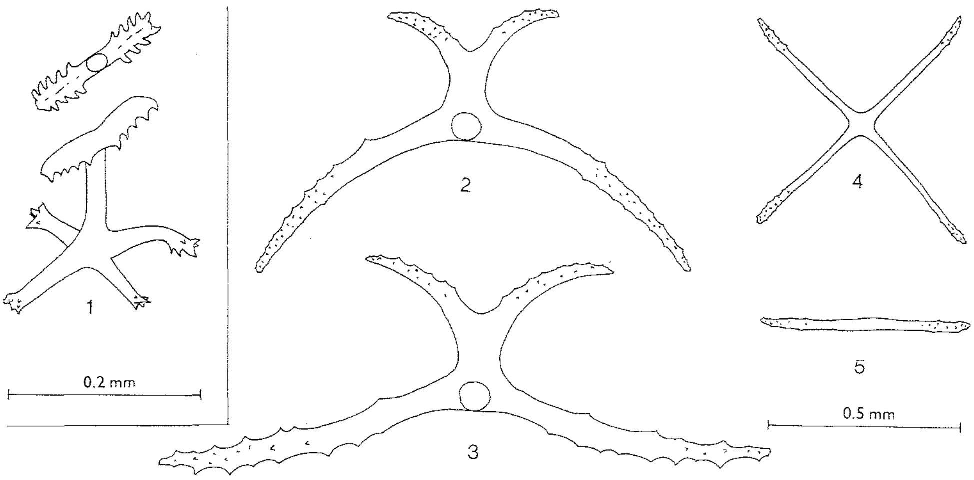


Fig. 28. *Benthodytes incerta.* St. 716. Deposits. 1, small cross from dorsum; 2–3, large crosses from dorsum; 4–5, cross and rod from ventrum.

Deposits (Fig. 28). The crosses of the dorsal warts possess a large bifurcate apophysis which projects from the skin. The arms of the crosses are usually about 0.75 mm long, although they may be only 0.50 mm. The arms vary greatly in appearance, being upwardly or downwardly curved, and with rather differently developed spines.

Scattered small crosses of a peculiar type (Fig. 28: 1) occur in the dorsal skin. The arms are about 0.07 mm long and possess spines only in their distal part which is somewhat downwardly curved. The apophyses are high and smooth, and end in two horizontal arms which are provided with downwardly directed spines on their margin.

The ventral deposits are few and usually reduced to rods. The few cross-shaped deposits present have reduced apophyses.

Synonymy: *Benthodytes incerta* Ludwig was taken by the *Albatross* near the locality of the *Galathea* specimens, one specimen (11.5 cm long) at St. 3400 (depth 2417 m), another (8.4 cm long) at St. 3415 (depth 3436 m). The specimens (in USNM) were re-examined and found to agree in external morphology with the *Galathea* specimens. (The large size of the papillae in Ludwig's figure applied to the freshly caught large specimen. The specimen in the preserved state had papillae similar in shape and size to those of the largest of the *Galathea* specimens). The skin was covered with warts. A number of 10 and 12 tentacles respectively were present. The deposits (not re-examined) were somewhat different in the two specimens. The large specimen had sturdy and spinous ventral crosses with 0.30–0.45 mm long arms and spinous, undivided apophyses. The arms of the dorsal crosses were shorter (up to 0.3 mm long) and more slender; the apophyses were high and bipartite. The small specimen possessed no ventral deposits; the dorsal crosses had up to 0.5 mm long arms and a bipartite apophysis.

The dorsal deposits of the *Galathea* specimens differ from those of the large *Albatross* specimen (i.e. the deposits illustrated by Ludwig), by their large size and their more regularly shaped, outwardly curved and tapering apophyses. On the other hand, the small specimen of Ludwig's *B. incerta* had dorsal deposits which fell within the variation in the *Galathea* specimens.

The small type of deposit in the *Galathea* specimens was not described from Ludwig's specimens. This is, however, not surprising in view of the fact that these deposits occurred very sparsely, and that the ends of the apophyses were rarely preserved.

The species identity of the *Galathea* specimens with the large *Albatross* specimen may be questioned, but they agree well with the small specimen which Ludwig designated as the type.

Benthodytes gotoi Ohshima is known from four specimens, taken at 3292 m in the Okhotsk Sea. The agreement with the *Galathea* specimens, as seen from the illustrations in the Japanese edition of Ohshima's work, is very fine. Both types of deposit were present, large crosses with 0.3–0.8 mm long arms, and sparsely occurring small ones with 0.10–0.18 mm long arms and a central apophysis ending in two horizontal branches with downwardly directed spines. The identity between *B. gotoi* and *B. incerta* is strongly supported by the occurrence in both species of this peculiar type of small crosses.

Benthodytes regularis H. L. Clark is known from one specimen, taken at 4087 m between the Galapagos Islands and South America. According to Clark, the species is characterized by the regular arrangement of the dorsal papillae; but actually, this feature is common to a number of species of *Benthodytes*. The deposits were not illustrated, and the shape of the apophyses not mentioned. The dorsal deposits were said to measure about 0.125 mm across, but fragments of double-sized crosses were also present. A re-examination of the specimen (in USNM) showed fragments of crosses measuring about 1.4 mm across, but with no apophyses preserved. Smaller crosses measuring 0.2–0.3 mm across, with straight, rather slender and spinous arms occurred in the deeper layer of the skin. Deposits as small as the type mentioned by Clark were not found; in size they agreed with the small type in the *Galathea* specimens. The identity of the *regularis* specimen, like that of the large *incerta* specimen described by Ludwig, cannot be established until the deposits can be shown to fall within the range of variation in *B. incerta*.

Relationships: *B. incerta* and *B. lingua* differ in the following features: (1) The small type of deposit, with the apophyses ending in two horizontal branches, are absent in *B. lingua*. (2) The tentacle discs in *B. incerta* have about 12 smooth, marginal knobs; in *B. lingua* the discs are larger, and the margin is irregularly indented. (3) Most of the known specimens of *B. lingua* have a remarkably thick and gelatinous skin, and the brim is completely retracted; the ventral sole is barely delimited from the remaining part of the body, and the specimens are circular in cross section. In contrast, the known specimens of *B. incerta* have a rather thin and firm skin, and the ventral sole is well delimited by a distinct, although narrow brim. However, the species *B. lingua* varies in external appearance, and some of Perrier's specimens were indistinguishable in body shape from the *Galathea* specimens of *B. incerta*.

B. incerta differs from all other species of *Benthodytes* by the peculiar small type of cross.

Distribution: Eastern Pacific, 2417–3570 m. *B. regularis*, which may be identical with *B. incerta*, was taken at a depth of 4087 m.

Type: USNM, labelled "Type".
Type locality: *Albatross* St. 3415 (14°46'N, 98°40'W).

Benthodytes lingua R. Perrier, 1896
Figs. 29, pls. IX: 3–5, XII: 2–3

Benthodytes lingua R. Perrier, 1896, p. 902; R. Perrier 1902, pp. 456–461, pls. XII: 1–2, XXI: 1–9; Deichmann 1930, pp. 124–125; Deichmann 1940, pp. 200–201, pl. XXXV: 3–4; Heding 1942, p. 15; Deichmann 1954, p. 384.
Benthodytes janthina von Marenzeller, Grieg 1921, p. 11; Heding 1942, p. 15.
Pannychia glutinosa Hérouard, 1902, p. 32, pl. IV: 17.

Diagnosis: Body usually rounded in cross section. Skin usually thick and gelatinous. Tentacles (12–)15. Brim narrow and completely retractile. Ventral sole usually feebly delimited from the remaining part of the body. Dorsal papillae in single rows, up to 12 pairs, filiform or slightly conical. Dorsal deposits large crosses with bipartite apophyses, the two arms of which are outwardly curved and gradually tapered. Ventral deposits rudimentary or absent.

Material:
St. 32, Monrovia–Takoradi (4°05'N, 2°13'W), 2100 m. – 4 specimens.
In addition, 7 specimens from South Africa (without further information about locality), kept in ZMUC, were examined.

Description: *Galathea* St. 32. – Length of specimens 26–38 cm. The specimens in external appearance agree with the specimen illustrated by Perrier (1902, pl. XII: 1–2).

Skin soft, thick, and light violet.

Tentacles 12–14. Discs in the extended state resembling those of the *Ingolf* specimens (Pl. IX: 3). However, most of the discs are to some degree retracted into the broad stalk (Pl. IX: 5). The stalks with the retracted discs are usually pressed together, forming elongated, radial pockets, the inside of which is lined with the disc surface.

Circum-oral papillae visible as minute violet spots. A partially contracted *oral membrane* is present in some of the specimens.

Brim narrow, in most of the specimens completely retracted. The ventral sole passes gradually into the body side, the body being rounded in cross section.

Midventral tubefeet minute and usually retracted. They are absent on the anteriormost 2–3 cm of the ventral sole.

Dorsal papillae filiform and varying in length, from quite inconspicuous to about 4 mm long. Owing to their small diameter at the base they are easily lost, and the number is, therefore, difficult to make out; it probably varies between 10 and 20 pairs.

Deposits resembling those of the South African specimens (q. v.). The dorsal crosses have 0.4–0.7 mm long arms and a central apophysis which is bipartite almost from the base. Both arms and apophyses are robust and spinous. Preparations from the ventral skin contained no deposits in three of the specimens, while a few large crosses were present in the fourth specimen; apophyses not preserved.

The South African specimens. – Length 15–24 cm. Body form, brim, and midventral tubefeet as in the *Galathea* specimens.

Tentacles 12–15 (Pl. IX: 4). The discs are similar in shape to those of the *Galathea* specimens, and show a similar retractility into the stalks.

Circum-oral papillae visible in three specimens.

Dorsal papillae filiform and varying in length, from being quite inconspicuous to about 10 mm long. The papillae are single-rowed; the highest number found was 10–12 pairs.

Deposits (Fig. 29: 1-2) similar in shape and size to those of the *Galathea* specimens. The ventrum, examined in three specimens, contains no deposits. The ovaries contain cross-shaped, tripartite, and rod-shaped deposits, all devoid of vertical apophyses.

Synonymy: *Benthodytes lingua* was taken at several North Atlantic stations of the *Travailleur* and the *Talisman*. A detailed description of the specimens was given by R. Perrier (1902), who noted the presence of circum-oral papillae and a contractile oral membrane. The tentacle discs were irregularly shaped and feebly lobated. The body was shaped like the tongue of an ox, whence the name of the species.

During re-examination the specimens were seen to resemble the *Galathea* specimens in external features as well as deposits. A few specimens had a flattened (apparently collapsed) body. The tentacle discs were irregularly shaped and differed greatly in size within one and the same specimen. They showed a similar retractility into the

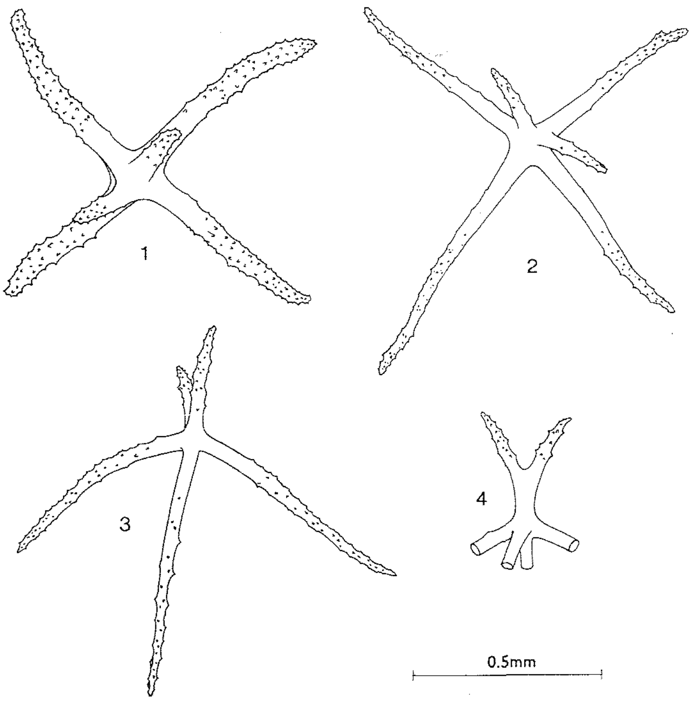


Fig. 29. *Benthodytes lingua.* Dorsal deposits. 1–2, South African specimens, 20 and 22 cm long; 3–4, *Ingolf* St. 18, a 7 cm long specimen.

stalks as those of the *Galathea* and the South African specimens.

Pannychia glutinosa Hérouard, erected on a 6 cm long specimen taken at a depth of 2202 m east of the Azores, was by Deichmann (1930) synonymized with *B. lingua,* but without comment. The specimen, to judge from Hérouard's description, resembled the small specimens of *B. lingua* taken by the *Ingolf* (see below).

The specimens from the *Ingolf* which Heding referred to *B. lingua* and *B. janthina,* are in the present work all referred to *B. lingua.* The specimens were re-examined.

The specimen from *Ingolf* St. 20, by Heding determined to *B. janthina,* is 14 cm long and uniformly whitish all over. The ventrolateral tubefeet are completely retracted, distinguishable only as small pits in the thick and soft skin. Only around the head do the tubefeet project slightly from the skin, forming a clear border between the dorsal and ventral side. Otherwise, the ventral sole passes gradually into the lateral body wall, and the pits from the ventrolateral tubefeet do not in any way delimit a well-defined ventral sole. The 15 tentacles resemble those of the small specimen from *Ingolf* St. 18 (Pl. IX: 3). The dorsal papillae are small and placed at irregular intervals throughout the length of the dorsal radii. Only few papillae are visible, but a number of small pits indicate additional, retracted papillae. The dorsal deposits agree perfectly with those of Perrier's specimens of *B. lingua* and with those of the *Galathea* and the South African specimens. The arms are about 0.5 mm long.

The specimen from *Ingolf* St. 18, by Heding determined to *B. lingua,* is 7 cm long and whitish-transparent. The skin is thick and soft, except ventrally, where it is quite thin. A few canals for the ventrolateral tubefeet are seen through the skin, but no tubefeet are visible on the surface. At least four pairs of small, radial dorsal papillae are present. Tentacles 15; discs (Pl. IX: 3) rounded in outline and covered with papillae; at the periphery of the disc the papillae are arranged into radial fields which continue into irregularly shaped marginal processes. The tentacles are thus more regularly shaped than is usual in the above described specimens. The deposits (Fig. 29: 3–4) are rather slender, though not more slender than in some of the large specimens. The ventral skin has no deposits.

Two additional specimens from St. 18, not mentioned in the Ingolf Report, were examined. They are 2.7 and 3.0 cm long and similar to the 7 cm long specimen both in external features and deposits (the deposits are slightly more slender, but of the same size and shape). Four pairs of low, conical dorsal papillae are visible in the 3.0 cm long specimen.

Benthodytes janthina von Marenzeller, Grieg 1921. Re-examination of the specimen (22 cm long) revealed agreement in external features with *B. lingua.* Deposits dissolved.

Relationships: Most closely related to *B. incerta* (q. v.).

Distribution: North and South Atlantic, 860–3192 m.

Type: MNHN.
Type locality: *Talisman* 1883, St. 39 (30°08'N, 14°02'W).

Benthodytes valdiviae n. sp.

Figs. 30–31

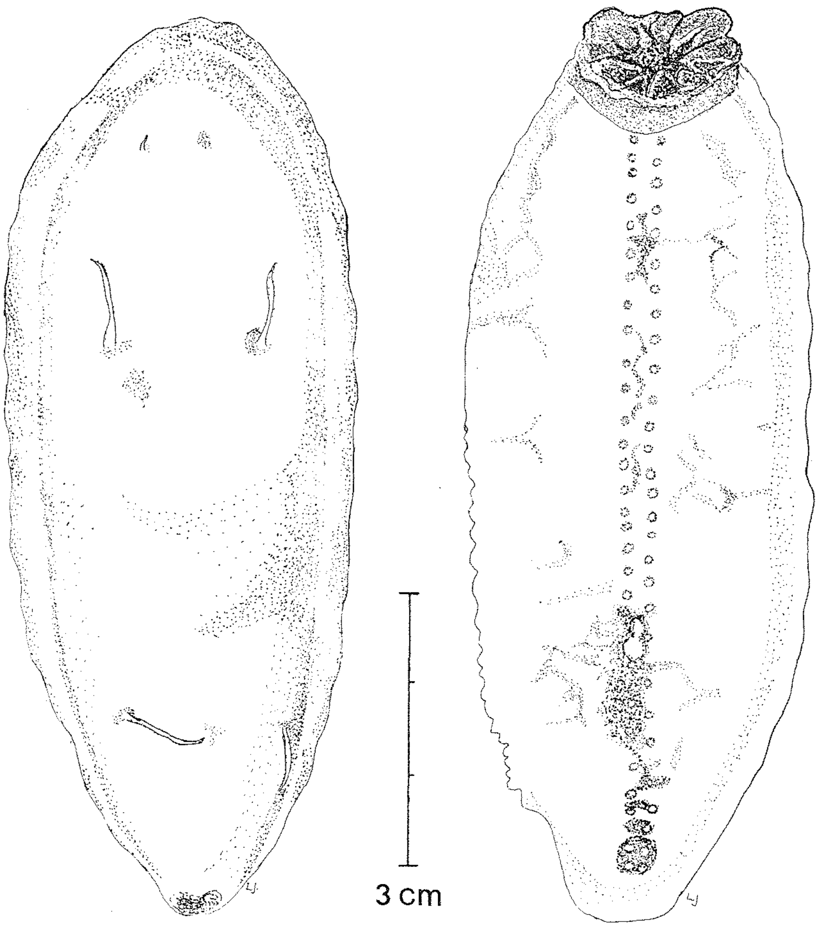
Benthodytes lingua R. Perrier, Heding 1940, p. 368.
Benthodytes janthina von Marenzeller, Heding 1940, p. 368.

Diagnosis: Body flattened, somewhat tapered at both ends. Tentacle crown adjoining anterior edge of body. Tentacles (12–)15. Brim broad, but retractile. Dorsal papillae 5–10 pairs, slender from base to tip. Deposits, dorsally large crosses with a bipartite apophysis; ventrally absent, or reduced to small rods.

Material:
Valdivia St. 33, south of the Canary Islands (24°35'N, 17°05'W), 2480 m. – 7 specimens.

Description:
Two specimens are large (10–11 cm long), five are small (5–7 cm long). Heding (1940), in his report on the *Valdivia* holothurians, referred the large specimens to *Benthodytes lingua,* and the small ones to *B. janthina.* A re-examination of the specimens (at present in ZMUC) resulted in the decision to unite them into a new species.

Fig. 30. *Benthodytes valdiviae. Valdivia* St. 33. The type specimen in dorsal and ventral view. LJ.



The type specimen (Fig. 30) is 10 cm long, 3 cm broad (exclusive of the lateral brim) and 1.7 cm high. Dorsal side light violet and smooth. Ventral side light violet, but with small patches of a dark violet superficial layer. Tentacles dark violet.

Tentacles with retractile, soft discs similar in shape to those of *B. lingua*. Some of the stalks containing retracted discs form radial pockets. The number of tentacles could not be made out.

Circum-oral papillae not visible.

Brim retractile, up to 7 mm broad along the body side and 2 mm broad round the anterior and posterior ends. The edge of the body is smooth, the tubefeet of the brim being completely fused.

Midventral tubefeet arranged in a double row throughout length of ventral sole.

Dorsal papillae. Two right and three left papillae are seen, varying in length from 2 to 10 mm. Additional completely retracted papillae were possibly present.

Deposits (Fig. 31) dorsally robust, spinous crosses with about 0.7 mm long arms and a large, bipartite apophysis. No deposits were present in a preparation from the ventral skin.

The other large specimen is 11 cm long, 3 cm broad (exclusive of the brim), and 2 cm high. Both dorsal and ventral side light violet and smooth; tentacles and midventral tubefeet dark violet.

Tentacles 12, resembling those of the type specimen.

Circum-oral papillae not visible.

Brim similar to that of the type specimen.

Midventral tubefeet present throughout length of ventral sole.

Dorsal papillae retracted, their presence indicated by slight depressions of the skin. The number is probably between 5 and 10 pairs.

Genital opening 18 mm from anterior edge of body.

Deposits similar to those of the type specimen.

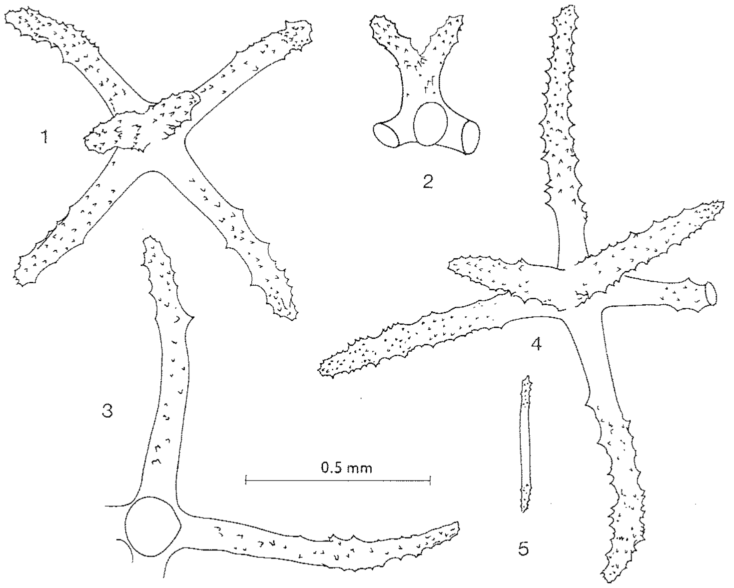


Fig. 31. *Benthodytes valdiviae. Valdivia* St. 33. 1–4, crosses from dorsum; 5, rod from ventrum.

Of the five small specimens, the largest (7 cm long) is the best preserved. The dorsal side is light violet, while the ventral side bears remnants of a superficial dark violet layer. The tentacles are dark violet.

Tentacles 15; discs regularly rounded and only slightly retracted. They are similar in shape to those of the 7 cm long specimen of *B. lingua* from *Ingolf* St. 18 (Pl. IX: 3). A few papillae are present posterior to the tentacle crown, probably forming part of a circum-oral ring.

Brim about 2 mm broad.

Dorsal papillae radial, 6 or 7 pairs, slender, and up to 7–8 mm long.

Deposits, dorsally similar to those of the large specimens. The ventrum contains small, scattered rods.

The four remaining small specimens are defective and provide no additional information.

Four of the five small specimens (including the largest one) show a strong contraction of the dorsal longitudinal muscles, and in two of the specimens this had led to a total rupture of the ventral skin. The complete extension of all the tentacles in the small specimens may be due to the strong contraction of the body.

Relationships: *B. valdiviae* may be most closely related to *B. plana.* The latter species has a more thick and soft skin, and its body is more regularly rounded at both ends. The tentacle crown in *B. plana* is placed at some distance from the anterior margin of the body, while in *B. valdiviae* its adjoins the anterior edge of the body. The deposits are similar to the largest and most robust deposits of *B. lingua* and much more robust than those of *B. plana.*

Benthodytes sibogae Sluiter, 1901

Figs. 32–33

Benthodytes sibogae Sluiter, 1901a, pp. 17–18; Sluiter 1901b, pp. 55–58, pls. I: 1–2, IX: 11, X: 1.

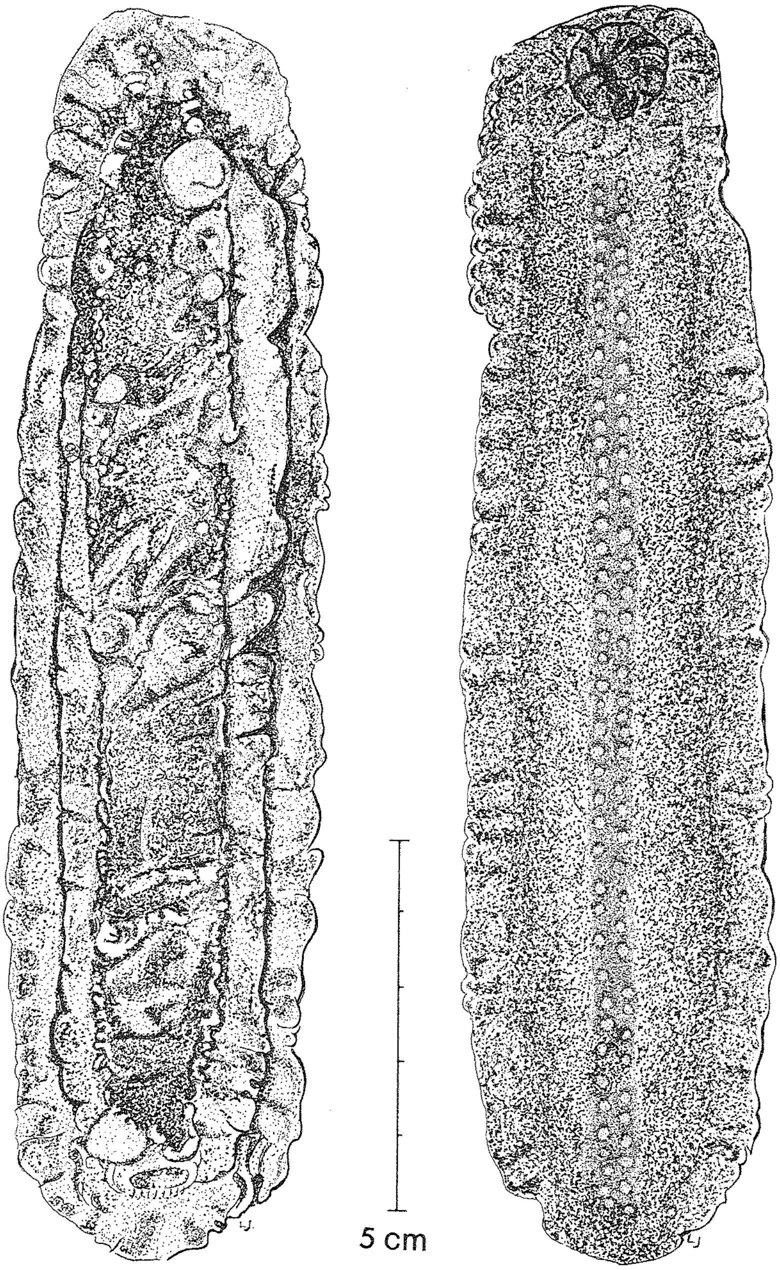
Benthodytes hystrix Sluiter, 1901a, pp. 19–20; Sluiter 1901b, pp. 59–60, pls. IV: 4, IX: 10; Heding 1940, p. 367.

Diagnosis: Body flattened. Colour uniformly dark violet. Tentacles (14–)15. Brim broad. Dorsal papillae 5–6 pairs, conical, in single rows. Dorsal deposits crowded, spinous crosses, usually with bipartite apophyses. Ventral deposits rod-shaped, tripartite, or cross-shaped; apophyses absent, or rudimentary and undivided.

Description: The species *B. sibogae* and *B. hystrix,* here synonymized, are known from seven specimens, taken in Indonesian seas by the *Siboga* and the *Valdivia.* The specimens, all re-examined, came from the following stations:

Siboga St. 18: *B. sibogae,* one specimen, 19 cm long. The specimen, although not designated as type specimen, formed the basis of Sluiter's description.

Fig. 32. *Benthodytes sibogae. Valdivia* St. 186. The 17 cm long specimen in dorsal and ventral view. LJ.



- St. 314: *B. sibogae,* one specimen, 11 cm long.
- St. 175: *B. sibogae,* one specimen, 6 cm long.
- St. 221: *B. hystrix,* one specimen, 20 cm long.

Valdivia St. 186: *B. hystrix,* two specimens, 15 and 17 cm long.

- St. 189: *B. hystrix,* one specimen, 11 cm long.

The variation in external appearance is illustrated by Sluiter's figures of *B. sibogae* and *B. hystrix,* and the *Valdivia* specimen shown in Fig. 32.

Colour uniformly dark violet, with whitish regions wherein the deposits are particularly dense. This uniformly dark violet colour seems to be the natural one in the species. The specimen from *Siboga* St. 314 had this colour still, whereas the specimen from *Siboga* St. 18, which, according to Sluiter's description, was dark violet, was found on re-examination to be light violet. The small specimen from *Siboga* St. 175 was likewise light violet, but all the internal organs were dark violet.

Tentacles (14–)15. Discs in the 15 cm long specimen from *Valdivia* St. 186 unretracted, resembling those of the 7 cm long specimen of *B. lingua* from *Ingolf* St. 18 (Pl. IX: 3). In the

17 cm long specimen from *Valdivia* St. 186 (Fig. 32) the retracted discs covered the inside of the stalks, the latter forming radial pockets.

Circum-oral papillae visible in the specimen from *Valdivia* St. 189.

Brim varying in breadth. Sluiter referred to the broader brim of *B. hystrix* as one of the features distinguishing this species from *B. sibogae*. However, the agreement in other external features, as well as in deposits, indicates that the different breadth of the brim is due to a different degree of contraction, or to individual variation.

In the two specimens from *Valdivia* St. 186 the brim is as broad as in the specimen which Sluiter illustrated as *B. hystrix;* but its edge is smooth, the tips of the tubefeet only slightly projecting here and there. Owing to the strong pigmentation of the skin and the dense crowding of the deposits, the canals are in most places invisible. In the specimen from *Valdivia* St. 189 the brim, only partially preserved, agrees more with that in Sluiter's figure of *B. sibogae,* being rather narrow and thin, with the canals of the tubefeet clearly visible through the skin.

The 6 cm long specimen of *B. sibogae* from *Siboga* St. 175 had the ventrolateral tubefeet almost completely retracted into the soft and gelatinous skin. In external appearance the specimen resembled juvenile specimens of *B. lingua.* Unfortunately, the determination to *B. sibogae* could not be supported by a comparison of the deposits, none of which had the apophyses preserved.

Dorsal papillae 5–6 pairs, placed in a single row along each dorsal radius. In addition to these papillae, which are conspicuous and conical with pointed or blunt tips, a number of minute, radial papillae are seen in the two specimens from *Valdivia* St. 186.

Some of the papillae of *B. sibogae* and *B. hystrix* illustrated by Sluiter are singly or doubly divided distally. A re-examination confirmed Sluiter's supposition that the splitting of the papillae is an artifact.

Deposits (Fig. 33). The dorsal crosses are so crowded in the *Valdivia* specimens and in the specimen from *Siboga* St. 314 that the external layer of the skin has become quite hard and has taken on a whitish tinge here and there. In the specimens from *Siboga* Sts. 18 and 175 the deposit layer was almost completely worn off, and usually little more than arm fragments remained. The specimen from *Siboga* St. 221, the type specimen of *B. hystrix,* possessed remnants of a strongly developed deposit layer, seen in Sluiter's drawing as small spinous patches.

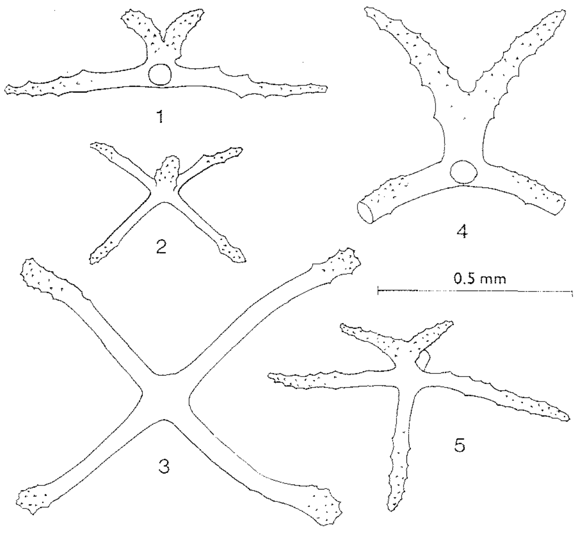


Fig. 33. *Benthodytes sibogae.* Deposits. 1–2, *Valdivia* St. 186, dorsal crosses; 3, same, crosses from the gonadal wall; 4–5, *Siboga* St. 314, dorsal crosses.

According to Sluiter, the deposits of *B. sibogae* resembled those of *B. incerta.* However, bipartite apophyses were not mentioned, and the deposit figured from the dorsal skin had an undivided apophysis. The arms of the crosses were slender, 0.3 mm long, and provided with spines only in the distal part. In contrast to this, the deposits of *B. hystrix* were of a heavy structure; the arms measured about 1.0 mm and were provided with spines throughout almost their whole length; the apophyses had a smooth, undivided proximal part, continuing into a pair of outwardly-curved, pointed, and spinous arms.

Comparing the two deposits illustrated in the Siboga Report an identity between *B. sibogae* and *B. hystrix* seems to be excluded. However, a re-examination revealed that the deposit illustrated from *B. sibogae* was not typical, the deposits being, in actual fact, indistinguishable from those of *B. hystrix.*

The deposits of the specimen which Sluiter described as *B. hystrix* were found to agree in shape with that illustrated in the Siboga Report; but the arms were only 0.6–0.8 mm long. The deposits of the two *B. sibogae* from *Siboga* Sts. 18 and 314 (Fig. 33: 4–5) had arm lengths of 0.3–0.4 and 0.4–0.6 mm, respectively. No apophyses were preserved in the preparations of the specimen from *Siboga* St. 18, but in the specimen from St. 314 the apophyses were nearly all bipartite and similar in shape to those described for *B. hystrix*. The arms of the deposits were in both specimens as robust as those of *B. hystrix* (their smaller size taken into account), and spines were present throughout almost their whole length. The deposits of the juvenile specimen from St. 175 were too defective to be examined.

According to Heding, the dorsal deposits of the *Valdivia* specimens agreed with those of Sluiter's *B. hystrix,* except that they possessed coarser spines. However, a re-examination of the deposits (Fig. 33: 1–2) revealed that they differed, both in size and shape, from those of the *Siboga* specimens. The arms were only about 0.25–0.40 mm long and nearly always horizontal. The apophyses were remarkably spinous and often irregularly shaped, varying from undivided to bipartite, with intermediates in the form of undivided apophyses with a side-branch.

The ventral deposits in the *Siboga* and *Valdivia* specimens varied from crosses with reduced apophyses, to rods.

Remarks: Pawson (1965c), with some doubt, identified two specimens taken at a depth of c. 1100 m in Palliser Bay (Cook Strait, New Zealand) as *B. hystrix*. However, in the external features the specimens, which were "extensively damaged", appear to be more similar to *B. lingua*. The body was rather cylindrical, and the body wall was thick and soft. (Brim, or ventrolateral tubefeet not mentioned).

Variation: While the differences in the external features between the above specimens are probably due to individual variation, the differences between the deposits of the *Valdivia* specimens on one hand and those of the *Siboga* specimens on the other suggest a geographic variation. The *Valdivia* stations are situated west of Sumatra, whereas the *Siboga* stations are situated farther east.

Relationships: The most closely related species are probably *B. incerta* and *B. lingua,* both of which differ from *B. sibogae* by the body being arched or rounded in cross-section and by the feebly developed brim.

Distribution: Indonesia, 694–2798 m.

Benthodytes plana n. sp.

Figs. 34–35

Diagnosis: Body flattened, regularly rounded at both ends. Skin thick, soft, and semi-transparent. Tentacle crown placed some distance from anterior edge of body, leaving ample space for the ring of circum-oral papillae. Tentacles 15. Brim broad and thick, passing gradually into the body proper. Deposits large crosses with bipartite apophyses.

Material:

St. 186, Cape Town–Durban (32°33'S, 32°01'E), 3620 m. – 1 specimen.

St. 281, Seychelles–Ceylon (3°38'N, 78°15'E), 3310 m. – 1 specimen.

Description:

St. 186. – The specimen (Fig. 34), selected as type, is 13 cm long. The flat ventral sole is regularly rounded at both ends. Breadth of body, including the brim, 4.5–5.0 cm. Height 2.5 cm.

Skin thick, soft, and semi-transparent both dorsally and ventrally. The ventral skin has a brownish tinge, and the tentacles and midventral tubefeet are dark brown.

Tentacles 15; discs with 20–30 small, rounded processes on the margin. Surface of discs smooth, possibly due to retraction of the papillae. The discs may not differ significantly in shape from those illustrated for the small specimen of *B. lingua* (Pl. IX: 3).

Circum-oral papillae present. Most of the papillae are totally embedded in the soft and gelatinous skin; viewed by transmitted light they are seen to form a complete circle.

Brim broad and passing gradually into the body proper. The transition between body and brim is indicated by a faint depression in the dorsal skin. The canals of the enclosed tubefeet are visible from the ventral side; in dorsal view they are seen by transmitted light only. The broad and thick brim gives the species a flattened appearance.

Dorsal papillae not distinguishable with certainty, due to the defective state of the dorsal skin.

Deposits (Fig. 35), dorsally spinous crosses with up to 0.4 mm long arms and a bipartite apophysis. A few deposits have 3 or 5 arms, and some have tripartite apophyses. The deposits are pre-

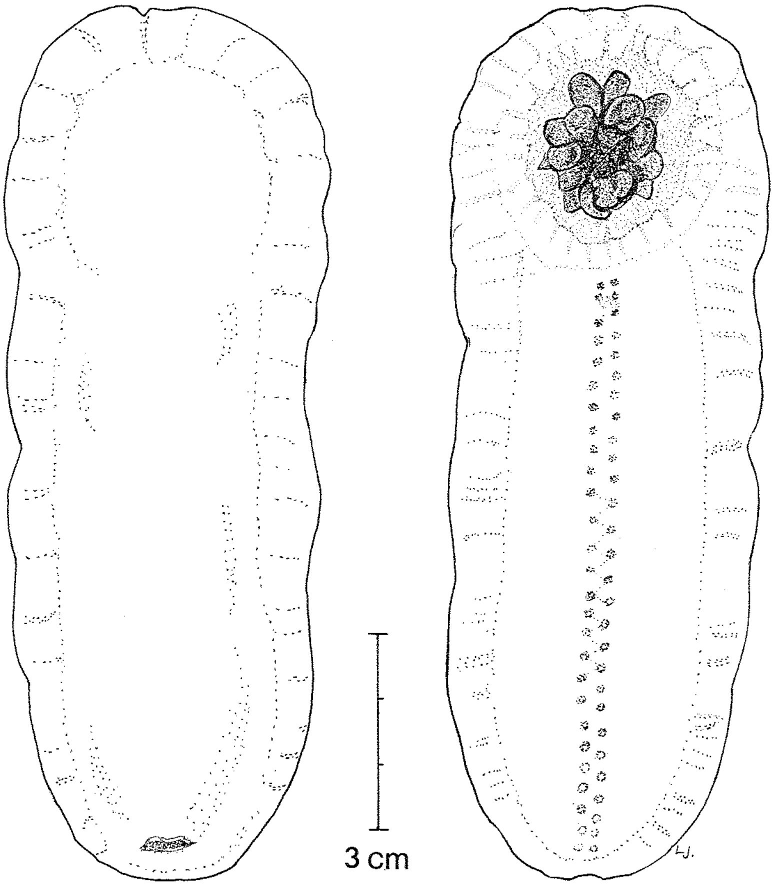


Fig. 34 *Benthodytes plana*. St. 186. The type specimen in dorsal and ventral view; the absence of dorsal papillae is possibly due to incomplete preservation of the dorsal skin. LJ.

served only in patches dorsally. No deposits were found in the ventrum.

St. 281. – The specimen is 13 cm long. Breadth of body, including the brim, 3.0–3.5 cm.

Skin soft and gelatinous as in the type specimen. A brown, superficial layer is preserved to some degree ventrally, and to a lesser degree dorsally. Tentacles brown.

Tentacles 15. Marginal processes are barely distinguishable on the discs, but otherwise the tentacles are similar to those of the type specimen. A few of the tentacles are slightly retracted.

Circum-oral papillae visible only here and there. They are partly fused at their base.

Brim similar to that of the type specimen, but owing to the body being more strongly vaulted, the transition between body and brim is less gradual than in the type specimen. The water-vascular canals of its tubefeet are difficult to distinguish, even from the ventral side, owing to the stronger pigmentation of the skin.

Dorsal papillae not distinguishable with certainty, due to the defective state of the dorsal skin.

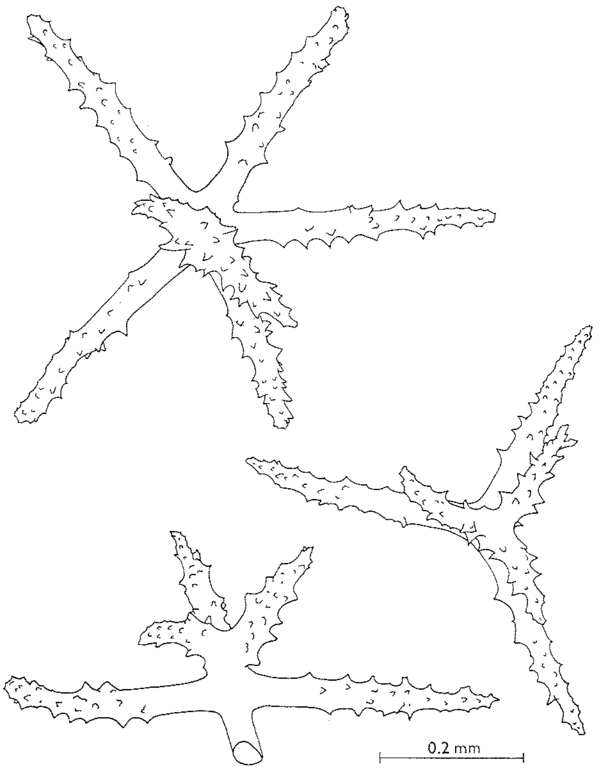


Fig. 35. *Benthodytes plana*. St. 186. Dorsal deposits from the type specimen.

Deposits resembling those of the type specimen, although the arms are more tapered. No deposits with abnormal arm numbers or with tripartite apophyses were present in the preparations.

Relationships: Probably closest related to *B. valdiviae* (q. v.).

Benthodytes superba Koehler & Vaney, 1905

Benthodytes superbus Koehler & Vaney, 1905, pp. 74–75, pls. VII: 1–2, XII: 11–12.

Diagnosis: Tubefeet of brim free in the greater part of their length. Dorsal papillae about 10 pairs, large, in single rows. Dorsal deposits large and very robust crosses with arm spines resembling short branches. Ventral deposits rod-shaped or tripartite.

Record: Arabian Bay, 2754 m. Two specimens.

Remarks: The species was considered most closely related to *B. hystrix* (here synonymized with *B. sibogae),* differing by the tubefeet of the brim being free in the greater part of their length and by the irregularly shaped and spinous dorsal crosses which apparently lack bipartite apophyses. Circum-oral papillae not mentioned.

Benthodytes typica Théel, 1882
Fig. 36, pls. I–II

Benthodytes typica Théel, 1882, pp. 103–104, pls. XXVII: 7, XXXV: 4, XXXVIII: 5, XLIV: 8; Théel 1886b, p. 2; von Marenzeller 1893a, p. 12; Grieg 1921, p. 10, fig. 8, pl. III: 6–7; Hérouard 1923, pp. 101–102, pl. VI: 4; Deichmann 1930, pp. 123–124; Deichmann 1940, p. 200, pl. XXXV: 1–2; Heding 1940, p. 368; Madsen 1953, pp. 160–161, fig. 8; Deichmann 1954, p. 384.

Benthodytes papillifera Théel, 1882, pp. 102–103, pl. XXXIV: 14.

Benthodytes glutinosa R. Perrier, 1896, pp. 902–903; R. Perrier 1902, pp. 462–465, pls. XIII: 5, XX: 31; Koehler & Vaney 1905, pp. 72–74, pl. XII: 10; Clark 1920, p. 141; Grieg 1921, pp. 10–11, pl. III: 1–2.

Benthodytes janthina von Marenzeller, Hérouard 1902, p. 30; Hérouard 1923, p. 103.

Diagnosis: Tentacles 15–20; discs irregularly incised at the margin, and retractile into the stalks. Circum-oral papillae present. Brim well developed, the dark pigmented canals of the enclosed tubefeet often clearly visible both from the dorsal and ventral side. Dorsal papillae minute and few, placed in a single row along the anterior part of the dorsal radii. Skin soft and usually mucous. Deposits absent or rod-shaped.

Material:
St. 186, Cape Town–Durban (32°33'S, 32°01'E), 3620 m. – 4 specimens.
St. 190, off Durban (29°42'S, 33°19'E), 2720 m. – 2 specimens.
St. 192, off Durban (32°00'S, 32°41'E), 3430 and 3530 m (two hauls). – 5 specimens.
St. 217, Mozambique Channel (14°20'S, 45°09'E), 3390 m. – 24 specimens.
St. 281, Seychelles–Ceylon (3°38'N, 78°15'E), 3310 m. – 1 specimen.
St. 282, Seychelles–Ceylon (5°32'N, 78°41'E), 4040 m. – 1 specimen.
St. 299, Bay of Bengal (17°10'N, 84°30'E), 2820 m. – 26 specimens.
St. 314, Bay of Bengal (15°54'N, 90°17'E), 2600 m. – 1 specimen.
St. 575, Tasman Sea (40°11'S, 163°35'E), 3710 m. – 21 specimens.
St. 668, Kermadec Trench (36°23'S, 177°41'E), 2640 m. – 1 specimen.
St. 726, Gulf of Panama (5°49'N, 78°52'W), 3270–3670 m. – 1 specimen.
St. 758, Puerto Rico Trench (18°45'N, 66°27'W), 2840 m. – 3 specimens.

Description: The specimens here referred to *Benthodytes typica* show a considerable variation. In actual fact, there are such conspicuous differences between some of the specimens that only the presence of intermediary forms speaks against referring the specimens to more than one species. In order to illustrate the variation in the material the specimens are described separately for each station, beginning with stations comprising a large material.

Tasman Sea: St. 575. – The 21 specimens (Fig. 36) are 7–13 cm long; the breadth of the body (including the broad brim) is about one-fourth to one-third of the length.

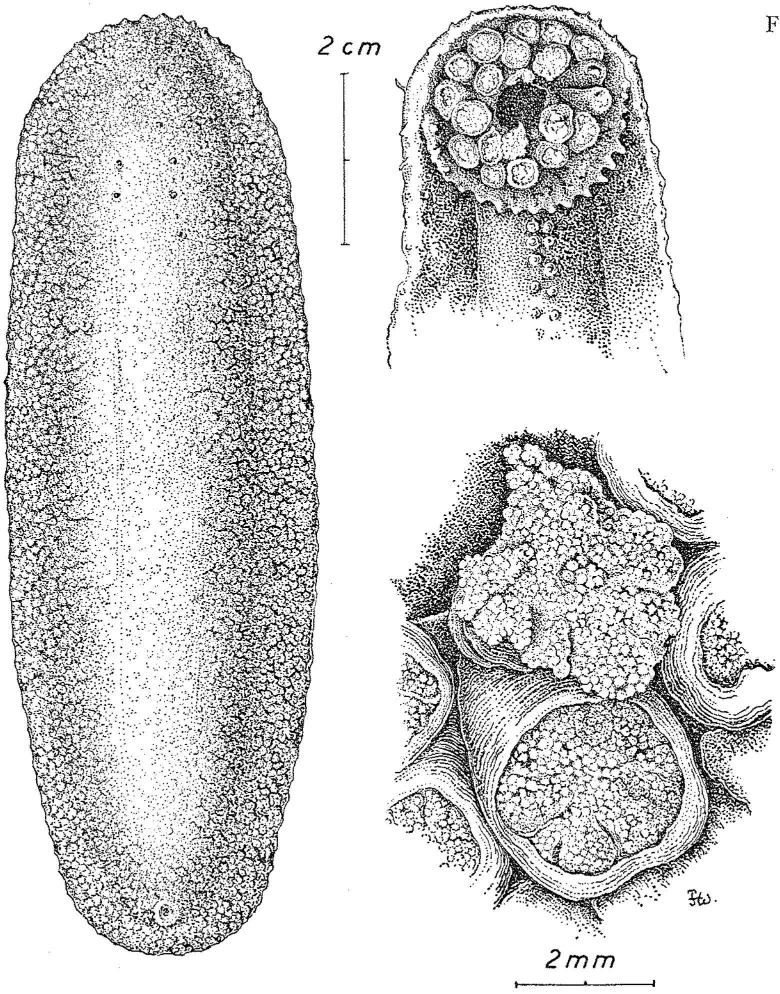


Fig. 36. *Benthodytes typica.* St. 575. PHW.

Dorsal skin covered with small, light violet knobs surrounded by dark interspaces; the dorsal skin has apparently been covered with a very fine, superficial, pigmented layer, only preserved in the grooves between the knobs. The knobs are most conspicuous laterally, and give the skin a mottled appearance.

Ventral skin uniformly dark violet, in strong contrast to the light coloured dorsal side.

Tentacles 17–20; discs covered with papillae and irregularly incised at the margin.

Circum-oral papillae present in all the specimens, although rarely as well developed as in the figured specimen. In some specimens most of the circum-oral papillae are retracted, only a few being visible posterior to the oral disc. A membrane originating from inside the circum-oral ring covers the tentacles wholly or partially in some of the specimens. In addition, each tentacle disc is retractile into its stalk.

Brim well developed. The margin of the brim is usually bent downwards. Although the brim is rather thin in most specimens, the tubefeet composing it are not visible from the dorsal side. Ventrally, the dark water-vascular canals of the tubefeet are clearly seen after removal of the superficial, strongly pigmented layer of the skin.

Dorsal papillae minute, placed along the anterior part of the radii. A number of 3–4 pairs could be counted in nearly all the specimens.

Deposits consisting of scattered rods in ventrum, dorsum, and tentacles.

Bay of Bengal: Sts. 299 and 314. – The 26 specimens from St. 299 are 5.5–9.0 cm long, and in many respects similar to those from the Tasman Sea.

Dorsal skin mucous, light reddish violet, and transparent, the longitudinal muscles and the water-vascular canals of the brim being in most of the specimens clearly visible through the skin. Some specimens, however, have an opaque skin like those from the Tasman Sea. The dorsal knobs characteristic of the Tasman Sea specimens are vaguely indicated in a few specimens from St. 299. (The absence of knobs in most of the specimens might be due to preservation, the soft skin being liable to swell in the formalin). Small patches of a pigmented superficial layer are preserved in some of the specimens.

Ventral skin with a darkly pigmented, superficial layer (partially worn off in most of the specimens).

Tentacles 18–20, with discs similar to those of the specimens from the Tasman Sea; in some specimens the discs are retracted into the stalks.

Circum-oral papillae are seen in almost all the specimens. Tentacle crown in some of the specimens covered by an oral membrane.

Dorsal papillae minute; 3 pairs are usually present anteriorly, and in some specimens a few papillae are also present more posteriorly. However, in many specimens no papillae at all could be found.

The material from St. 299 comprises specimens which are indistinguishable from some of the Tasman Sea specimens (Pl. I: 3–4) as well as specimens belonging to the typical form of the species, characterized by the mucous and transparent skin through which the dark violet tubefeet of the brim are clearly visible (Pl. I: 1–2). All intermediates are present between the two forms.

The specimen from St. 314 is more slender than any of the specimens from St. 299. The body is 1.2 cm broad and at least 8 cm long (the hind end of the body is missing). Tentacles 20, of the usual shape. One disc was partly retracted into the stalk. A transversal line of papillae is present posterior to the tentacle crown but it is uncertain whether they are part of a circum-oral ring. Three small and filiform papillae are present anteriorly along the left dorsal radius. Deposits not found.

Mozambique Channel: St. 217. – The 24 specimens are 6–12 cm long. They all belong to the typical form of the species, having a mucous, whitish, and transparent skin, through which the dark violet tubefeet of the brim are clearly visible.

Skin in most of the specimens more thick and mucous, and less pigmented than in the specimens from St. 299. In a few of the specimens the violet pigment is completely absent, even from the tentacles and the ventrolateral tubefeet. Remnants of a dark, superficial, ventral layer are present in some of the specimens, but in most specimens no trace of this layer is seen. The small knobs present on the skin in the specimens from St. 575, and feebly indicated in some of the specimens from St. 299, are absent from the specimens from St. 217, possibly because of the mucous state of the skin.

Tentacles 15–20, and similar to those from Sts. 575 and 299. A few tentacles have the discs partly retracted into the stalks, and in one specimen the tentacles are concealed by an oral membrane similar to that found in several specimens from Sts. 575 and 299.

Circum-oral papillae visible in most of the specimens.

Dorsal papillae inconspicuous, few, and placed in a single row along the anterior part of each dorsal radius. However, in most of the specimens the papillae could not be detected at all, being, apparently, totally embedded in the thick and soft skin.

The two specimens illustrated (Pl. II: 1–4) indicate the variation at the station. As at St. 299, all intermediates are present between the two forms.

Southwestern Indian Ocean: Sts. 186, 190, 192. – The 11 specimens taken are 5.5–8.5 cm long and resemble those from St. 217.

Dorsal skin mucous and whitish.

Ventral skin in some specimens partially covered with a dark violet layer, of which, however, only a few patches usually remain. The degree of pigmentation in the superficial layer varies; in two specimens the pigmentation is almost absent from both the skin and the radial papillae. In this respect the specimens show the same variation as those from St. 217.

Tentacles 16–20, of the usual type in the species. Some of the tentacles were partly retracted into their stalks.

Circum-oral papillae visible in two specimens from St. 192. In none of the specimens was the tentacle crown covered by an oral membrane.

Dorsal papillae visible only in one of the specimens from St. 186; this specimen has three minute, anterior papillae on the right side, and one on the left.

Deposits scattered rods.

Northern Indian Ocean: Sts. 281 and 282. – The specimen from St. 281 is 2 cm broad and 9 cm long (posterior end of body missing).

Tentacles concealed by an oral membrane covering the area between the circum-oral ring of papillae and the mouth.

Circum-oral papillae fused into a brim.

Skin whitish, but partially covered with a superficial, violet layer.

Dorsal papillae 6–7 pairs, minute, radial, and confined to the anterior third of the dorsum.

Brim with sturdy and strongly pigmented canals, which are very conspicuous from the ventral side.

Deposits scattered rods.

The specimen from St. 282 is 1.5 cm broad and 15 cm long (the posterior end is missing). The external layer of the skin is whitish and mucous. Head dark violet. Tentacles 20, of the usual shape in the species. One disc was partly retracted into the stalk. A few papillae are present posterior to the tentacle crown. It could not be made out whether they form part of a circum-oral ring. Deposits not found.

Kermadec Trench: St. 668. – The specimen is 5 cm long and 1.2 cm broad, including the brim.

Skin light violet and transparent, with remnants of a dark violet superficial layer on the ventral side.

Tentacles probably 17, most of them partly retracted into their stalks. A number of papillae are present posterior to and somewhat lateral to the tentacle crown, but they could not be followed round the whole of the crown.

Brim with the dark canals clearly visible from both the dorsal and the ventral side.

Dorsal papillae. Three slender papillae visible anteriorly.

Deposits rod-shaped, present in the dorsal and ventral skin, and in the tentacles.

Gulf of Panama: St. 726. – The specimen is 5 cm long and 1 cm broad, including the lateral brim.

Dorsal skin light violet, mucous, and transparent, with the longitudinal muscles visible through it.

Ventral skin less transparent. Only traces of a superficial, dark layer preserved.

Tentacles probably 16, of the usual type in the species. None of the tentacles are retracted into their stalks. A number of papillae are present posterior to and lateral to the tentacle crown, probably forming part of a circum-oral ring.

Brim with the dark tubefeet clearly visible from both the dorsal and the ventral side.

Dorsal papillae small and radial; four pairs are seen on the anterior part of the dorsum.

Deposits rod-shaped, scattered in the dorsal and ventral skin, and abundant in the tentacle stalks.

Puerto Rico Trench: St. 758. – The three specimens are 1 cm broad and 3.5–7.0 cm long (the hind end is missing in all the specimens). Tentacles 20 in all the specimens, of the usual shape. Papillae visible behind tentacle crown in two of the specimens. It could not be seen whether they form part of a circum-oral ring. Two short and filiform dorsal papillae present anteriorly. Deposits rod-shaped, of scattered occurrence in the dorsal and ventral skin, and more numerous in the tentacles.

Synonymy:

Benthodytes papillifera Théel is known from three Pacific *Challenger* stations. Specimens from each of the stations were re-examined.

Challenger St. 300, near Juan Fernandez (33° 42'S, 78°18'W). Three of the five specimens taken (two in BM and one in ZMUC) were re-examined. The two specimens in BM in external appearance resembled the specimens from *Galathea* St. 575; the dark violet ventral side was clearly delimited from the light coloured dorsal side, and the lateral parts of the dorsum were (especially in one of the specimens) covered with numerous small, conical knobs. The margin of the brim was bent downwards. In the ZMUC specimen, on the other hand, the dorsum is smooth all over. The body is flattened; the ventral side in this specimen also is dark violet, whereas the dorsal side is whitish. The name *"papillifera"* referred to the dorsal knobs. Théel did not find the true radial papillae (called "processes"), but a few papillae were actually present in all the re-examined specimens.

A number of 20 tentacles were present, according to Théel (this number was even used in the key to the species). However, the re-examined specimen in ZMUC has only 18 tentacles. The tentacles are similar to those in the illustrated specimen from *Galathea* St. 575, and in all three specimens some are partly retracted into their stalks. Théel found a transversal row of papillae behind the tentacle crown. The specimen in ZMUC has a complete ring of papillae.

Challenger St. 184 (Coral Sea). The four specimens were, according to Théel, "in such an incomplete state as to render examination impossible". Two of the specimens were re-examined. One agreed in external appearance with the usual form of *Benthodytes typica,* except for the presence of numerous small, conical knobs all over the dorsum, each knob containing a calcareous rod. Ventrum light violet; the midventral radius dark violet. Tentacles similar to those portrayed in the specimens from *Galathea* St. 575. It could not be made out whether the tentacles were retractile, or whether a circum-oral ring of papillae was present.

The other re-examined specimen from the same station was slender and elongated. It was too poorly preserved to be determined to species.

Challenger St. 271 (Central Pacific near the Equator). Of the four specimens, one (in BM) was re-examined; like those from St. 300, it resembled the specimens from *Galathea* St. 575. Both dorsum and ventrum were light violet. Dorsum covered with conical knobs. Tentacles of the usual shape, but it could not be established whether they were retractile. Papillae present posterior to the tentacle crown.

Benthodytes janthina von Marenzeller, Hérouard 1902 and 1923. The material described by Hérouard came from the North Atlantic Monaco Sts. 443, 673 and 2111. Re-examination was made of 15 specimens from St. 443 (one in ZMUC, one in MCZ, one in MNHN, and 12 in MOM), 3 specimens from St. 673 (all in MOM), and one from St. 2111 (in MOM). The specimens were found to resemble *B. typica.* Ventrum dark violet, dorsum light violet and mucous. Tentacles 17–20. Discs of the usual type in *B. typica;* in the specimen in ZMUC most of the discs are partly or completely retracted into their stalks, and remnants of a circum-oral ring of papillae are present. Dorsal papillae few and minute. The specimen in ZMUC has 7 pairs of small (1–2 mm long) papillae, distributed all along the dorsal radii. Deposits, very scattered rods.

The specimens are very different from the type specimen of *B. janthina;* this specimen was uniformly dark violet and had four pairs of large dorsal papillae (and, in addition, a number of small ones). Although the deposits were so incompletely preserved that *B. janthina* is disregarded in the present survey of the species of *Benthodytes,* it could be seen that the deposits were cross-shaped.

Variation: *Benthodytes typica* shows a considerable variation in the proportions of the body, the development of the brim, and in the degree of skin pigmentation. Most of this variation seems to be individual, as indicated by the variation found in specimens from St. 299 in the Bay of Bengal.

The specimens most unlike the usual type are those from St. 575 in the Tasman Sea, characterized by the presence of knobs on the dorsal side, by the strongly pigmented ventral side, and the opaque skin, which almost completely conceals the enclosed tubefeet. The fact that these features are found also in the *Challenger* specimens of *B. papillifera* (here synonymized with *B. typica)* suggests the presence of a geographic variation in the species (the *Challenger* specimens came from the southern and central Pacific). On the other hand, specimens which are indistinguishable from some of the Tasman Sea specimens occurred as individual variants at St. 299 in the Bay of Bengal.

Relationships: A relationship to *B. sanguinolenta* is indicated by the reduced state of the deposits, the small size of the dorsal papillae, and the tentacle number exceeding 15. *B. sanguinolenta* differs from *B. typica* by the high number of dorsal papillae which are arranged in two bands, by having post-oral instead of circum-oral papillae, and by the constant number of 18 tentacles.

Biology: Grieg (1921) recorded a 13 cm long pelagic specimen caught in the eastern North Atlantic about 1400 m below surface and at least 1600 m above the bottom.

Distribution: Cosmopolitan, 1873–4700 m. According to Deichmann (1954) it ascends to remarkably shallow depths in the western part of the North Atlantic, being distributed "in the West Indies, common in the Gulf of Mexico, along the Lesser Antilles and also known from off the coast of New England, from 172–766 fathoms" (315–1401 m).

Type locality: *Challenger* St. V (35°47'N, 8°23' W). All the *Challenger* specimens came from this station, but no type specimen was selected.

Benthodytes sanguinolenta Théel, 1882
Pls. III–VI, IX: 6–7, XII: 4–5

Benthodytes sanguinolenta Théel, 1882, pp. 104–105, pls. XXIII, XL: 4–5, XLII: 6; Ludwig 1894, pp. 53–60, pl. I: 1–8; Koehler & Vaney 1905, p. 72; Clark 1913, p. 233; Ohshima 1915, p. 245; Ohshima 1916–1919, with one figure; Clark 1920, p. 142; Clark 1923a, p. 162; Clark 1923b, p. 420; Heding 1940, p. 367; Hansen 1956, pp. 44–45.

Non *Benthodytes sanguinolenta* var. *marginata* Théel, 1882.

Diagnosis: Body elongated and flattened. Tentacles 18, retractile into pockets of the skin; discs with papillae in radial fields which continue into c. 12–14 marginal knobs or processes of varying length. Post-oral papillae present. Oral membrane absent. Brim well developed. Dorsal papillae minute and numerous, scattered in position or forming two longitudinal bands. Deposits rod-shaped, or absent.

Material:

St. 495, Banda Trench (5°26'S, 130°58'E), 7250–7290 m. – 5 specimens.

St. 497, Banda Trench (5°18'S, 131°18'E), 6490–6650 m. – 3 specimens.

St. 607, Tasman Sea (44°18'S, 166°46'E), 3580 m. – 2 specimens.

St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 1 specimen.

St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – 1 specimen.

Description:

Several authors have recorded this species; however, only Théel and Ludwig accompanied their records with detailed descriptions, including illustrations of taxonomic features. The two descriptions differ in a number of points, suggesting that the name *Benthodytes sanguinolenta* embraces more than one species.

Differences of the same magnitude are shown by the specimens taken by the *Galathea*. However, the presence of specimens which combine the features of Théel's and Ludwig's specimens makes it inadvisable at present to erect new species on specimens which are within the variation of *B. sanguinolenta*, as hitherto defined. Increased knowledge may show that the specimens belong to different species, or to different geographic forms of one species.

St. 607 (Pl. III: 1–2). – The two specimens are 20 and 16 cm long, respectively. Body flattened, 2.5–3.5 cm broad (varying with the degree of contraction of the lateral brim), the posterior end somewhat tapering. Colour light violet; the larger specimen is dark violet in the ventral midline and on the underside of the head.

Tentacles (Pl. IX: 6) 18 in both specimens; discs with papillae on the surface and about 12–14 retractile processes on the margin. Each tentacle is completely retractile into a pocket of the skin.

Post-oral papillae clearly visible in the 16 cm long specimen (Pl. III: 2). Their canals are seen as radial elevations of the skin while their free parts form low conical knobs. The papillae do not form part of a circum-oral ring. There is no indication of an oral membrane.

Ventrolateral tubefeet enclosed in the broad brim, with only the tips emerging from the edge. Their water-vascular canals are only indistinctly seen, except by transmitted light.

Dorsal papillae minute and almost completely embedded in the skin, although their dark colour makes them clearly visible. They are mainly arranged in two radial bands, although a few are present in the dorsal interradius.

Deposits apparently absent from dorsal and ventral skin. A few rods are present in the midventral tubefeet and in the tentacle discs.

St. 663 (Pl. V: 3–4). – The specimen is 15 cm long. Owing to contraction of the brim, the body is only 1.5 cm broad. Colour light violet all over.

Tentacles 18. Discs resembling those of the specimens from St. 607, but none are retracted.

Post-oral papillae forming about one-third of a circle, close to the tentacle crown. An oral membrane not indicated.

Ventrolateral tubefeet only slightly emerging from the sides of the body; around the anterior and posterior ends of the body the tubefeet form a brim resembling that of *B. typica,* with the canals clearly visible through the skin.

Dorsal papillae minute, dark violet, and almost completely embedded in the light coloured skin. The papillae are arranged in two longitudinal bands, here and there forming an irregular line.

St. 716 (Pl. III: 3–4). – The specimen is 20 cm long and 2.5–3.0 cm broad (including the brim), with a tapering posterior end. Colour light violet, the head dark violet. The specimen very much resembles that illustrated by Ludwig (1894, pl. I: 1–2).

Tentacles 17 (or 18), unretracted; discs resembling those of the above-mentioned specimens, although the margin is more deeply incised between the processes.

Post-oral papillae forming a dark violet fringe along the posterior third of the tentacle crown. Oral membrane not present.

Brim broad, with the dark pigmented canals clearly visible from the ventral side. The margin of the brim is thin as paper, dark violet, and with a frayed edge. The thin margin is almost totally worn off along the side of the body. The brim is well preserved round the anterior end of the body. The long canals for the tubefeet of the anterior part of the brim are conspicuous on the dorsal side of the head.

Dorsal papillae similar to those of the above-mentioned specimens.

Deposits not preserved.

St. 495. – Five specimens from this station and three specimens from St. 497 were described previously (Hansen 1956). A few supplementary remarks are given below.

The 21 cm long specimen (Pl. IV: 1–2) has features in common both with the specimens from St. 607 and the specimen from St. 716. The canals of the ventrolateral tubefeet are clearly visible from the ventral side of the brim, but less clearly from the dorsal side. The tips of the tubefeet project a little from the edge of the brim. The brim round the head is intermediate in shape between that of the specimens from the Tasman Sea and that from St. 716. The tentacles (Pl. IX: 7) are deeply incised at the margin. A few tentacles are retracted into pockets of the skin – a similarity to the specimens from the Tasman Sea. Post-oral papillae present, similar in appearance to those of the specimen from St. 716.

The four 7–8 cm long specimens (Pl. IV: 3–4) have almost completely lost the gelatinous, external layer of the skin, except on the rather well preserved head. This is light violet as the rest of the body, and the papillae which form the marginal brim of the head are visible also from the dorsal side. The tentacles are partially embedded in the soft gelatinous layer of the skin, but none are retracted into pockets of the skin. The discs of some of the tentacles are as deeply incised as those of the large specimen. Post-oral papillae not preserved.

St. 497. – One, 15 cm long, specimen is complete (Pl. V: 1–2) while two specimens have lost the hind end of the body. The outer gelatinous layer of the skin is to a large degree torn off, which explains the more fringed appearance of the anterior margin.

Re-examined specimens:

All *Challenger* specimens were re-examined. Théel mentioned three specimens from St. 298 and one from St. 295, both stations situated off the coast of Chile. However, four specimens were, in actual fact, found to originate from St. 298 (two in BM, one in MNHN, and one in ZMUC; the specimen from St. 295 is in BM).

The specimens (Pl. VI: 1–2) agree with those from the Tasman Sea in the shape of the body and the brim (in the ZMUC specimen the brim is contracted round the head), and in the number and shape of the tentacles (one specimen has, however, only 17 tentacles). The tentacles, like those of the Tasman Sea specimens, form a regular circle round the mouth, and several of them are retracted into pockets of the skin.

The specimens of *B. sanguinolenta* var. *marginata* Théel possessed traces of cross-shaped deposits and should, therefore, not be included in the synonymy of *B. sanguinolenta.* Due to insufficient preservation of the deposits, the specimens are unidentifiable.

One specimen from *Albatross* St. 3400 (Gulf of Panama), belonging to the material described by Ludwig (1894), is kept in ZMUC. It is 10 cm long and less than 1 cm broad. The skin is almost totally worn off down to the muscular coat, and the brim is represented only by the slender and freely pendent ambulacral canals of some of the tubefeet. Only around the head are the papillae long and fused into a broad brim. Tentacles 18, unretracted, with long and slender stalks and deeply and irregularly incised discs.

Four other eastern Pacific specimens from the material described by Clark (1913, 1920) were re-examined (all in MCZ). They were 6–19 cm long and as slender as the specimen in ZMUC.

No additional information could be gained from them.

The specimen taken by the *Valdivia* at a depth of 768 m west of Sumatra was, according to Heding (1940), too poorly preserved to permit a closer examination, although it was regarded as a typical representative of the species. Re-examination of the specimen (Pl. VI: 3–4), at present in ZMUC, revealed the following features: Tentacles 18, unretracted, with only slightly incised discs. Post-oral papillae forming a conspicuous brim posterior to the tentacle crown; they do not form part of a circum-oral ring. A few minute dorsal papillae preserved; probably, the papillae were arranged in bands. Remnants of a dark violet brim present here and there on the body side. Brim complete round the head.

Relationships: See *Benthodytes typica.*

Distribution: Distributed throughout almost the whole of the Indo-Pacific region. Depths 768–7250 m. Most records are deeper than 2000 m, although it has been recorded from bathyal depths in several regions: Japan (805–1187 m), Bay of Bengal (1223–1353 m), west of Sumatra (768 m), and South Africa (1372 m).

Benthodytes spp.

Three specimens are too damaged to be identified to species.

St. 474. One specimen, 16 cm long and 5 cm broad. The external features are well preserved and indicate a relationship to *B. lingua.* The deposit-containing layer of the skin is almost entirely worn off, leaving only some fragments of crosses.

St. 664. One specimen, 27 cm long and 5 cm broad, and uniformly dark violet. Tentacles 12. Marginal brim composed of rather few and large tubefeet. Dorsal papillae and midventral tubefeet rudimentary. Deposits absent (probably dissolved).

St. 665. One specimen, 12 cm long and 2 cm broad. Colour light violet, with remnants of a brown superficial skin layer both dorsally and ventrally. Tentacles 15. Marginal brim preserved only round the head. Skin soft. Papillae not preserved. Deposits, preserved only in patches, dorsally crosses with bipartite apophyses; ventrally absent.

Genus ***Psycheotrephes*** Théel, 1882

Fig. 118

Théel 1882, p. 92. – Type species: *Psycheotrephes exigua* Théel, 1882, by monotypy.

Diagnosis: Anus ventral. Unpaired dorsal appendage absent. Circum-oral papillae absent. Tentacle discs of a fixed shape, rounded in outline and with marginal knobs.

Remarks: *Psycheotrephes* seems to be more closely related to *Psychropotes* than to *Benthodytes,* as indicated by the ventral anus, the absence of circum-oral papillae, and the number (16–18) and shape of the tentacles. (The 10 tentacles in *Psycheotrephes exigua* may be a juvenile feature). The large size of the posterior pair of papillae in *Psycheotrephes recta* also suggests a relationship to *Psychropotes.*

Key to the species of *Psycheotrephes*

1.	Posterior pair of dorsal papillae large	*recta*	(p. 99)
1.	Dorsal papillae, all minute	2	
2.	Tentacles 10	*exigua*	(p. 96)
2.	Tentacles 16–18	*magna*	(p. 97)

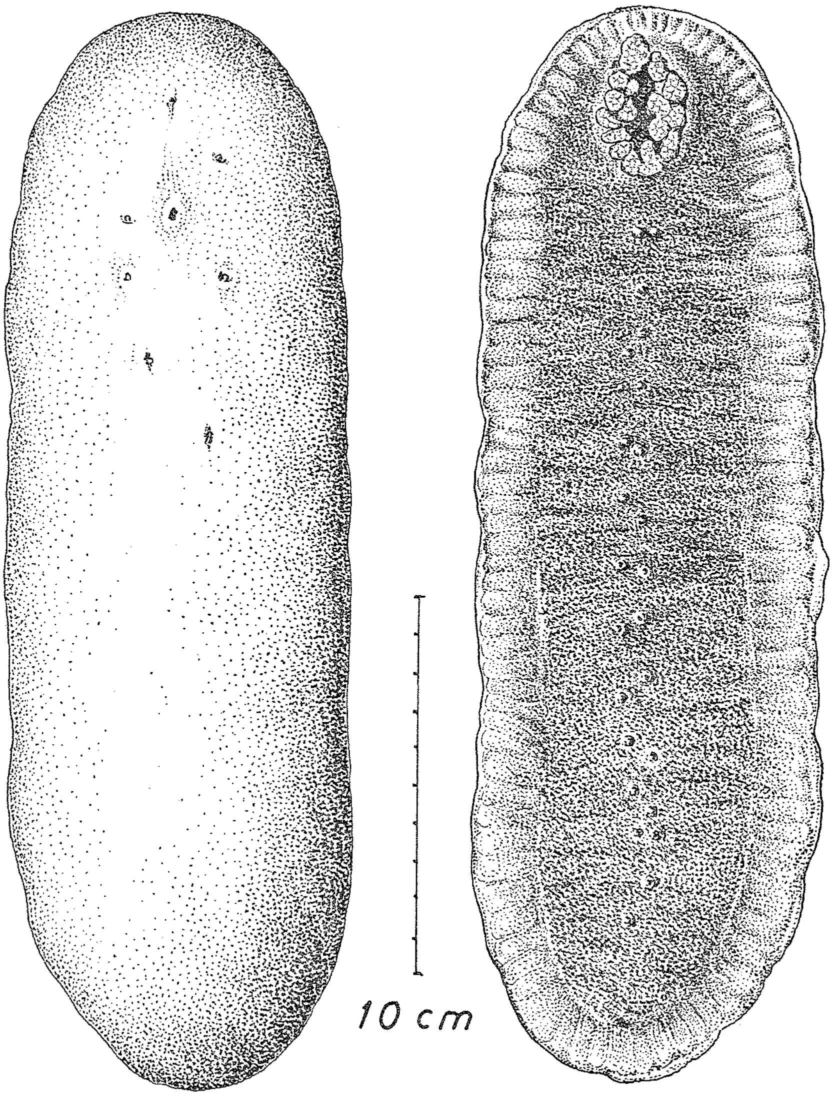
Psycheotrephes exigua Théel, 1882

Théel 1882, pp. 92–93, pls. VIII: 8, XXXV: 12, XLIV: 1.

One specimen, 2.5 cm long, taken by the *Challenger* at a depth of 5029 m in the Central Pacific (7°25'S, 152°15'W).

The species may represent a juvenile stage of *P. magna.*

Fig. 37. *Psycheotrephes magna.* St. 234. The type specimen in dorsal and ventral view. PHW.



Psycheotrephes magna n. sp.
Figs. 37–38, pl. XII: 6

Diagnosis: Tentacles 16–18. Dorsal papillae 2–3 pairs, all small and placed anteriorly. Deposits cross-shaped, the dorsal ones with the distal part of the arms curved upwards.

Material:

St. 234, Madagascar–Mombasa (5°25'S, 47°09'E), 4820 m. – 4 specimens.

St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 3 specimens.

Description:

St. 234. – Type specimen (Fig. 37) 28 cm long and 9 cm broad.

Dorsal skin light violet, soft, gelatinous, and perfectly smooth, without wrinkles, knobs, or other irregularities.

Ventral skin dark violet, rather firm, and slightly wrinkled. The dorsal skin is 7–8 mm thick, the ventral skin only half this thickness. (This difference in thickness is not shown by all the specimens).

Tentacles 16; discs firm and vaulted, with c. 20 marginal knobs. The tentacles are probably unretractile.

Brim surrounding the entire body, but only visible from the ventral side. It is 1.5–2.0 cm broad, decreasing to 0.5 cm on the anterior margin of the head. The presence of water-vascular canals in the brim is indicated by furrows in the ventral skin.

Midventral tubefeet extremely small and completely retracted, their presence indicated by a double row of minute pits from mouth to anus.

Dorsal papillae completely retracted; when extended they are scarcely more than a few

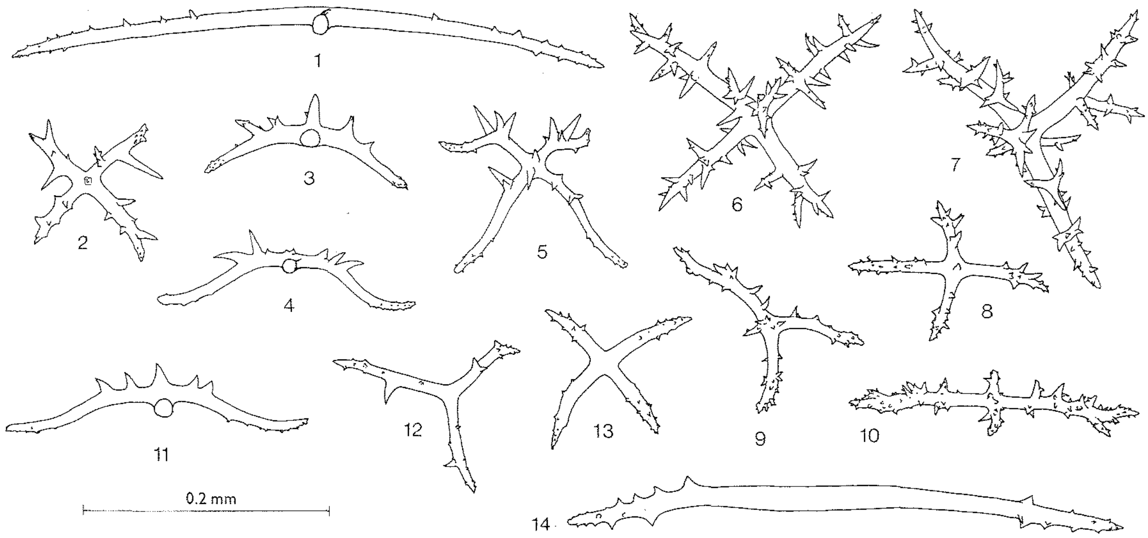


Fig. 38. *Psycheotrephes magna.* Deposits. 1–3, St. 234, dorsal crosses from an 11 cm long specimen; 4–10, deposits from the type specimen, 28 cm long (4–5, anterior part of dorsum; 6–7, posterior part of dorsum 8, ventrum; 9–10, muscles); 11–14, St. 663 (11, dorsum; 12–14, ventrum).

millimeter long. The papillae are all placed anteriorly; two are visible on each side.

Deposits (Fig. 38: 4–10). The dorsal deposits (4–5) have curved arms, which are downwardly bent proximally and horizontal in the distal part. The arms bear oblique or vertical spines which are irregularly arranged. Larger and strongly spinous deposits (6–7) are present in the posterior part of the dorsum. While the former type of deposits was also found in other specimens, the latter type is peculiar to the type specimen. The ventral deposits (8) have usually less curved arms and smaller spines than the dorsal ones; they are occasionally tripartite. The muscles contain spinous tripartite and rod-shaped deposits (9–10).

The other three specimens from St. 234 are 10, 11, and 13 cm long. They are similar in appearance to the type specimen, except that one of the specimens is strongly vaulted and has a narrow brim due to body contraction.

Dorsal skin light violet, soft, and perfectly smooth.

Ventral skin more firm, and dark violet.

Tentacles 17 in two of the specimens, and 16 in the third specimen.

Midventral tubefeet could not be detected in the middle part of the body in two of the specimens.

Dorsal papillae not visible.

Deposits (Fig. 38: 1–3) with rather straight arms occur in the dorsum of one of the specimens, scattered between the usual type with curved arms. Most of them are of the usual size in the species, with arms 0.1 mm long but a few deposits are more than twice as large.

St. 663. – The specimens are 30, 11, and 6 cm long. They resemble the type specimen, although the smallest specimen is remarkable for its rather thin brim, in which the pigmented canals for the papillae are visible both from the dorsal and ventral side.

The largest specimen has 18 tentacles, which are similar in shape to those of the specimens from St. 234. One right and two left dorsal papillae are present, all placed anteriorly. In the two other specimens the tentacles cannot be counted and no dorsal papillae are visible.

Deposits (Fig. 38: 11) similar to the usual type at St. 234. One specimen has large rods (14) in the ventrum in addition to the usual cross-shaped (13) and tripartite (12) deposits.

Slender crosses are present in the ovaries, and spinous rods, tripartite deposits, and rudimentary crosses in the muscles.

Relationships: The species is possibly identical with *Psycheotrephes exigua.* The presence of only ten tentacles in the latter species might be a juvenile feature, the single specimen known being only 2.5 cm long. The supposed absence of midventral tubefeet in *P. exigua* can hardly be considered taxonomically significant, as in two of the specimens of *P. magna* they could not be followed along the entire midventral radius.

Psycheotrephes recta (Vaney, 1908)

Benthodytes recta Vaney, 1908, pp. 417–418, pls. II: 23, III: 37–38.

Diagnosis: Tentacles 16. Dorsal papillae consisting of about three pairs of small, anterior papillae and one pair of large posterior ones. Deposits cross-shaped with unequally reduced arms.

Records: Antarctic, 4572 m. Three specimens.

Remarks: The species is here referred to *Psycheotrephes* because the anus, according to Vaney, is "plûtot ventral que terminal". Likewise, the presence of 16 tentacles suggests that the species does not belong to the genus *Benthodytes,* in which this tentacle number does not occur (apart from *B. typica* where the number is 15–20).

The species is characterized by the large-sized posterior pair of dorsal papillae and the irregularly shaped deposits.

Genus ***Psychropotes*** Théel, 1882
Figs. 117–118

Psychropotes Théel, 1882, p. 96. – Type species, designated by Deichmann (1930): *Psychropotes longicauda* Théel, 1882.
Euphronides Théel, 1882, p. 93.
Triconus Hérouard, 1909, pp. 1–5.
Nectothuria Belyaev & Vinogradov, 1969, p. 711.

Diagnosis: Anus ventral. Unpaired dorsal appendage present. Circum-oral papillae absent. Tentacle discs of a fixed shape, rounded in outline and with marginal knobs.

Remarks: The genera *Euphronides* and *Psychropotes* were distinguished by the position and size of the unpaired, dorsal appendage. In *Euphronides* the appendage was low and placed at a considerable distance from the posterior end of the body, whereas in *Psychropotes* it was long and placed close to the posterior end. However, *P. semperiana* and *P. belyaevi* combine the features of the two genera, having a long appendage placed far from the posterior end of the body.

The genus *Nectothuria* was erected for the species *N. translucida,* which is here regarded as a synonym of *Psychropotes longicauda.*

Key to the species of *Psychropotes*

1.	Dorsal appendage placed close to posterior end of body	2	
1.	Dorsal appendage placed at least $^{1}/_{5}$ body length from posterior end of body	3	
2.	Tentacles 10–12	*loveni*	(p. 126)
2.	Tentacles 18	*longicauda*	(p. 115)
3.	Dorsal skin covered with warts, each containing a giant cross	4	
3.	Dorsal skin smooth	5	
4.	Dorsal appendage short	*verrucosa*	(p. 112)
4.	Dorsal appendage very long	*mirabilis*	(p. 111)
5.	Dorsal appendage at the most $^{1}/_{6}$ length of the body	6	
5.	Dorsal appendage at least $^{1}/_{3}$ length of the body	7	
6.	Tentacles 18	*depressa*	(p. 106)
6.	Tentacles 16	*scotiae*	(p. 111)
7.	Brim broad. Dorsal appendage $^{1}/_{3}$–$^{1}/_{2}$ length of the body, usually bipartite. Arm spines of deposits usually arranged in rings	*belyaevi*	(p. 100)
7.	Brim narrow. Dorsal appendage $^{1}/_{3}$–$^{1}/_{1}$ length of the body, placed on the most elevated part of the body. Arm spines of deposits not arranged in rings	8	

8. Deposits belonging to two types, one with spines throughout arm length, the other with a smooth, proximal arm part and a high, central apophysis ending in three or four downwardly bent hooks .... *semperiana* (p. 102)
8. Deposits belonging to one type only, being small, slender crosses with a low, central apophysis .... *minuta* (p. 106)

Psychropotes belyaevi n. sp.

Figs. 39–40, pls. XII: 9, XIV: 3–5

Diagnosis: Tentacles 16. Brim broad and flattened. Dorsal papillae minute. Unpaired dorsal appendage gelatinous, measuring about $^1/_3$–$^1/_2$ body length, usually bipartite almost from the base, and placed $^1/_4$–$^1/_3$ body length from posterior end of body. Dorsal and ventral deposits robust crosses with the spines usually placed in pairs or rings down the arms; central apophysis rudimentary or absent, except on the scattered larger crosses of the deeper layer.

Material:
St. 231, Madagascar–Mombasa (8°52'S, 49°25'E), 5020 m. – 2 specimens.
St. 235, Madagascar–Mombasa (4°47'S, 46°19'E), 4930 m. – 1 specimen.
St. 234, Madagascar–Mombasa (5°25'S, 47°09'E), 4820 m. – 3 specimens.
St. 235, Madagascar–Mombasa (4°47'S, 46°19'E), 4810 m. – 19 specimens.

Description: One specimen is 5.5 cm long, the others 11–19 cm (Fig. 39). The type specimen, from St. 235, is 18 cm long.

Skin. The small specimen has a soft and light violet skin both dorsally and ventrally, and the inner organs also are only feebly pigmented. The other specimens are dark violet (darkest on the ventrum), and the inner organs are strongly pigmented.

Tentacles 16 (one 15 cm long specimen has only 14 tentacles).

Brim flattened and 1–2 cm broad in the larger specimens. In the small specimen the brim resembles that of *Benthodytes typica.* The brim is somewhat contractile, but never completely retracted into the body. The species has a flattened appearance owing to the broad brim, but the body proper is semicircular in cross-section.

Midventral tubefeet small and conical, present throughout whole length of ventral sole.

Dorsal papillae up to 3 pairs, the posterior pair largest. In a 16 cm long specimen with especially well-developed papillae those of the hindmost pair are 5 mm long, whereas those of the two anterior pairs measure 2 mm. In the

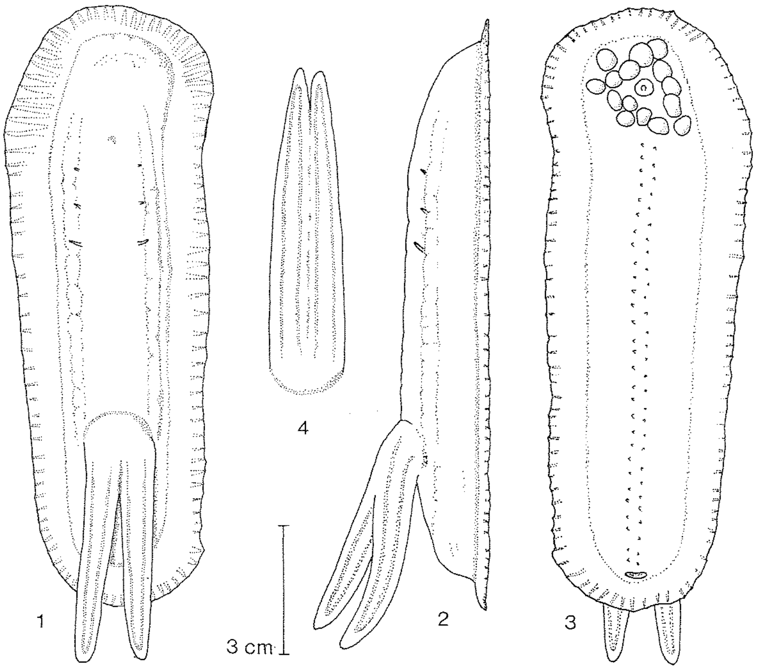


Fig. 39. *Psychropotes belyaevi.* St. 234. 1–3, a specimen in dorsal, lateral and ventral view; 4, an almost undivided dorsal appendage from another specimen.

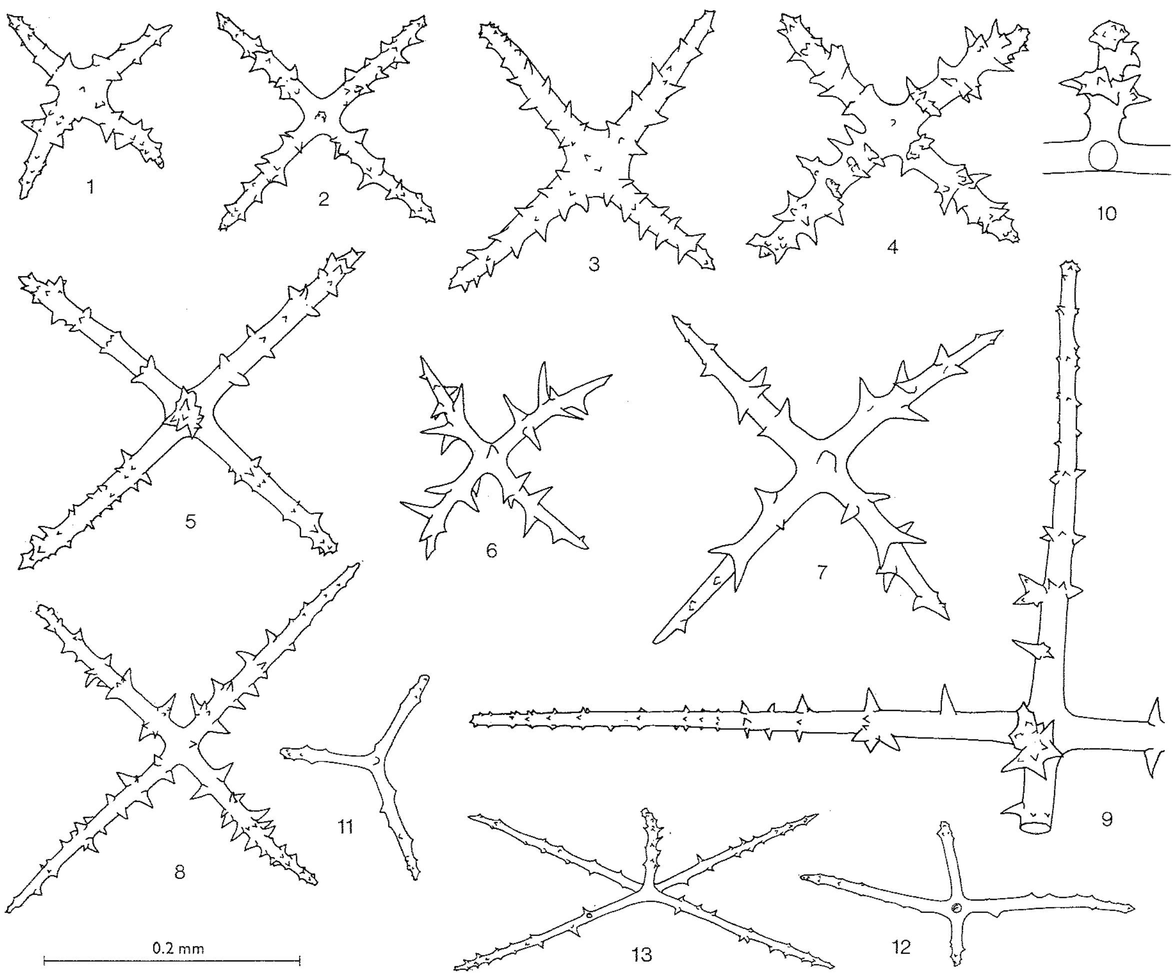


Fig. 40. *Psychropotes belyaevi.* Deposits. 1–4, dorsal crosses from outer layer (1–2, St. 231; 3, St. 234; 4, St. 232); 5, dorsal cross from deeper layer (St. 234); 6–7, crosses from unpaired appendage (St. 234); 8, ventral cross from outer layer (St. 234); 9–10, ventral cross from deeper layer (St. 234); 11–13, peritoneum (11–12, St. 231; 13, St. 232).

small specimen the papillae of the posterior pair measure 4 mm, while anterior to this pair only one pair of 1 mm long papillae is seen.

Unpaired, dorsal appendage very soft and gelatinous, and fully preserved in only a few specimens. It measures $^{1}/_{3}$ to almost $^{1}/_{2}$ body length; it is usually bipartite almost from the base, although in some specimens the two halves are almost completely fused. A broad and darkly pigmented water-vascular canal is clearly visible in each half of the appendage. The appendage is placed $^{1}/_{4}$ to $^{1}/_{3}$ body length from the posterior end of the body.

Deposits (Fig. 40). The dorsal crosses (1–4) are crowded, most of them very robust, with small spines usually placed in pairs or rings on the arms. This spine arrangement was found in all the specimens, and is apparently characteristic of the species. Crosses with larger and more irregularly placed spines (6–7) are present in the unpaired appendage in one specimen; however, in two other appendages examined the crosses belong to the usual type. The central apophysis is rudimentary or absent. The ventral crosses (8) are usually more slender than the dorsal ones, but otherwise of the same type.

Crosses possessing a central apophysis (5, 9–10) occur scatteredly beneath the outer layer of densely packed crosses. Both in dorsum and ventrum they may occasionally reach 0.4–0.5 mm in arm length.

Peritoneum, gonads, and muscles (11–13) with very slender cross-shaped and tripartite deposits, often with a high, central apophysis.

Tentacles with large, obliquely or longitudinally placed rods in the stalk; the tentacle discs possess large, radially placed rods, and small, curved rods round the bases of the papillae.

Relationships: *P. belyaevi* is well characterized by the gelatinous dorsal appendage which usually shows an incomplete fusion of its two papillae, by the broad brim, and the shape of the deposits. It does not appear particularly closely related to any of the other species. The combination of 16 tentacles and a dorsal appendage placed far from the posterior end of the body is also found in *P. verrucosa* and *P. semperiana.* In *P. verrucosa* the dorsal appendage may be bipartite to a large extent (as in the specimen described as *Euphronides bifurcata* Koehler & Vaney); however, the appendage is very short. Moreover, *P. verrucosa* is distinguished by the dorsal warts, which each contains a giant cross. In *P. semperiana* the appendage is long and undivided, the brim is narrow, and the deposits very different from those of *P. belyaevi.*

Remarks: The bivalve *Galatheavalva holothuriae* Knudsen, 1970, lives as a commensal in the oral cavity, anchored in the tissue by means of its byssus. The bivalve attains a length of 20 mm.

One specimen of *Galatheavalva* came from St. 234 and nine from St. 235. As most of the specimens were found loose in the vial, it is not known how many specimens can be present simultaneously in an oral cavity. All the Indian Ocean specimens of *P. belyaevi, P. longicauda, P. semperiana,* and *P. mirabilis* were searched for commensalistic bivalves by means of X-ray photography, but no additional specimens of bivalves were found.

The species is named after the Soviet deep-sea biologist and holothurian specialist, Dr. G. M. Belyaev.

Psychropotes semperiana Théel, 1882
Figs. 41–42

Psychropotes semperiana Théel, 1882, pp. 100–101, pl. XXXIV: 10–11.

Psychropotes kerhervei Hérouard, 1902, pp. 27–30, pl. IV: 1–9.

Euphronides kerhervei (Hérouard), Hérouard 1923, p. 104, pl. III: 4–5; Deichmann 1940, pp. 202–203, pl. XXXV: 9–12; Madsen 1953, pp. 161–163, fig. 9.

Benthodytes kerhervei (Hérouard), Deichmann 1930, pp. 125–126.

Euphronides anchora Hérouard, 1912, pp. 6–7, fig. 5; Hérouard 1923, p. 103, pls. I: 22–30, VI: 3.

"Holothurid" from *Challenger* St. 89, Théel 1886a, p. 244, pl. X: 12.

Diagnosis: Tentacles (15–)16. Brim narrow. Dorsal papillae minute. Unpaired, dorsal appendage varying from $^1/_3$ to the same length as the body, placed on an elevated part of the dorsum, $^1/_4$–$^1/_3$ body length from posterior end of body. Dorsal deposits of two types – one with irregularly placed spines throughout the length of the arms and a low and irregularly spinous central apophysis, the other with the proximal part of the arm smooth, and a smooth and often rather high central apophysis which ends in three or four downwardly bent hooks; in Indian Ocean specimens a few downwardly bent hooks are nearly always present also on the stalks of the apophyses. Ventral deposits varying from crosses to rods.

Material:

St. 235, Madagascar–Mombasa (4°47'S, 46°19'E), 4810 m. – 4 specimens.

St. 279, Seychelles–Ceylon (1°00'N, 76°17'E), 4320 m. – 1 specimen.

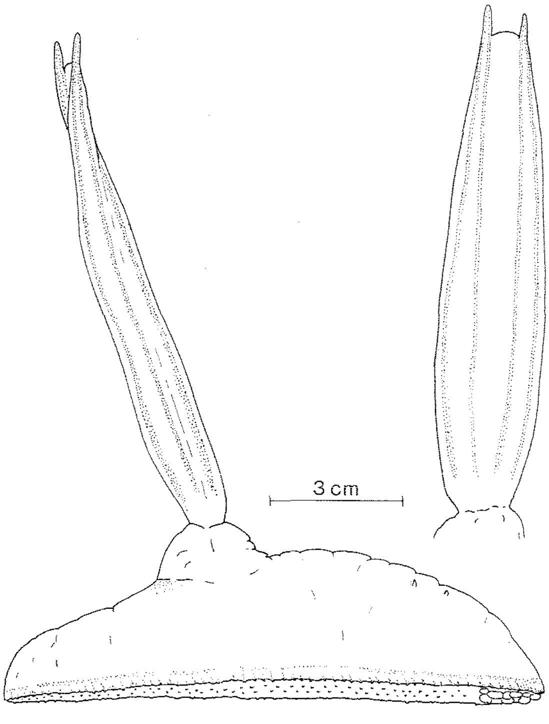


Fig. 41. *Psychropotes semperiana.* St. 235.

Description: The specimens (Fig. 41) are 7.5–12.0 cm long and very similar to each other both in external features and deposits.

Colour dark violet, darkest on the ventrum.

Tentacles 16 (except in one specimen with 15).

Brim narrow and retractile, composed on each side of approximately 60 conical, one millimeter long tubefeet which are fused at their bases.

Midventral tubefeet present throughout whole length of ventral sole.

Dorsal papillae 1–2 mm long. One specimen has two papillae on the left side; the other specimens have only one or no papilla preserved.

Unpaired, dorsal appendage fully preserved only in the illustrated specimen where it was almost the same length as the body. In the other specimens it is torn off close to the base. In all the specimens the appendage is placed on an elevated part of the dorsal side, about one-third body length from the posterior end of the body.

Deposits (Fig. 42: 1–11). The dorsal deposits consist of crosses of two types. By far most of the crosses (4–5, 9–11) possess large and irregularly placed spines throughout arm length. The centre of the cross sometimes has a low and irregularly spinous apophysis, but often the apophysis is absent or replaced by a number of irregularly shaped spines. The apophyses start as tripartite structures, but no trace of this structure is seen in the fully developed deposits. The arms are 0.1–0.2 mm long in the specimen from St. 279 (7.5 cm long), and 0.1–0.3 mm long in the specimens from St. 235 (8–12 cm long). In the smallest specimen from St. 235 almost no crosses of this type had arms longer than 0.2 mm. One of the specimens (10 cm long) from St. 235 had very robust and spinous crosses (11).

Another type of dorsal deposit (1–3), occurring more rarely, has smooth proximal arm parts, and a true central apophysis which ends in three downwardly bent hooks; in addition, a few hooks are practically always present on the stalks. Most of the apophyses, however, are broken off at the base, leaving only a fractured surface in the centre of the cross. The arms are 0.2–0.3 mm long and usually show an irregular, horizontal curvature at the end; this type of curvature is rarely found in the crosses of the first type.

Very few deposits are intermediate in shape between the two types.

Deposits with 3, 5, or 6 arms, commonly found in Atlantic specimens, are very rare in the *Galathea* specimens.

The ventral deposits (6–7) consist of curved, up to 0.7 mm long rods. The rods are crowded in a preparation from the specimen from St. 279, but very scarce in those from the specimens from St. 235.

Synonymy: *Psychropotes semperiana* Théel was taken at two South Atlantic *Challenger* stations (Sts. 101 and 133), one specimen at each. The specimens (both in BM) were re-examined; deposits dissolved in the specimen from St. 101.

The specimens agreed with the *Galathea* specimens in the number and shape of the tentacles, the shape of the brim, and in the dorsal appendage being placed on an elevated part of the body, about one-third body length from the posterior end. The appendage measured one third body length in both *Challenger* specimens.

The dorsal deposits, as in the *Galathea* specimens, comprised two types. Those of the first type (Fig. 42: 13–15) were strongly spinous. Some of the deposits had 3, 5, or 6 arms. The apophyses, when present, were low and spinous. The second type was represented by only one deposit (12) in the preparation made during re-examination. The arms of this deposit were irregularly curved at the end, as usually found in the *Galathea* specimens; the apophysis was high, smooth, and slender, and ended in three, downwardly curved hooks. Théel illustrated both types of deposit, although he did not find the hooked ends on the second type, and also failed to recognize the crosses as belonging to two distinct types.

The ventral deposits (16–20), also illustrated by Théel, were rod-shaped and irregularly 3- or 4-armed.

A third specimen was taken at *Challenger* St. 89 (off Cape Blanco, West Africa; depth 4389 m). The specimen, 6.5 cm long, was listed as a "holothurid" among specimens "too fragmentary for accurate diagnosis" (Théel 1886a). However, the two deposits illustrated by Théel refer the specimen to *Psychropotes semperiana*. The fact that the anchor-shaped apophyses ended in four hooks instead of three is hardly important. The hooked ends are so rarely preserved that it is uncertain whether the hook number is constant even in one and the same specimen.

Euphronides anchora Hérouard is known from one specimen taken southwest of the Azores. The

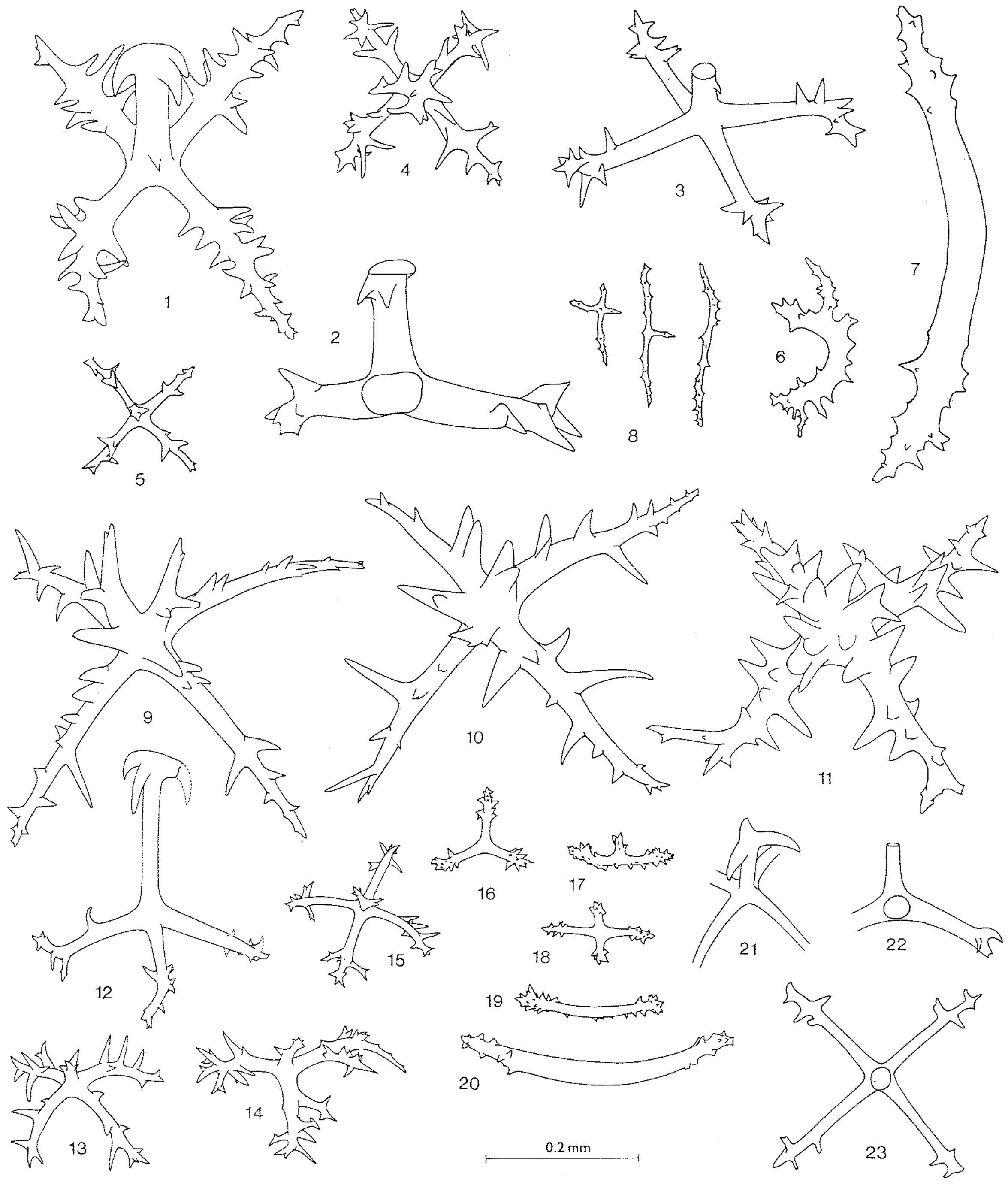


Fig. 42. *Psychropotes semperiana.* Deposits. 1–8, *Galathea* St. 279 (1–5, dorsum; 6–7, ventrum; 8, peritoneum); 9–11, *Galathea* St. 235, dorsum; 12–20, *Challenger* St. 133 (12–15, dorsum; 16–20, ventrum); 21, Swedish Deep-Sea Exp., tråldrag 6 *(Euphronides kerhervei),* dorsum; 22, Monaco St. 749 *(E. kerhervei),* dorsum; 23, Monaco St. 1757 *(E. kerhervei),* dorsum.

specimen (in MOM) is in a poor state of preservation, and the external features can no longer be made out.

The specimen had 15 tentacles and a narrow brim. Size and position of the dorsal appendage not mentioned, but as the specimen was referred to the genus *Euphronides,* it was probably placed some distance from the posterior end.

The deposits illustrated by Hérouard are similar to the two types found in the re-examined specimen of *P. semperiana*. The type with anchor-shaped apophyses had arm spines on the distal half of the arms only.

Psychropotes kerhervei Hérouard is known from eleven North Atlantic specimens. The four specimens described by Hérouard (1902, 1923) and one of the specimens described by Madsen (1953) were re-examined; in addition, skin preparations were examined from the other four specimens in Madsen's material. The re-examination revealed good agreement with the *Galathea* specimens, both in external features and deposits.

Body colour, brim, and number of tentacles as in the *Galathea* specimens. (One of Madsen's specimens had only 15 tentacles).

Dorsal papillae 3–4 pairs, minute. Unpaired dorsal appendage in all the specimens torn off at the base.

Deposits. The dorsal crosses in *P. kerhervei* belong to the same two types as in *P. semperiana, E. anchora,* and the *Galathea* specimens. The deposits of the first type have irregularly placed spines throughout arm-length, and a low and spinous central apophysis; the arms are 0.10–0.15 mm long. A number of deposits with 3, 5, or 6 arms are present in both Hérouard's and Madsen's specimens. The deposits of the second type (Fig. 42: 21–23) have about 0.16 mm long arms with distal spines. The deposits are usually of a slender structure, although some are more strongly built; the latter deposits possess only a few spines at the end of the arms, and are similar to those which Hérouard illustrated for *E. anchora.* A vertical, smooth apophysis with three, downwardly bent hooks is preserved in a few deposits of the second type. The hooked ends were overlooked by Hérouard and Madsen.

The ventral deposits in the re-examined specimens consist of rods up to 0.3 mm in length, and reductional stages of crosses.

Hérouard (1902) considered the posterior elevation of the body to be a characteristic feature of *P. kerhervei,* but in his later work he suspected that this body form was caused by contraction. However, Madsen again stated that "the dorsal side is vaulted, usually highest in the posterior part of the body". This shape of the body is a similarity to the *Challenger* specimens of *P. semperiana* and to the *Galathea* specimens.

Deichmann (1930) "with some doubt" recorded a specimen of *Benthodytes kerhervei* (Hérouard) from a depth of 4345 m off the West Indies. The deposits were stated to agree with those illustrated by Hérouard (which, however, did not include the type with anchor-shaped apophyses).

Another West Indian specimen, recorded by Deichmann (1940) as *Euphronides kerhervei* (Hérouard), was taken at the *Atlantis* St. 2966 (22°47'N, 80°24'W) at a depth of 3886 m. (Deichmann cited a wrong position and depth (625 fathoms) of the station). The specimen (in MCZ) was re-examined and found to agree with *P. semperiana* in external features as well as deposits, although the unpaired appendage was lost and no hooked ends of apophyses were preserved in a preparation made.

Remarks: The species synonymized agree with the *Galathea* specimens in the number and shape of the tentacles, the narrow brim, and the dorsal appendage being placed on an elevated part of the body, about one-third body length from the posterior end. (Only the *anchora* specimens were too poorly preserved to make out the shape of the body). The unpaired appendage was fully preserved only in one *Galathea* specimen (where it was almost as long as the body) and in the two *Challenger* specimens (where it measured about one-third body length).

A geographic variation may be present in the size and shape of the dorsal deposits, which in all the specimens belong to the same two types. In the Indian Ocean the deposits of both types have arm lengths up to 0.3 mm. The type with anchor-shaped apophyses has one or more of the arms irregularly curved at the ends, and the apophyses usually possess a few hooks on the stalk in addition to the three large terminal hooks.

In the Atlantic Ocean the arms reach only 0.2 mm in length. Deposits with 3, 5, or 6 arms are not uncommon in the Atlantic, while they are very rare in the Indian Ocean. The deposits with anchor-shaped apophyses are slender and the apophyses possess no spines other than the terminal hooks. In the specimens from the North Atlantic the arms are sometimes straight and often with a few terminal spines only.

Relationships: Most closely related to *P. minuta* (q. v.).

Distribution: North and South Atlantic, and western part of the Indian Ocean. Depth 3465–5600 m.

Psychropotes minuta Koehler & Vaney, 1905

Psychropotes minutus Koehler & Vaney, 1905, pp. 76–78, pls. VIII: 4–5, XII: 23–24.

Diagnosis: Resembling *P. semperiana,* but deposits with anchor-shaped apophyses have not been found.

Record: Off the Laccedives (Indian Ocean), 2085 m. One specimen.

Remarks: The similarities to *P. semperiana* include the number of 16 tentacles, the narrow brim composed of small and closely placed tubefeet, and the posterior vaulting of the body, with the unpaired appendage placed on the highest point about one third body length from the posterior end. The appendage was almost as long as the body, a similarity to the appendage preserved in one of the *Galathea* specimens.

Koehler & Vaney figured two crosses with spinous, c. 0.16 mm long arms, resembling the smallest crosses in the *Galathea* specimens. The deposit type especially characteristic of *P. semperiana,* with smooth basal arm parts and a hooked apophysis was not mentioned by Koehler & Vaney. For this reason *P. minuta* is retained as a separate species.

Psychropotes depressa (Théel, 1882)

Figs. 43–44, pls. VII: 1–3, XII: 8, XIV: 1–2

Euphronides depressa Théel, 1882, pp. 93–96, pls. XXVI, XXX: 5–6, XL: 7, XLVI: 4; Ohshima 1915, pp. 244–245, fig. 1; Ohshima 1916–1919, with three figures.

Euphronides depressa var. *minor* Théel, 1886b, p. 2.

Euphronides cornuta Verrill, 1884, p. 217; Verrill 1885, pp. 518, 538, figs. 32–33; Deichmann 1930, pp. 127–128; Heding 1940, p. 368.

Euphronides tanneri Ludwig, 1894, pp. 39–44, pls. III: 7, IV, V: 17–19.

Euphronides auriculata R. Perrier, 1896, pp. 901–902; R. Perrier 1902, pp. 434–438, pls. XIII: 1–2, XX: 12–13; Grieg 1921, pp. 8–9.

Euphronides violacea R. Perrier, 1896, p. 902; R. Perrier 1902, pp. 438–441, pl. XX: 14; Deichmann 1930, pp. 128–129; Deichmann 1940, pp. 201–202; Heding 1942, pp. 15–16; Madsen 1947, p. 16; Deichmann 1954, p. 384.

Euphronides talismani R. Perrier, 1896, p. 902; R. Perrier 1902, pp. 441–444, pl. XX: 15; Hérouard 1902, pp. 30–31, pl. II: 19–22; Deichmann 1930, p. 129; Heding 1942, p. 15, fig. 15.

Benthodytes assimilis Théel, 1886b, pp. 2–3.

Diagnosis: Tentacles 18, retractile; discs rather soft with c. 20 marginal knobs. Brim broad, but retractile. Dorsal papillae 3–4 pairs; the two posterior pairs vary in size, whereas the others are always minute. Unpaired dorsal appendage short, placed about one-third body length from posterior end of body. Dorsal deposits cross-shaped, with a high and usually smooth central apophysis; arms 0.2–1.0 mm long, most often with one high spine. Ventral deposits, rods and reduced crosses.

Material:

St. 32, Monrovia–Takoradi (4°05'N, 2°13'W), 2100 m. – 13 specimens.

St. 52, San Tomé–Cameroon (1°42'N, 7°51'E), 2550 m. – 5 specimens.

St. 65, off Gabon (2°17'S, 8°10'E), 2770 m. – 2 specimens.

Description: The specimens (Pl. VII: 1–3) are 7–20 cm long.

Colour violet, very dark on the ventral sole.

Tentacles 18 in all the specimens. Discs rather soft, with c. 20 radial elevations, each ending in a marginal knob. In one, 12 cm long, specimen from St. 52 some of the tentacles are completely retracted into pockets of the skin. Only a few of the other specimens show slight indications of retractility of the tentacles.

Brim greatly varying in breadth and thickness. In some specimens the brim is so thick that it passes gradually into the body proper, whereas in other specimens the brim is thin and clearly set off from the body.

Midventral tubefeet present throughout length of ventral sole.

Dorsal papillae 2–5 pairs (the whole variation in number is present in the specimens from St. 52). The posterior pair is placed midway between the anterior end of the body and the unpaired appendage. The posterior papillae in a 20 cm long specimen are 2.5 cm lang and 1 cm broad at the base; in most of the other specimens the posterior papillae are contracted, but they are in all the specimens very broad at the base. The remaining papillae are all minute.

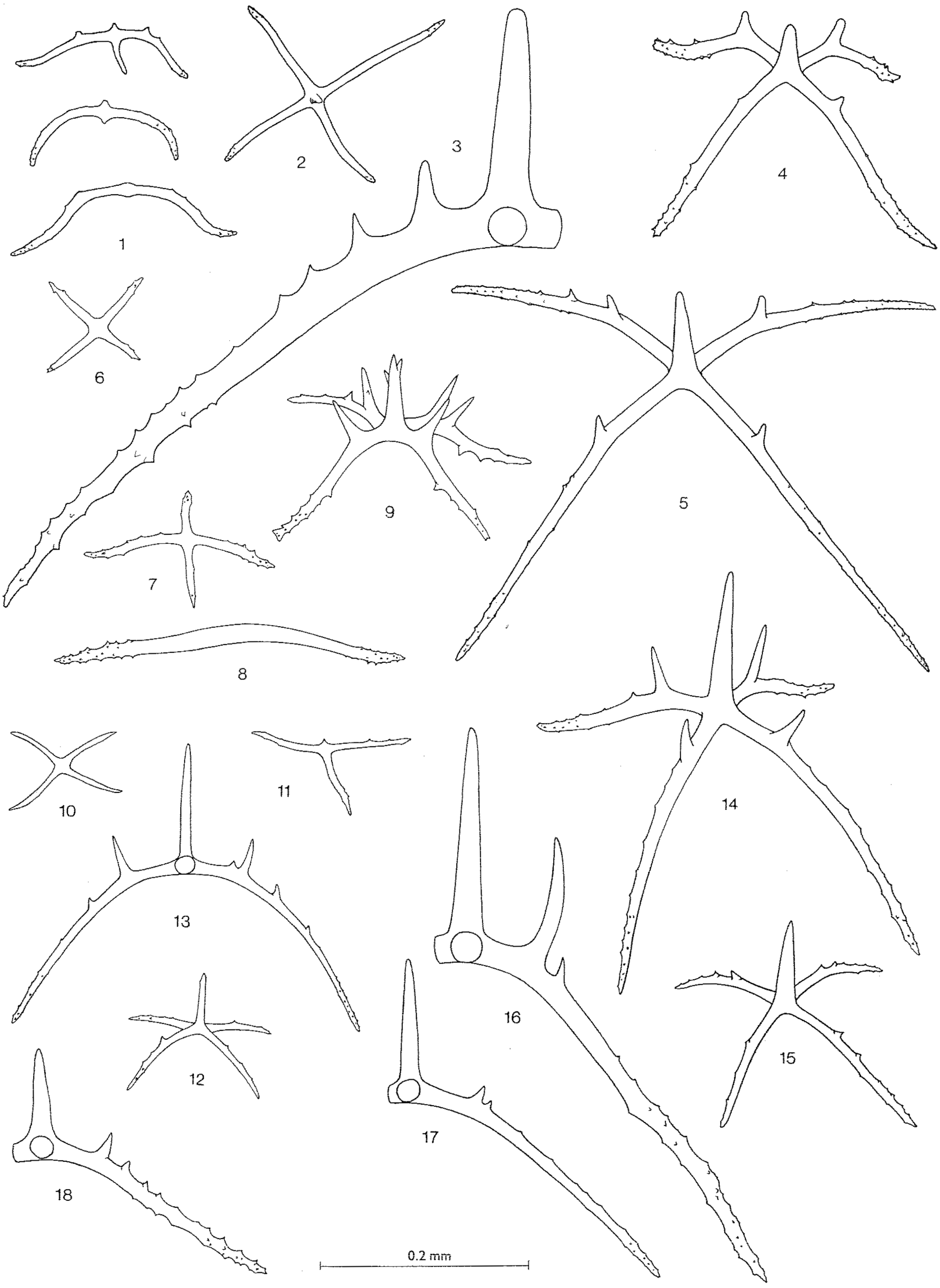


Fig. 43. *Psychropotes depressa.* Deposits. 1–5, *Galathea* St. 52 (1–2, ventrum; 3–5, dorsum); 6–9, *Challenger* St. 300 (6–8, ventrum; 9, dorsum); 10–17, *Ingolf* St. 18 (10–12, ventrum of a 1.8 cm long specimen; 13, dorsum of same; 14–17, dorsum of a 7.2 cm long specimen); 18, *Thor* St. 166, dorsum of a 12 cm long specimen.

Unpaired dorsal appendage placed about one-third body length from posterior end of body. The appendage may be as long as one-sixth of the body length, but is usually contracted (in some specimens scarcely visible).

Deposits (Fig. 43: 1–5). The dorsal deposits (3–5) are cross-shaped with a high, smooth central apophysis and slender, slightly spinous arms. The arms vary considerably in length. In the preparations from most of the specimens the arms are 0.2–0.4 mm long, but in some specimens crosses with arms up to 1.0 mm occur. (The whole variation is present in the specimens from St. 32). No correlation was found between size of deposits and body size. The arm spines are vertical (except for the distal, reduced spines). On most deposits only one large spine is present on each arm, placed at some distance from the centre of the cross; but on the largest deposits a number of vertical arm spines are usually present, of which none is especially high. The proximal spine on these deposits is placed very near the centre of the cross. Deposits intermediate in shape between these two types do occur, and deposits of the latter type are not only found among the large deposits.

The ventral deposits consist of small crosses (2) with reduced apophyses and spines. Numerous curved rods (1) were found in all the specimens from Sts. 52 and 65, but not in those from St. 32. The rods possess an enlargement in the middle, derived from two reduced arms of a cross. Intermediate stages in which two reduced arms are still present show that the curvature of the rods is horizontal, not originating from the downward curvature of the arms of the crosses.

Synonymy: *Euphronides depressa* Théel was taken in three specimens by the *Challenger,* one off Gibraltar, and two off the coast of Chile. Théel based his description mainly on the Pacific specimens, in spite of the fact that the specimen taken off Gibraltar was selected as the type. This selection of the type was unknown to the subsequent authors, who all regarded *E. depressa* as a species restricted to the Pacific.

Ohshima (1915) regarded the Pacific species *E. tanneri* as a synonym of *E. depressa* and, moreover, suggested the synonymy between all the Atlantic species of *Euphronides* mentioned in the present synonymy list. He did not discuss the possible identity between Pacific and Atlantic specimens; apparently, this synonymy was considered out of the question for zoogeographic reasons.

The species synonymized in the present paper were distinguished from each other by the shape of the body, the size of the two posterior pairs of dorsal papillae, the size of the unpaired appendage, the body colour, and the size and shape of the deposits.

The variation found in the *Galathea* specimens and in the specimens re-examined (see below), compared with that recorded in the literature, indicates that none of the differences are valid species characters. On the other hand, some of the differences appear to represent geographic variations. In addition, an age variation is present in some features.

Deichmann (1930) is the authority of the synonymy of *Benthodytes assimilis* Théel with *Euphronides violacea.*

Material re-examined:

(1) South and southwest of Iceland. Heding (1942) referred 27 of the specimens taken by the *Ingolf* and the *Thor* to *E. talismani,* and two to *E. violacea.* (He relied upon a determination made by Deichmann but remarked that he would otherwise have referred all of them to *E. talismani).* The 23 specimens from *Ingolf* St. 18 measure 1.7–7.2 cm and include the smallest known specimens of the species. The specimens were all re-examined; preparations were made from the dorsal and ventral skin of eight specimens.

(2) Eastern North Atlantic. R. Perrier (1902) referred eight of the specimens taken by the *Travailleur* and the *Talisman* to *E. auriculata,* six to *E. violacea,* and one to *E. talismani.* The number of specimens found during re-examination of Perrier's material in MNHN did not quite agree with the numbers stated in his report, and, moreover, the depths indicated for the different stations in some cases disagreed with those stated in the report. In all, five specimens of *E. auriculata,* 16 specimens of *E. violacea,* one of *E. talismani* (very poorly preserved), and 43 specimens not determined to species were found during re-examination. They are 3–12 cm long. The deposits were examined in one specimen of *E. auriculata,* but had dissolved in four specimens examined of *E. violacea.*

The type specimen of *E. depressa* (in BM), and skin preparations (in ZMUC) of the specimen of *E. violacea* taken by the *Skagerak* (Madsen 1947) were re-examined. (Both specimens were taken off Gibraltar).

(3) Western North Atlantic (off the coast of the United States, about 40°N). Six of Verrill's specimens of *E. cornuta* from the *Albatross* Sts. 2036, 2568, and 2570, and ten of Théel's specimens of *E. depressa* var. *minor* were re-examined, all by means of skin preparations. (One specimen of *E. cornuta* is kept in BM, three in MCZ, and two in ZMUC; eight of the specimens of *E. depressa* var. *minor* are kept in MCZ, and two in ZMUC).

(4) Gulf of Guinea. The *Valdivia* specimen of *E. cornuta* (at present in ZMUC) was re-examined by means of skin preparations.

(5) Japan. Two of Ohshima's specimens (in USNM) were re-examined by means of skin preparations.

(6) Eastern Pacific. The two *Challenger* specimens from off Chile were re-examined. One is in BM, the other in ZMA; skin preparations were made from the latter.

Description of the re-examined specimens:

Colour. According to Deichmann (1930), the body colour is different in the three Atlantic species, *E. cornuta* (brownish), *E. talismani* (whitish to rose-coloured), and *E. violacea* (dark violet). However, eleven re-examined specimens of *E. violacea* from *Talisman* St. 38 varied from whitish to light violet with a dark violet ventral sole. Although the colours are those of specimens long kept in alcohol, the differences indicate that variations in body colour can hardly be considered taxonomically significant.

Skin in specimens smaller than c. 6 cm usually soft, transparent, and light-coloured.

Tentacles resembling those of the *Galathea* specimens. According to Théel, the tentacles are retractile; this could be verified for one of his Pacific specimens, in which some of the discs were retracted into their stalks. The discs were partly retracted also in some of the *Ingolf* specimens. In all other re-examined specimens the discs were unretracted.

The full tentacle number is 18. This number may be attained already at a body length of 3 cm and is nearly always found in specimens larger than 10 cm. The specimens from the *Ingolf* and the *Thor,* measuring 1.7–12.0 cm, showed a variation of 10–18 tentacles, largely increasing with the size of the specimens (Fig. 44).

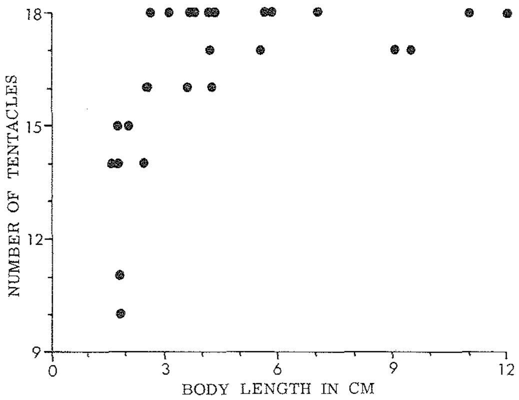


Fig. 44. *Psychropotes depressa.* Number of tentacles in relation to body length in 25 North Atlantic specimens taken by the *Ingolf* and the *Thor.*

Posterior pair of dorsal papillae large in all the Atlantic specimens of larger size. In the specimens from *Ingolf* St. 18, which are only 1.7–7.2 cm long, they are small, except in the largest specimen. Large posterior papillae have been found in Atlantic specimens as small as 4 cm. The pair preceding the posterior pair of papillae is, according to Deichmann (1930), large in the species *E. cornuta,* although smaller than the posterior pair. In the three re-examined specimens of *E. cornuta* from off Delaware the pair preceding the posterior pair of papillae was intermediate in size between the large posterior pair and the small anterior pairs; but in the other two it was scarcely larger than the anterior pairs.

Ohshima (1915) found a large variation in size of the posterior pair of papillae in 23 Japanese specimens. He did not mention whether the small posterior papillae were found in specimens of small size.

In the three specimens known from the eastern Pacific (the two *Challenger* specimens from off Chile, and Ludwig's specimen of *E. tanneri* from the Gulf of Panama) the posterior papillae were small. The specimens measured 22–37 cm.

Unpaired dorsal appendage completely retractile. Supposed differences in appendage size represent different states of contraction rather than differences of taxonomic value.

Dorsal deposits, all having a high and conical central apophysis. A few spines were present on the central apophyses in Ohshima's Japanese specimens and in the two *Challenger* specimens taken off Chile (Fig. 43: 9). The apophyses were smooth in the specimen of *E. tanneri* from the Gulf of Panama. Perrier mentioned that one or two small spines were present on some of the central apophyses in his specimens of *E. violacea,* but otherwise such apophyses have not been found in Atlantic specimens. Crosses with an arm length up to 0.5–0.7 mm are represented at all the Atlantic localities, although usually not in all the specimens. In the Pacific specimens (the two *Challenger* specimens from off Chile, the Japanese specimens described by Ohshima, and the specimen of *E. tanneri* from the Gulf of Panama) the arms did not exceed 0.35 mm in length. (In the Japanese specimens most of the crosses had arms only 0.15–0.20 mm long).

The arm spines are vertical (apart from the inconspicuous spines on the distal half of the arms). The proximal arm spine is usually much larger than the others, and is often the only large spine present. Crosses with a number of vertical spines on each arm occur along with the crosses with only one large spine on each arm in specimens from all the Atlantic localities. The two types of cross are interconnected by crosses intermediate in shape. No correlation was found between type and size of the crosses.

In six re-examined specimens from *Ingolf* St. 18 (south of Iceland) the arm spines and the central apophyses of the dorsal crosses (13–17) varied greatly in height, and many of them were unusually high. Heding supposed that the high spines and apophyses were a juvenile feature. However, the re-examination revealed no difference in this respect between the smallest and the largest specimens, although they ranged in size from 1.7 to 7.2 cm.

Crosses with a number of rather low arm spines prevail in re-examined *E. cornuta* and *E. depressa* var. *minor* taken off the east coast of the United States, and are also common in *E. talismani* from *Ingolf* St. 11 and *Thor* St. 166 (Fig. 43: 18), both situated in the same area as *Ingolf* St. 18.

One high spine was present on the arms in most of the crosses of the re-examined Pacific *Challenger* specimen (9), although some crosses possessed two or three high spines on each arm.

Ventral deposits. Crosses which lack the central apophysis and the four arm spines predominate in all examined specimens. One or two arms are often reduced, and rod-shaped deposits (often with a central enlargement derived from the reduction of two opposite arms) are found in both Atlantic and Pacific specimens. Most of the rods are horizontally curved. Large rods (8) occurred in the re-examined Chile specimen. In the others the rods were equal in length to the span of the crosses.

Variation: A *geographic variation* may be present in the size of the posterior pair of dorsal papillae. These were large in specimens longer than 4–5 cm from all the Atlantic localities; in the three known specimens from the eastern Pacific, measuring 22–37 cm, they were as small as the other papillae. In Ohshima's Japanese specimens the posterior papillae varied in size, but it is not known whether the small papillae were found in juveniles only.

The deposits show a geographic variation in size. Crosses with an arm length up to 0.5–0.7 mm were present in some of the specimens re-examined from all the Atlantic localities. In the three eastern Pacific specimens the arms were up to 0.3–0.4 mm long. In Japanese specimens few crosses had arms longer than 0.2 mm.

Spines were present on the central apophyses in the Japan and Chile specimens while those from other localities, with almost no exception, had completely smooth apophyses.

A *local varation* may be present in the shape of the deposits. Thus the specimens from *Ingolf* St. 18 (south of Iceland) possess four, often very high, arm spines on practically all the dorsal crosses, whereas this type of cross is rare in the specimens taken off the east coast of North America.

An *age variation* is shown in Atlantic, and possibly also in Japanese, specimens in the increase in relative size of the posterior pair of dorsal papillae. The tentacle number increases from 10 to 18 with the body size (Fig. 44). Finally, the skin is more soft and transparent in small specimens.

Distribution: *P. depressa* is one of the few species of Elasipoda ranging over the deeper bathyal and the upper abyssal zone. Depth range, 957–4060 m.

The species is common throughout the North Atlantic and has been found on several occasions in the Gulf of Guinea. Widely separated from these localities are the Pacific occurrences from Japan, the Gulf of Panama, and off Chile.

The Atlantic and Pacific areas of distribution are probably parts of one continuous distributional area. The coasts round South America from the West Indies to Chile are unexplored at the depths where *P. depressa* occurs, and this is partly true also of the Indian Ocean.

Type: BM, labelled "Type".
Type locality: *Challenger* St. V (35°47'N, 8°23'W).

Psychropotes scotiae (Vaney, 1908)

Euphronides scotiae Vaney, 1908, pp. 418–419, pls. I: 8–9, III: 39–40.

Diagnosis: Resembles *P. depressa*, but differs in having 16 tentacles, and triradiate deposits interspersed among the dorsal crosses.

Record: Antarctic, 3246 m. One specimen.

Remarks: The specimen was 14 cm long and had, therefore, probably attained the full tentacle number in the species.

Psychropotes mirabilis n. sp.

Figs. 45–46

Diagnosis: (Tentacle number not known). Unpaired, dorsal appendage placed about $^1/_5$ body length from posterior end of body, exceeding the body in length, and reaching some distance from the base about the double breadth of the body. Brim composed of about 75 pairs of slender, closely placed tubefeet, which are fused almost to their tips. Dorsal skin covered with warts, each containing a giant cross; the remaining part of the dorsal skin and the whole ventral skin with small crosses only.

Material:
St. 299, Bay of Bengal (17°10'N, 84°30'E), 2820 m. – 1 specimen.

Description: The specimen is 11 cm long, slender, flattened anteriorly, increasing in height towards the base of the unpaired appendage (Fig. 45).

Colour of body dark violet, darkest on the ventrum. The unpaired appendage is light violet. The dorsal skin is covered with conspicuous warts, each containing a giant cross. The appendage is smooth-skinned.

Tentacles. Only six are preserved, of the usual shape in the genus.

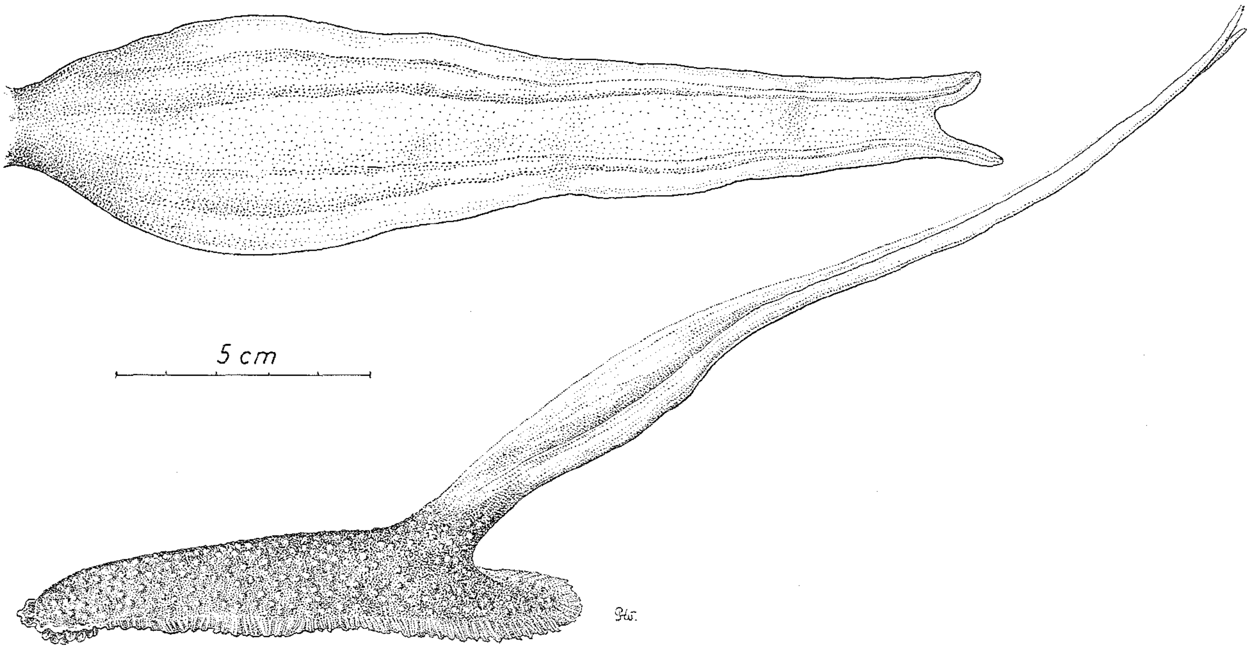


Fig. 45. *Psychropotes mirabilis.* St. 299. PHW.

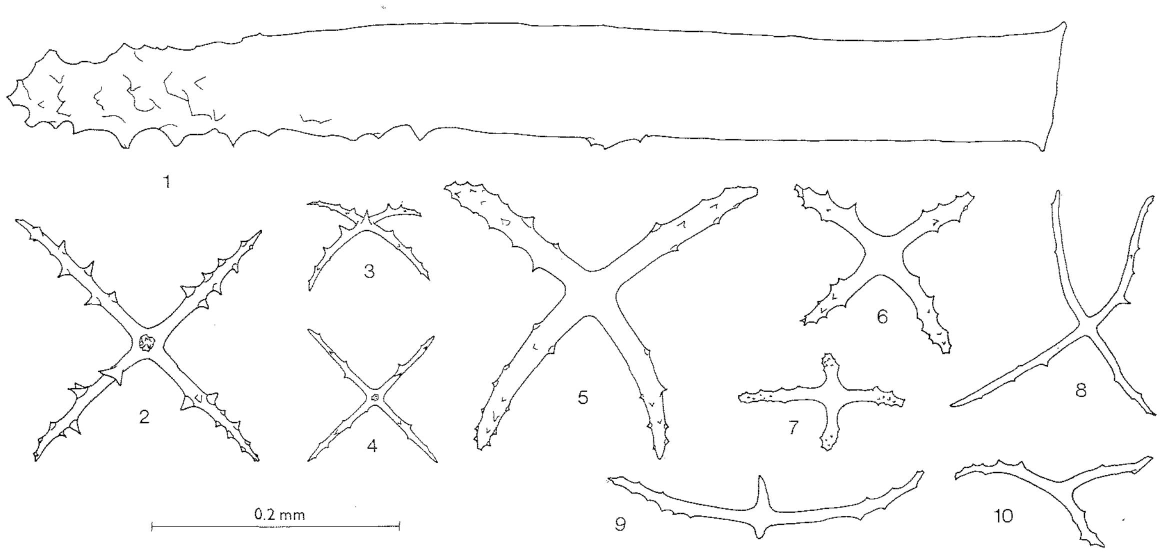


Fig. 46. *Psychropotes mirabilis*. Deposits. St. 299. 1–4, dorsum; 5–7, ventrum; 8, intestine; 9–10, gonad.

Brim composed of about 75 pairs of slender, almost completely fused tubefeet.

Midventral tubefeet about 30 pairs, present throughout length of ventral sole.

Dorsal papillae not found.

Unpaired dorsal appendage 15 cm long. At the base it is almost as broad as the body, and it increases to about the double that breadth some distance from the base. The distance from the base to the posterior end of the body is 2.5 cm.

Deposits (Fig. 46). The warts of the dorsal skin are mostly worn off, but fragments of one very large cross (1) are still present at the base of most of them. The arms of the crosses are 0.8–0.9 mm long, very robust and only slightly spinous; a 0.3 mm high, smooth, central apophysis is preserved on one of the crosses. Smaller and much more slender crosses (2–4) are present between the warts; most of these crosses have about 0.1 mm long arms, but some reach 0.2 mm. The spines are rather small and irregularly placed, and the central apophysis is reduced. Only few crosses are present in the ventrum (5–7). They are more sturdy and on an average larger than the dorsal crosses, and have only very small spines; some of the crosses have two opposite arms reduced. No giant crosses are present in the ventrum. Rods are present in the tentacles, and slender, reductional stages of crosses are present in the gonads (9–10) and intestines (8).

Relationships: Probably most closely related to *P. verrucosa* (q. v.).

Psychropotes verrucosa (Ludwig, 1894)
Figs. 47–48

Euphronides verrucosa Ludwig, 1894, pp. 44–48, pl. III: 1–6; Clark 1920, p. 140, pl. I: 2; Hansen 1956, p. 45.

Euphronides bifurcata Koehler & Vaney, 1905, pp. 75–76, pls. VIII: 1–2, XII: 22.

Diagnosis: Tentacles (15–)16. Brim well developed. Dorsal papillae up to four pairs, minute. Unpaired dorsal appendage low, conical, and completely retractile. Dorsal skin covered with warts; larger specimens have in addition two longitudinal bands of transversal skin elevations. Dorsal deposits consisting of numerous crosses of varying robustness, with 0.10–0.15 mm long, spinous arms and a rudimentary central apophysis; in addition, each wart of the dorsal skin contains a slightly spinous giant cross with 0.9–1.6 mm long, strongly curved arms and a high central apophysis, Ventral deposits cross-shaped, tripartite, and rod-shaped.

Material:

St. 192, off Durban (32°00'S, 32°41'E), 3530 m. – 1 specimen.

St. 234, Madagascar–Mombasa (5°25'S, 47°09'E), 4820 m. – 2 specimens.

St. 495, Banda Trench (5°26'S, 130°58'E), 7250–7290 m. – 3 specimens.

St. 497, Banda Trench (5°18'S, 131°18'E), 6490–6650 m. – 1 specimen.

St. 574, Tasman Sea (39°45'S, 159°39'E), 4670 m. – 1 specimen.

St. 575, Tasman Sea (40°11'S, 163°35'E), 3710 m. – 3 specimens.

St. 602, Tasman Sea (43°58'S, 165°24'E), 4510 m. – 1 specimen.

Description:

The specimens from the Banda Trench were described in a previous paper (Hansen 1956), where also the synonymy between *E. verrucosa* and *E. bifurcata* was proposed.

Western Indian Ocean: Sts. 234 and 192.

1. – The largest of the two specimens from St. 234 (the largest known specimen in the species) is 22.5 cm long and 6.5 cm broad (Fig. 47).

Colour light violet dorsally, the ventral sole darker.

Dorsal skin covered with warts, as usual in the species. In addition, two longitudinal fields of transversal elevations are present throughout the length of the dorsal side. The elevations in the freshly caught specimen were faintly subdivided into warts; in the preserved state the elevations are less clearly seen, whereas the warts stand out more clearly.

Ventral skin smooth, with the median part depressed.

Tentacles 16.

Brim 1.0–1.5 cm broad. The water-vascular canals of the enclosed tubefeet are visible only when viewed by transmitted light.

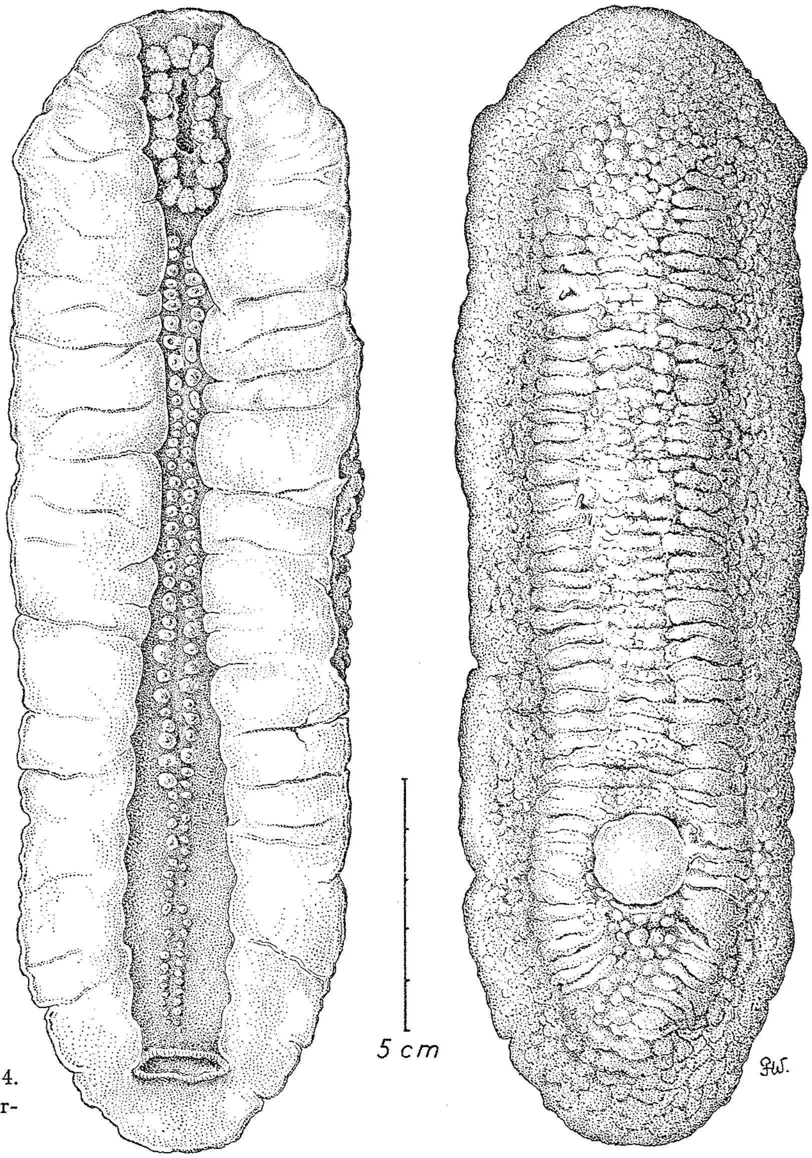


Fig. 47. *Psychropotes verrucosa*. St. 234. The large specimen in ventral and dorsal view. PHW.

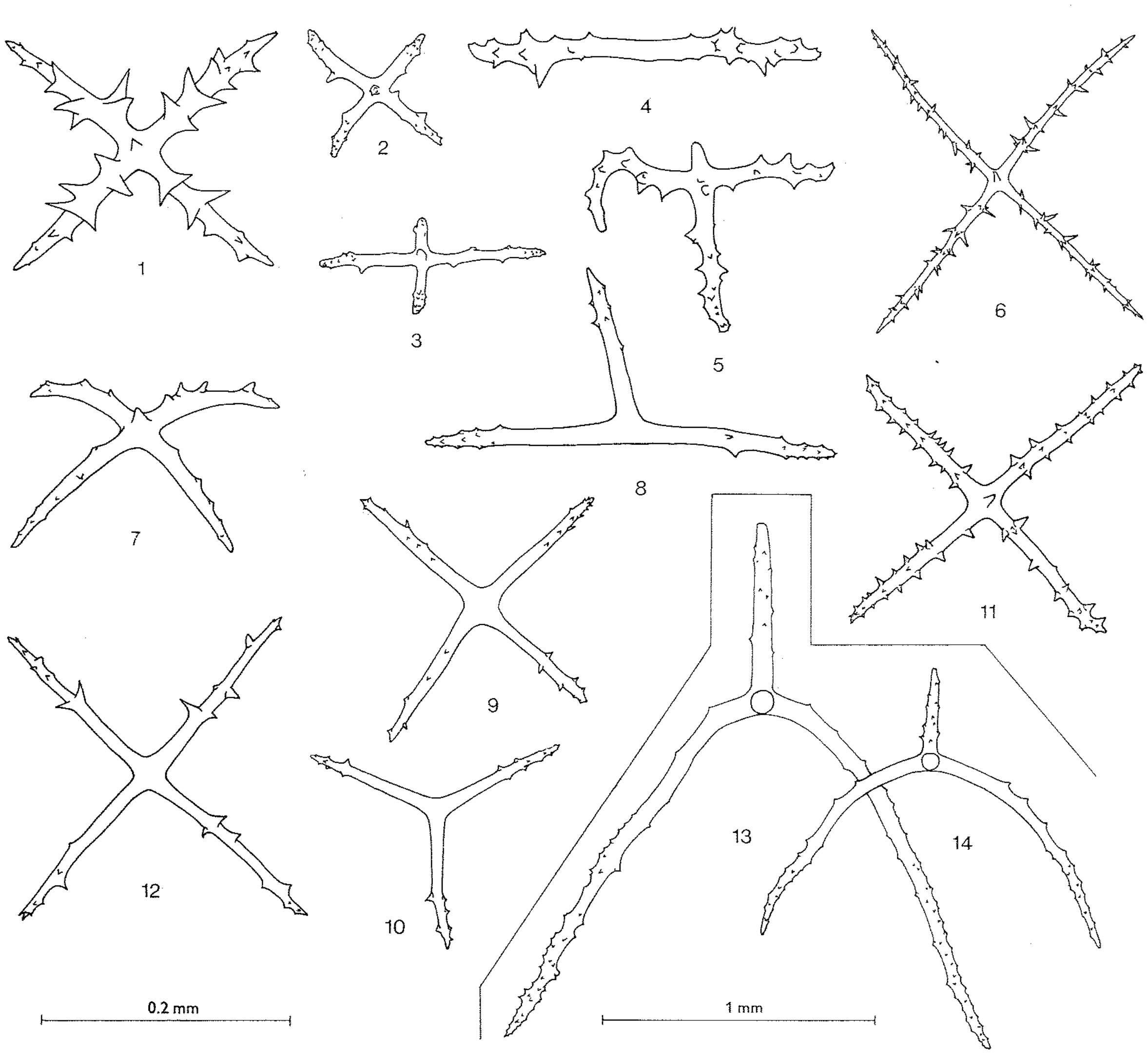


Fig. 48. *Psychropotes verrucosa.* Deposits. 1–6, St. 234, large specimen (1, dorsum; 2–5, ventrum; 6, deeper layer of skin); 7–11, St. 234, small specimen (7, dorsum; 8–10, ventrum; 11, deeper layer of skin); 12–13, St. 192, a normal-sized and a giant cross from dorsum; 14, St. 234, small specimen, giant cross.

Midventral tubefeet 56 pairs, present throughout length of ventral sole.

Dorsal papillae minute and easily lost. Three are present along the left dorsal radius.

Unpaired dorsal appendage level with the skin, apparently retracted; its presence is clearly indicated by a circular furrow, almost 2 cm in diameter, surrounding a smooth field with no warts. It is placed about one-fourth body length from the posterior end of the body.

Deposits (Fig. 48). Numerous, rather robust spinous crosses with a rudimentary central apophysis and 0.10–0.15 mm long arms are present in the dorsal skin (1). The giant crosses of the dorsal warts are broken in the preparations, but apparently they agreed with those found in other specimens of the species.

The ventral crosses (2) have 0.05–0.10 mm long arms. Stages leading to rods (3–5) are common; they are often larger than the complete crosses.

Slender, spinous crosses (6) were found in the deeper part of the body wall in a preparation from the dorsal side. They probably occur here and there all over the body wall.

2. – The other specimen from St. 234 is whitish, 5.5 cm long and 2 cm broad. Tentacles 16. Dorsal papillae and unpaired appendage not seen. (The unpaired appendage is retracted in most of the other specimens taken and often difficult to de-

tect). Brim about 2 mm broad. Dorsal skin covered with warts.

Dorsal deposits (7) less robust and spinous than those of the large specimen. A giant cross (14) is present in each wart of the dorsal skin. Some rather robust crosses from a deeper layer (11) were found in the preparation. The spines are to some degree arranged in rings, a similarity to the large specimen.

Ventral deposits (8–10) cross-shaped, tripartite, and rod-shaped. They are usually larger and less spinous than those of the large specimen.

3. – The specimen from St. 192 is 8 cm long and 5 cm broad, but apparently strongly contracted. In size and external appearance the specimen was probably very similar to the large specimen from St. 234. Tentacles 16; discs somewhat contracted, but apparently similar to those of the large specimen from St. 234. One left and two right dorsal papillae are present, all about one millimeter long. Unpaired appendage level with the skin. Midventral tubefeet small and conical. The dorsal side is covered with conspicuous warts, and, in addition, two longitudinal fields of transversal elevations are faintly visible.

Dorsal deposits (12) slender, with about 0.15 mm long arms. Giant crosses (13) with 1.6 mm long arms were present in a preparation. (The size variation of the giant crosses cannot be established, as practically all of them are broken; the figured crosses from St. 192 (13) and St. 234 (14) might fall within the size variation of one specimen). Slender crosses from a deeper layer were found in the dorsum, but not in the ventrum.

Ventral deposits cross-shaped, tripartite, and rod-shaped. In size and appearance they are intermediate between those of the large and the small specimen from St. 234.

Tasman Sea. The five specimens taken are 5.5–10.5 cm long and very similar to those from the western Indian Ocean, both in external features and deposits. The dorsal warts are conspicuous in all of them; the presence of two longitudinal fields of transversal elevations is indicated in the largest specimen. Colour light violet dorsally, and darker on the ventral sole; the two smallest specimens (5.5 and 8.0 cm long) are only faintly coloured Tentacles 15–16; the number of 15 tentacles was found in two of the three specimens from St. 575 (body length, 5.5 and 10.5 cm). Three pairs of minute dorsal papillae are present in the largest specimen. The unpaired appendage is retracted in all the specimens.

Dorsal deposits both in shape and size falling within the variation in the western Indian Ocean. Giant crosses with 1.1–1.2 mm long arms (i.e. intermediate in size between the two giant crosses figured from the western Indian Ocean); in shape the crosses are indistinguishable from the crosses figured.

Ventral deposits similar to those from the western Indian Ocean. As in the latter, the tripartite and rod-shaped deposits are often larger than the crosses.

Slender crosses from a deeper layer were found both in the dorsum and ventrum.

Banda Trench. The specimens were described previously (Hansen 1956). They are 6–7 cm long and very similar to the specimens of the same size from the Indian Ocean and the Tasman Sea. The two longitudinal elevated fields on the dorsal skin are not visible, but these have not been found in other specimens of similar size either. The unpaired appendage is low and conical (it is unretracted, in contrast to that of the other *Galathea* specimens). Both dorsal and ventral deposits agree with the usual types in the specimens from the Indian Ocean and the Tasman Sea. A few slender crosses are present both in dorsum and ventrum.

Relationships: *P. verrucosa* resembles *P. mirabilis* in the presence of dorsal warts, each with a giant cross. But the giant crosses are more robust in *P. mirabilis* which, moreover, has a more slender body and a very long unpaired appendage.

Distribution: Western Indian Ocean to eastern Pacific. Depth 2417–7250 m.

Psychropotes longicauda Théel, 1882

Figs. 49–54, pls. VII: 4–6, XII: 7

Psychropotes longicauda Théel, 1882, pp. 96–98, pls. XXVII: 1, XXVIII, XXXV: 13–17, XXXVII: 10; Agatep 1967b, p. 67, pl. XI: 1–7.
Psychropotes longicauda var. *monstrosa* Théel, 1882, pp. 98–99, pls. XXIX: 2, XXX, XXXIX: 1.
Psychropotes longicauda var. *fusco-purpurea* Théel, 1882, p. 99, pls. XXIX: 1, XXXV: 11.

Psychropotes longicauda var. *antarctica* Vaney, 1908, pp. 419–420.

Psychropotes buglossa E. Perrier, 1886, p. 283, fig. 200; R. Perrier 1902, pp. 445–453, fig. 7, pls. XIII: 3–4, XX: 16–28; Hérouard 1923, pp. 105–108, pls. I: 32, VI: 2.

Psychropotes raripes Ludwig, 1894, pp. 48–51, pl. V: 1–16; Ohshima 1915, p. 244; Ohshima 1916–1919, with one figure; Clark 1920, pp. 140–141, pl. I: 1.

Psychropotes dubiosa Ludwig, 1894, pp. 52–53, pl. II: 5–7.

Psychropotes grimaldii Hérouard, 1896, p. 167, fig. 2; Hérouard 1902, pp. 25–27, pl. III: 1–2.

Psychropotes fucata R. Perrier, 1896, p. 902; R. Perrier 1902, pp. 453–455, pl. XX: 29–30.

Psychropotes laticauda Vaney, 1908, pp. 420–422, pl. II: 14, 24.

Psychropotes brucei Vaney, 1908, pp. 422–423, pls. I: 13, II: 21–22, III: 41–42.

Euphronides dyscrita Clark, 1920, p. 139, pl. II: 3.

Nectothuria translucida Belyaev & Vinogradov, 1969, pp. 711–716, figs. 1–4.

Diagnosis: Tentacles 18. Anterior brim usually conspicuous and with the water-vascular canals of the enclosed tubefeet visible as low, radial elevations on the dorsal side of the flattened head. Free, ventrolateral tubefeet, 7–25 pairs. Posterior brim composed of 2–9 pairs of tubefeet. Dorsal papillae minute, 2–8 pairs. Unpaired dorsal appendage placed close to posterior end of body, the base almost as broad as the body, and varying in length from one-fifth to the same length as the body. Deposits, crosses of varying shape; dorsal crosses usually with about 0.1 mm long arms, although (especially in smaller specimens) the variation in arm length may amount to 0.1–1.0 mm; ventral crosses with arms curved upwards, and measuring 0.1 mm or less; central apophysis often reduced; scattered large crosses with 0.2–0.3 mm long arms, and the spines confined to the distal half of the arms, are often present in smaller specimens; the arms usually with a horizontal curvature. Body colour varying from light yellow to dark violet.

Material:

St. 234, Madagascar–Mombasa (5°25'S, 47°09'E), 4820 m. – 6 specimens.

St. 235, Madagascar–Mombasa (4°47'S, 46°19'E), 4810 m. – 5 specimens.

St. 601, Tasman Sea (45°51'S, 164°32'E), 4400 m. – 5 specimens.

St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 14 specimens.

St. 664, Kermadec Trench (36°34'S, 178°57'W), 4540 m. – 33 specimens.

St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – 5 specimens.

Description:

Kermadec Trench: Sts. 663 and 664 (Pl. VII: 5–6).

Six of the specimens (three from each of the stations) differ in some features from the other specimens. These specimens, as well as a juvenile specimen (3.2 cm long), are described separately.

1. – The 40 "typical" specimens.

Body length 8–23 cm at each station.

Colour. The specimens from St. 663 varied in colour from a uniformly yellow, to yellow with a violet ventral side. The specimens from St. 664 were coloured in various shades of violet, but no specimens were wholly or partially yellow. However, in alcohol the violet colour has, in all the specimens, changed into a light yellowish. There was no correlation between the size of the specimens and their colour.

Tentacles 18 in all the specimens.

Anterior brim composed of 11–14 pairs of tubefeet. The water-vascular canals are seen as low, but usually conspicuous, elevations on the dorsal side of the head.

Free, ventrolateral tubefeet 13–23 pairs, large and well spaced.

Posterior brim composed of 2–4 pairs of tubefeet, usually clearly distinguished from the free, ventrolateral tubefeet.

No correlation was found between tubefeet number and body size.

Dorsal papillae minute, 2–6 (usually 4) pairs.

Unpaired dorsal appendage placed close to posterior end of body. It varies in length from one-fourth to the same length as the body.

Deposits (Fig. 49). In most of the specimens the dorsal deposits (6–8) consist of spinous crosses with 0.07–0.10 mm long arms. Usually, the spines are irrregularly developed, both regarding shape and arrangement; but in some preparations most of the crosses possess one large, bipartite spine proximally on each arm. All intermediates are present between the two types.

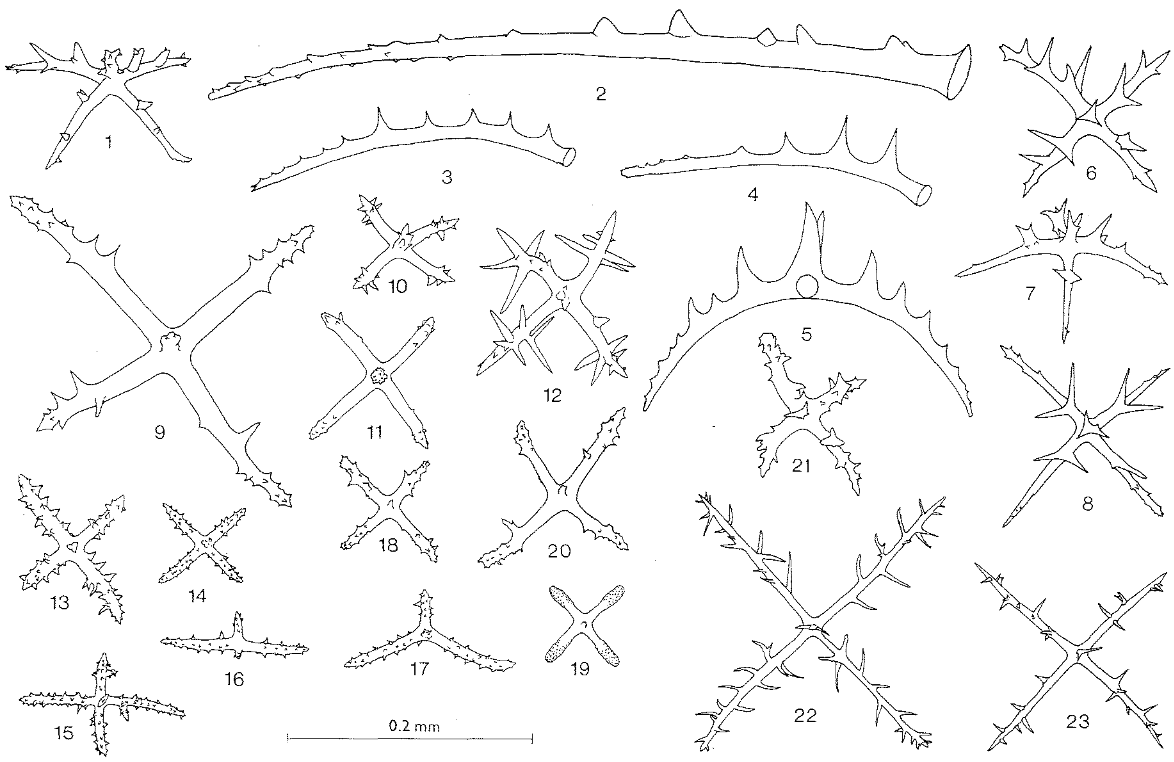


Fig. 49. *Psychropotes longicauda.* Deposits. Sts. 663 and 664. 1–2, small cross and arm of large cross from dorsum of the 13 cm long "deviating" specimen from St. 663; 3–4, arms of large crosses from dorsum of the 12 cm long "deviating" specimen from St. 664; 5, large cross from dorsum of the 17 cm long "deviating" specimen from St. 664; 6, dorsum (St. 664); 7–8, dorsum (St. 663); 9, giant cross from ventrum (St. 664); 10–17, ventrum (St. 663); 18–21, ventrum (St. 664); 22, dorsum, deep layer (St. 664); 23, dorsum, deep layer (St. 663).

The ventral deposits (10–21) show a remarkable variation in shape. Some are densely covered with small spines or knobs, others have a few large and irregularly placed spines, and others again have almost smooth arms. The arms are 0.04–0.10 mm long, and usually curved slightly upwards.

Scattered crosses (9), with 0.15–0.20 mm long arms, usually with an irregular horizontal curvature, are present in the ventrum of a 12 cm long specimen from St. 664. The spines are confined to the distal half of the arms, and are mainly horizontal.

Slender crosses (22–23) are found here and there in the deeper layer of the skin.

2. – The three deviating specimens from St. 663 are 6 cm (specimen a), 10 cm (b) and 13 cm long (c). They are violet, darkest on the ventral side and have retained the violet colour after twenty years in alcohol. The skin is thin and distended, due to a strong filling of the intestine. In all three specimens the external layer of the skin has partly ruptured and does not cover the entire body surface. Specimen c is stretched longitudinally, as shown by the long interspaces (c. 22 mm) between the free, lateral tubefeet. (Even in the largest of the "typical" specimens from the Kermadec Trench the gaps between the tubefeet are less than half this distance).

The anterior brim in specimens b and c is similar in shape to that of the "typical" specimens, with distinct radial elevations on the dorsal side corresponding to 12–13 pairs of tubefeet. Specimen a does not show these elevations, and the tubefeet of the anterior brim could not be counted with certainty.

The free, ventrolateral tubefeet amount to 8 pairs in specimen a, 10 in specimen c, and 12 in specimen b. All three specimens have 3 pairs of fused, posterior tubefeet.

In specimens a and c the dorsal crosses (1–2) measure 0.1–0.6 mm in arm length. The arm spines of the largest crosses are usually vertical and often very high; the spines are smooth or provided with a few secondary spines. Large crosses with irregularly shaped and arranged spines are also found. All intermediates are present, both in size and shape, between the giant crosses and the usual small type.

The same two specimens with large dorsal crosses have also large scattered crosses in the ventrum. The arms of these crosses are 0.2–0.3 mm long; the arm spines are mainly horizontal and confined to the distal half of the arms. Apart from their larger size, they resemble the large crosses found in one of the "typical" specimens (9). The large ventral crosses, unlike the large dorsal crosses, form a size group of their own.

Specimen b has normal-sized crosses both in dorsum and ventrum.

In other respects the three specimens agree with the other specimens from the Kermadec Trench (number and shape of the tentacles, position and length of the unpaired appendage, the characteristic shape of the anterior brim, the separation of the tubefeet into free and well-spaced lateral ones and about three pairs of fused posterior ones, and the shape of the smaller deposits).

3. – The deviating specimens from St. 664 comprise two complete specimens, 13 and 17 cm long, and fragments of a smaller specimen (c. 12 cm long). The skin in all three specimens is brownish-violet, darkest on the ventrum. In alcohol, they have preserved their colour better than the other specimens from the station, which have all changed to a light yellowish colour. The skin of the three specimens has partly ruptured and the outer, deposit-containing layer has partly separated from the subcutis.

The anterior brim lacks the dorsal, radial elevations which are otherwise characteristic of the species. The anterior brim includes about 12 pairs of tubefeet.

The tubefeet could be counted only in the 17 cm long specimen, where 14 pairs of free and three pairs of posterior fused tubefeet were present.

In all three specimens the dorsal crosses (3–5) have arm lengths up to 0.2–0.3 mm. The arm spines of the large crosses are mostly vertical. All intermediates occur, both in size and shape, between these deposits and the usual type.

Ventral giant crosses were not found in the specimens. The 13 cm long specimen possessed numerous short and sturdy rods in the ventrum, a difference from all other specimens of the Kermadec Trench.

The agreement with the "typical" specimens in many features (tentacles, unpaired appendage, tubefeet, and deposits) makes it unlikely that the three specimens represent a different species. Sexual dimorphism can also be ruled out as the three deviating specimens comprised two females and one male.

The dark colour, the fragile skin, and the presence of large crosses are similarities to specimens a–c from St. 663. The absence in the specimens from St. 664 of radial elevations on the head may be due to contraction of the water-vascular canals.

4. – The juvenile specimen (St. 663).

Body (exclusive of unpaired appendage) 3.2 cm long and 1.0 cm broad.

Skin whitish and soft.

Tentacles 12; discs with about 18 radial elevations, each ending in a small, marginal process.

Brim broad and flat. The brim is intact round the anterior and posterior ends of the body, while laterally it is preserved only in places. Probably, the brim was continuous round the body. Anteriorly, the brim is 3–4 mm broad and has a smooth edge. Posteriorly it is 2 mm broad and the ends of the enclosed tubefeet project from the edge. The number of tubefeet included in the brim is approximately 20–25 on each side.

Midventral tubefeet almost invisible, although present throughout length of ventral sole.

Dorsal papillae one pair, minute, placed in the middle of the body.

Unpaired dorsal appendage 2.5 cm long, placed close to posterior end of body. Base of appendage almost as broad as the body. The appendage passes gradually into the dorsal side of the body.

Deposits (Fig. 50). Dorsal crosses (1–4) up to 0.5 mm in arm length, and rather slender. Arm spines vertical. Central apophysis and larger arm spines usually with secondary spines. Ventral crosses (5–9) up to 0.3 mm in arm length. The largest crosses are rather numerous and, to some degree, form a size group of their own. Like the giant ventral crosses found in some of the larger specimens, they have the arms somewhat horizontally curved and with distal spines. However, the spines are more numerous than in the large specimens, and not only horizontal. A few of the

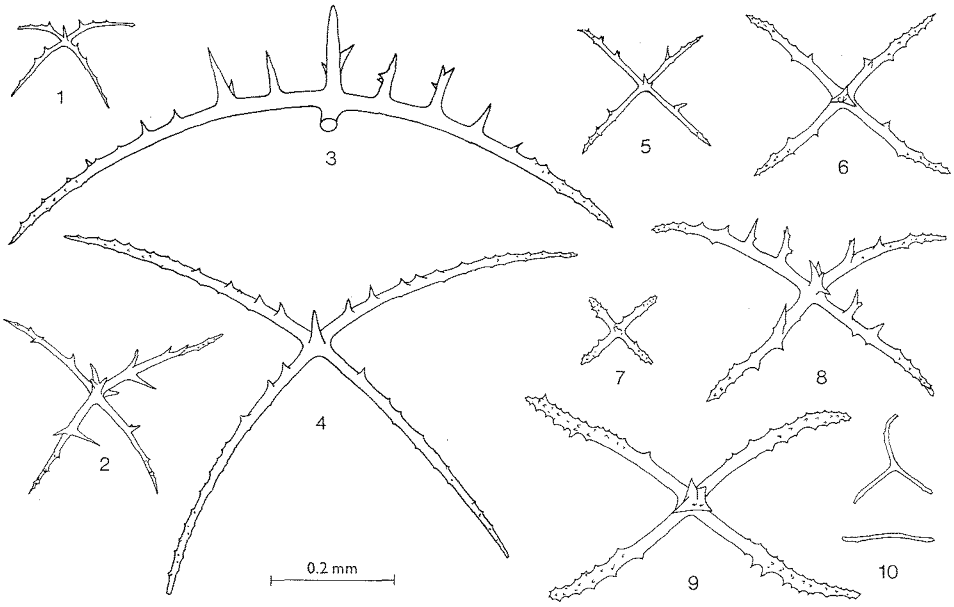


Fig. 50. *Psychropotes longicauda.* Deposits of the juvenile specimen from St. 663. 1–4, dorsum; 5–9, ventrum; 10, intestine.

large crosses (8) are strongly spinous throughout the length of the arms.

The small ventral crosses usually show an upward curvature of the arms like in the large specimens.

The determination of the specimen to *P. longicauda* is based on the shape, size, and position of the unpaired appendage, and on the similarity of the large dorsal and ventral crosses to the large juvenile types in *P. longicauda.*

Tasman Sea: St. 601.

Body length 14–24 cm.

Colour violet, darkest on the ventrum.

Tentacles 18 in three specimens (14, 14, and 19 cm long) and 17 in two specimens (18 and 24 cm long).

Anterior brim similar to that of the Kermadec specimens and composed of 12–14 pairs of tubefeet.

Free, ventrolateral tubefeet 14–15 pairs, large and well spaced.

Posterior brim composed of 2–3 pairs of tubefeet.

Dorsal papillae minute. In one specimen five papillae could be counted on the left side, but in the other specimens only one or two papillae were preserved.

Unpaired dorsal appendage varying from less than one-half to the same length as the body.

Deposits dissolved in all the specimens.

Eastern Pacific: St. 716. The five specimens are 6, 17, 17, 21, and 26 cm long, respectively.

Colour reddish violet, darker on the ventrum.

Tentacles 18 in all five specimens.

Anterior brim similar to that of the Kermadec specimens. The brim contains 24 tubefeet in the largest specimen and 16 in the others. No dorsal radial elevations are present in the smallest specimen.

Free, ventrolateral tubefeet 7–10 pairs, large and well spaced. In the smallest specimen the tubefeet are connected at the base by a low elevation of the skin.

Posterior brim composed of 5–7 pairs of tubefeet.

Dorsal papillae minute. They can be counted only in the two largest specimens where 6–7 pairs are present.

Unpaired dorsal appendage measuring ${}^1/_4$–${}^3/_4$ body length. In shape and position it is similar to that of the Kermadec specimens.

Deposits (Fig. 51). The dorsal crosses of the small specimen (1–4) have 0.1–0.8 mm long arms. The spines are irregularly placed and nearly always with secondary spines. On the largest crosses the spines are mostly simple and vertical. The ventral crosses of the small specimen (5–7) fall into two size groups; by far the greater number of crosses have arm lengths of 0.08–0.10 mm, but scattered crosses with about 0.3 mm long

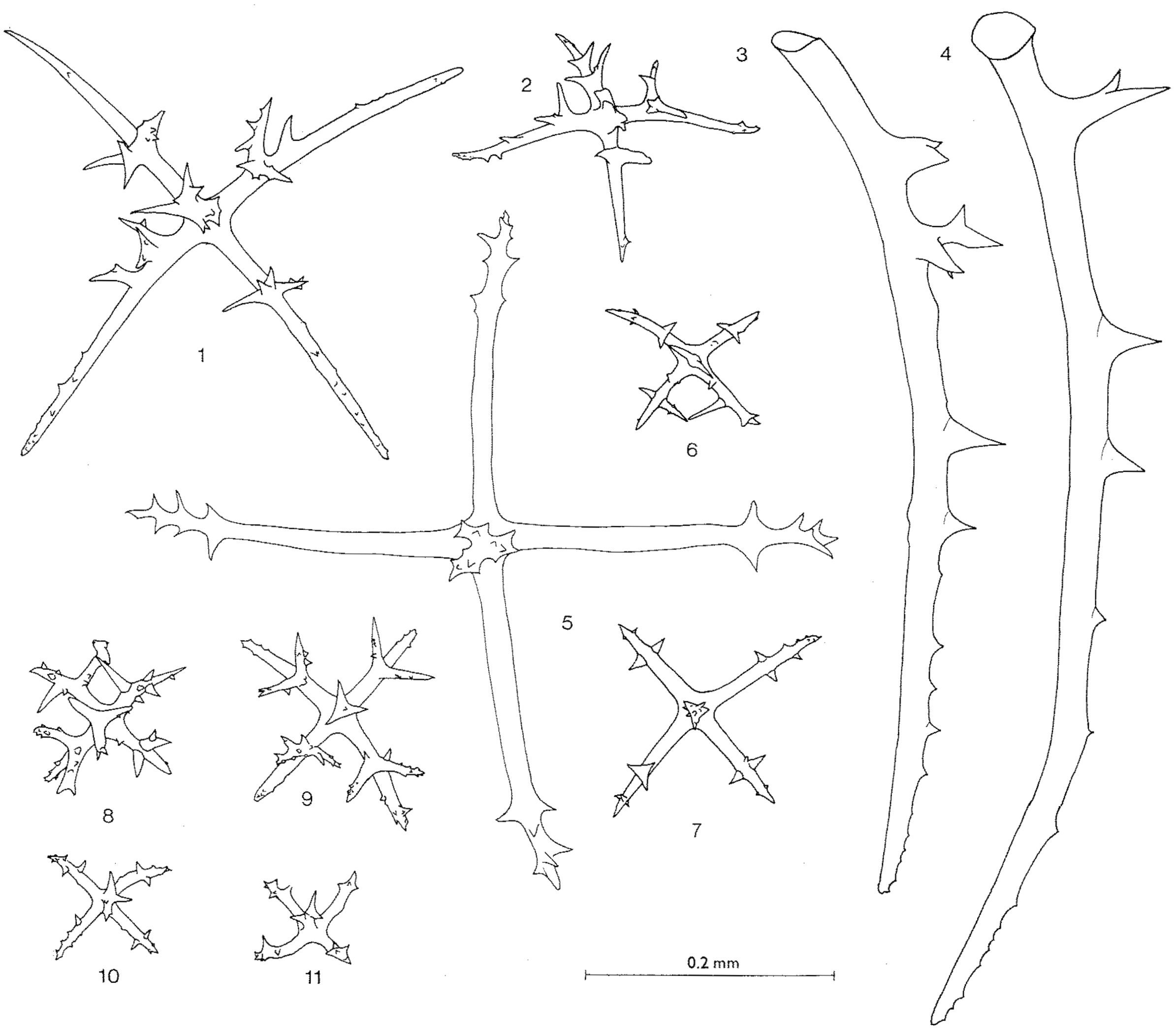


Fig. 51. *Psychropotes longicauda.* Deposits. St. 716. 1–4, dorsum of the 6 cm long specimen; 5–7, ventrum of same; 8–9, dorsum of a 17 cm long specimen; 10–11, ventrum of same.

arms do occur. The spines of the giant crosses are confined to the distal half of the arms and are almost exclusively horizontal. The central apophysis has a smooth proximal part, while the end is spinous and tripartite. The arms of the small crosses are curved upwards, while the arms of the large crosses are horizontally curved in an irregular manner.

Giant crosses are absent, both in dorsum and ventrum, in the four large specimens. The dorsal crosses of these specimens (8–9) have 0.07–0.10 mm long arms which are often strongly spinous. The proximal spine on each arm is, in most crosses, large and bipartite. The ventral crosses (10–11) are similar to those of the small specimen, but the arms are only 0.05–0.07 mm long.

Western Indian Ocean: Sts. 234 and 235 (Pl. VII: 4).

Body length 9–18 cm.

Colour varying from yellow with a yellow-brown ventral side, to light violet with a darker violet or violet-brown ventral side. The underside of the head is dark violet in all the specimens.

Tentacles 18 (in one specimen 17).

Anterior brim only feebly demarcated from the remaining part of the head. The dorsal radial elevations, which are usually conspicuous in the species, are absent, or only feebly developed. The tubefeet enclosed in the brim cannot be counted with certainty. Probably, about 10 pairs are present.

Free, ventrolateral tubefeet large and well spaced. The distinction between the free tube-

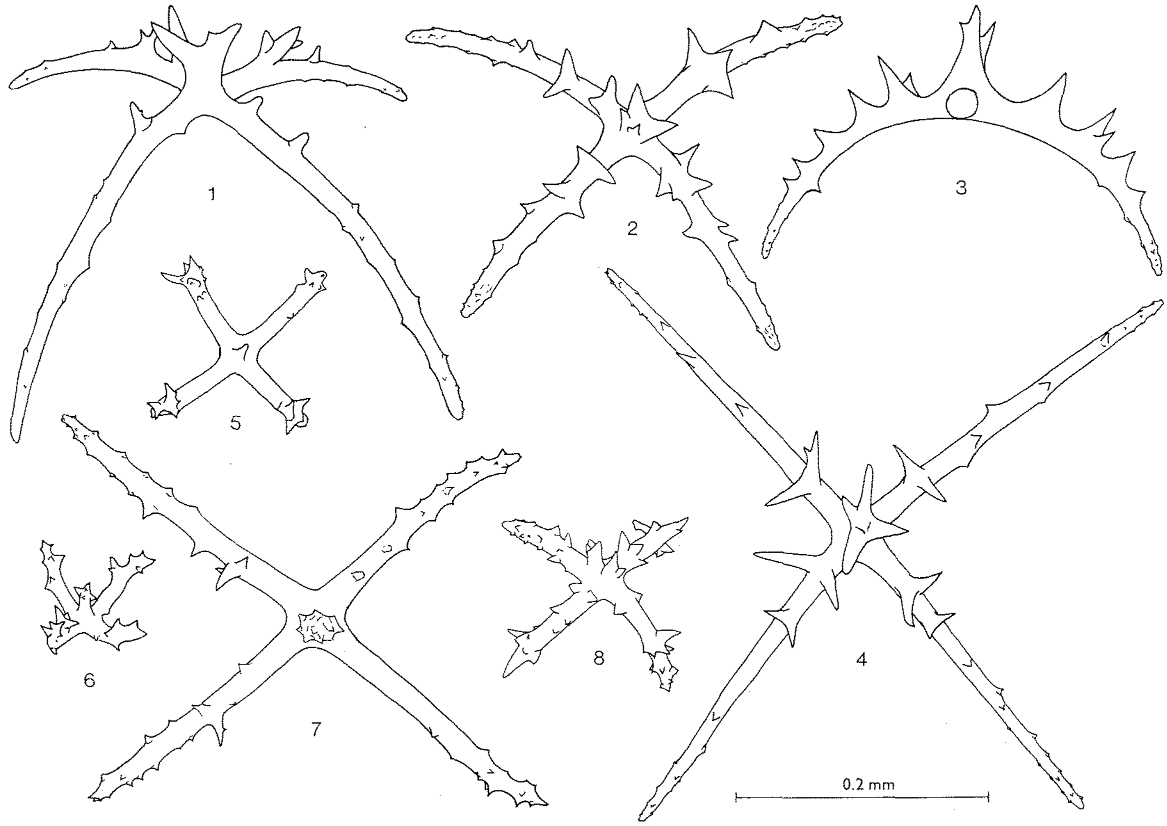


Fig. 52. *Psychropotes longicauda.* Deposits. 1–7, St. 234 (1–2, dorsum; 3–4, unpaired appendage; 5–7, ventrum); 8, St. 235, dorsum of the 18 cm long specimen (the other, and smaller, specimens from the station have dorsal deposits similar to those from St. 234).

feet and those of the anterior and posterior brim is more gradual than usually found in the species; 11–20 pairs of free, ventrolateral tubefeet are present.

Posterior brim with 6–9 pairs of tubefeet.

Dorsal papillae minute and few in number. Two specimens possess one papilla each (about 1 mm long), and one specimen (the largest one) has two papillae (1 and 2 mm long). No papillae were found in the other specimens.

Unpaired dorsal appendage measuring $^{1}/_{3}$–$^{2}/_{3}$ body length, and placed close to posterior end of body.

Deposits (Fig. 52). The dorsal crosses (including those of the unpaired appendage) are irregularly spinous. The largest of the specimens (an 18 cm long specimen from St. 235) has robust and spinous crosses (8) with arms only occasionally exceeding 0.15 mm in length. The other specimens (9–15 cm long) have dorsal crosses with a maximum arm length of 0.25–0.35 mm (1–4). Scattered crosses with predominantly vertical spines (3) are present in some preparations; all intermediates are found between these crosses and the normal, large type.

The ventral crosses (5–6) have 0.04–0.09 mm long, upwardly curved arms with distal spines and a central apophysis which is often rudimentary. Very scattered large crosses (7) with 0.2–0.3 mm long and slightly horizontally curved arms were present in the preparations from four specimens (9, 10, 11, and 13 cm long), but absent in those from the remaining seven specimens (12, 13, 14, 15, 16, 16, and 18 cm long). In this region also, the large type of cross is found mainly in smaller specimens.

Synonymy:

The *Galathea* specimens of *P. longicauda* vary strikingly in body colour, shape of the anterior brim, number of dorsal papillae, length of unpaired appendage, number of free, ventrolateral tubefeet, number of tubefeet included in the posterior brim, and shape and size of dorsal and ventral deposits. Owing to this variation a number of synonyms are proposed in the following. An analysis of the variation is attempted, based on a comparison of the *Galathea* specimens with previously described specimens, many of which have been re-examined.

Below, the previously described material is reviewed according to geographic regions.

North Atlantic. Three species *(P. buglossa, P. fucata,* and *P. grimaldii)* have been described from this region and are unknown from other regions. A total of 36 specimens (in MNHN and MOM) representing all the three species and ranging in size from 5 to 18 cm, were re-examined (24 by means of preparations of the dorsal and ventral skin). It was found that the differences used to distinguish the three species are individual variations only. Moreover, all the North Atlantic specimens have features in common which to some degree distinguish them from specimens from other regions, although scarcely to a degree which justifies the erection of a North Atlantic geographic subspecies.

Colour varying from yellow to violet. Tentacles 18 (only one specimen had 16), and similar in shape to those of the *Galathea* specimens. Anterior brim with conspicuous radial elevations on the dorsal side. Tubefeet, 8–10 pairs of free, and 5–6 pairs of fused posterior ones. (Perrier stated that in the smallest specimens the lateral tubefeet were connected by a brim; this feature could not be verified, because of the poor state of preservation). Unpaired appendage varying in length almost as much as in the specimens from the Kermadec Trench. Midventral tubefeet present in all the specimens, including that of *P. grimaldii.* (Hérouard doubted that midventral tubefeet were present in this species).

Dorsal crosses characteristically shaped. Their arms are strongly curved and have high, vertical, smooth spines and a central apophysis which is often subdivided. The proximal spine on each arm is usually much higher than the others; often no other large arm spines are present. The crosses figured by Perrier (1902) for *P. buglossa* and *P. fucata,* and by Hérouard (1902) for *P. grimaldii* all belong to this type, having predominantly vertical arm spines.

The dorsal crosses differ greatly in size range from one specimen to another. In all the specimens the smallest crosses have arm lengths of 0.1 mm or less, but the upper size limit varies from slightly more than 0.1 to about 0.6 mm in arm length. An inverse correlation is indicated between maximum size of crosses and size of specimens.

Ventral crosses with 0.05–0.10 mm long arms which are usually curved upwards. The arms possess small spines in their distal half and are not as varying in shape as those found in Kermadec specimens. In addition to these small crosses, some specimens have scattered crosses with 0.2–0.4 mm long arms. The large ventral crosses, like the large dorsal ones, are usually found in smaller specimens. Of 25 specimens examined, five possessed large, ventral crosses; these specimens measured 5–13 cm, whereas the specimens without large crosses measured 10–18 cm. In the 5 cm long specimen (the smallest known from the North Atlantic) the large crosses were particularly abundant.

Southern Ocean. The seven *Challenger* specimens of *Psychropotes longicauda,* all taken in this region, were re-examined. They have shrunk in the alcohol subsequent to the original examination by Théel. The body length mentioned below, unless otherwise stated, is the length found during re-examination.

St. 156 (Antarctic part of the Indian Ocean): One defective specimen, 8 cm long (according to Théel), in BM.

St. 157 (Antarctic part of the Indian Ocean): The type specimen, 10 cm long, in BM. Another specimen, 8 cm long, in MNHN. Two specimens of var. *fusco-purpurea:* One, 15 cm long (20 cm according to Théel), in BM; the other, 9 cm long, in MNHN. One specimen of var. *monstrosa,* 19 cm long (25 cm according to Théel), in BM.

St. 298 (off Valparaiso, Chile): One specimen, 20 cm long, in BM.

Agatep (1967b) reported 14 specimens of *P. longicauda* from eight Antarctic stations of the *Eltanin* (seven situated south of the Atlantic Ocean and one south of the eastern Pacific).

Vaney (1908) described three specimens from the Weddell Sea, not far from the seven *Eltanin* stations. One was described as *P. longicauda* var. *antarctica,* and the other two as new species, *P. brucei* and *P. laticauda,* both taken at the same station. Another specimen referred to the latter species was taken southwest of South Africa.

Colour. The specimen of *P. brucei* was yellowish grey. The others were violet.

Tentacles 18, of the usual shape in the species. Dorsal appendage placed close to posterior end of body, with a variation in length from one-fifth to almost the same length as the body. Anterior brim (verified in the *Challenger* specimens) of the usual type, with dorsal, radial elevations.

Most of the Antarctic specimens have a high number of tubefeet, placed almost without intervals. The transition to the fused tubefeet of the anterior and posterior brim is, accordingly, more gradual than usually found in the species. The ventrolateral tubefeet (as seen in some of the re-examined *Challenger* specimens) may be retracted, appearing only as low, inconspicuous elevations of the skin. The number of tubefeet (including those of the posterior brim) seems usually to be about 25–40 pairs, thus far exceeding the number in North Atlantic specimens, and also, with little overlapping, those in the Kermadec specimens. The specimens described as *P. laticauda* and *P. brucei* had only 16–17 pairs of tubefeet (according to Vaney), the free, lateral ones being widely spaced. This number is in the lower part of the variation found in the Kermadec specimens. The specimen figured by Agatep had more than 24 pairs.

The tubefeet included in the posterior brim amount to 5–9 pairs, thus exceeding the number in the Kermadec and Tasman Sea specimens.

The deposits in the specimens from *Challenger* Sts. 156 and 157 were found to resemble those in the *Galathea* specimens from the Kermadec Trench. (The deposits had dissolved, already at Théel's examination, in the specimen from St. 298).

According to Théel, the dorsal crosses measure 0.06–0.40 mm in arm length, and each arm is provided with "a number of strong, short spines directed outwards". The variety *fusco-purpurea* constituted an exception, the arms of the crosses being only 0.1 mm long and each with a conspicuous, bipartite spine.

The re-examination confirmed that both specimens of var. *fusco-purpurea* agreed with Théel's description. This was also the case with the other *Challenger* specimens, although differences were present both in the shape and size of the deposits. The largest dorsal crosses were found in the two smallest specimens.

The 8 cm long specimen from St. 157 had arms up to 0.6 mm long. The proximal arm spine was often much higher than the other spines (Fig. 53). The deposits resembled those found in North Atlantic specimens.

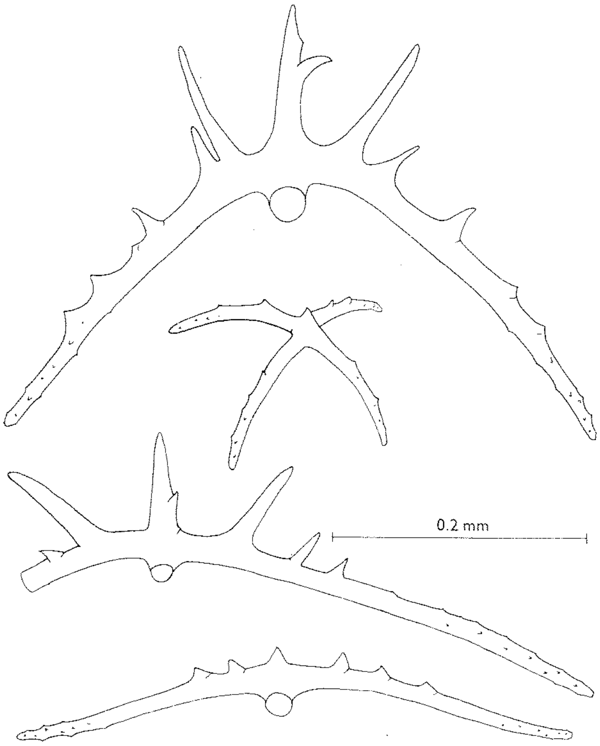


Fig. 53. *Psychropotes longicauda.* Dorsal deposits. *Challenger* St. 157 (the 8 cm long specimen in MNHN).

The 8 cm long specimen from St. 156 had arms up to 0.4 mm long. The arm spines were high and vertical as in the other small specimen, but the proximal spine was not notably higher than the other spines. The crosses resembled the larger crosses in the Kermadec specimens (Fig. 49: 1–4).

The 10 cm long specimen from St. 157 (the type) had arms up to 0.2 mm long. The arm spines were vertical but rather low. Some of the small crosses had bipartite arm spines.

The specimen of var. *monstrosa* had dorsal crosses with arms up to 0.2 mm long. The arm spines were either vertical, or irregularly placed. Often, the proximal arm spine was irregularly bipartite. The ventral crosses had 0.06–0.08 mm long upwardly curved arms. In shape they resembled some of those from the Kermadec Trench (Fig. 49: 17, 18, 20). The ventrum also possessed scattered large crosses, with arms 0.2–0.3 mm long. They were similar to the usual large type in the species – with horizontal spines confined to the distal half of the arms, and with the arms more or less horizontally curved.

The deposits of the *Eltanin* specimens, according to Agatep's illustrations, agree with the small type in the *Challenger* and *Galathea* specimens. Apparently, crosses with double arm spines were common. Large crosses were not mentioned. Vaney's two species, *P. laticauda* and *P. brucei,* had also similar deposits, with the exception that crosses with supernumerary arms occurred among the normal crosses. Vaney stated that deposits with six arms occur in *P. laticauda.* (Among the three figured crosses there is one with a bifurcate arm, but none with six arms; among the three crosses illustrated for *P. brucei* there is one with five arms, but for this species the occurrence of deposits with more than four arms was not mentioned in the text). The fact that the specimens of the two species came from the same station suggests that the presence of crosses with supernumerary arms is a local feature in the variation of the deposits.

Eastern Central Pacific. From this region are known the five specimens from *Galathea* St. 716; three specimens of *P. raripes,* comprising the type specimen described by Ludwig (1894) and the two specimens described by Clark (1920); the single specimen known of *P. dubiosa* Ludwig (1894); and the two specimens known of *Euphronides dyscrita* Clark (1920). Re-examination was made of one of Clark's specimens of *P. raripes* (17 cm long, in MCZ), and of both specimens of *E. dyscrita* (a 3.5 cm long specimen in MCZ, and a 7.5 cm long specimen in USNM).

Although the two specimens of *E. dyscrita* are in a poor condition, their identity with *P. longicauda* can scarcely be doubted. The unpaired appendage is inserted close to the posterior end of the body, and its length is within the variation of this species. The colour was yellowish-brown with the ventral side violet, a colour variation which is known to occur only in *P. longicauda.* According to Clark, both specimens possessed a "well-marked, lobed margin" round the body. This feature (which could no longer be verified) recalls the conditions mentioned by Perrier for small-sized North Atlantic specimens.

The specimen of *P. dubiosa* (in USNM), 3.1 cm long, was too defective to be re-examined. The juvenile features included the number of ten tentacles and the presence of large ventral crosses having 0.3 mm long arms with distal spines. (The central apophyses, which were smooth and pointed, might have lost the distal spines). The dorsal crosses were rather large (arm length 0.15–0.17 mm), but giant crosses were not mentioned. As typical of the eastern Pacific specimens there was one prominent spine on each arm; however, the spine was usually tripartite, not bipartite as in other eastern Pacific specimens examined. There was on each side 12 closely placed tubefeet, and five pairs were included in the posterior brim. The unpaired appendage was equal in length to the body and almost terminal in position.

In the number of free, ventrolateral tubefeet and in the number of tubefeet included in the posterior brim, the eastern Pacific specimens are similar to those from the North Atlantic. They differ in the shape of the dorsal crosses, which are characterized by the almost constant presence of a large, bipartite spine on each arm. As in the Kermadec Trench and the North Atlantic an inverse correlation is indicated between the size of the specimens and the maximum size of the crosses. While the larger specimens had arm lengths of about 0.1 mm, *E. dyscrita* and *P. dubiosa* had dorsal crosses with arm lengths up to 0.3 mm. The latter were similar both in size and shape to those in the small *Galathea* specimen (Fig. 51: 1–2); true giant crosses were, however, not present in *E. dyscrita* and *P. dubiosa.* The ventral deposits (examined only in the largest of the *dyscrita* specimens) were similar to the smallest ventral deposits in the *Galathea* specimens; giant crosses were not found.

Giant ventral crosses were present in the 3.1 cm long specimen of *P. dubiosa,* the 6 cm long *Galathea* specimen (arm length in both specimens 0.3 mm), and the 12 cm long type specimen of *P. raripes* (arm length 0.16 mm).

Okhotsk Sea. Ohshima (1915, 1916–1919) described five specimens of *P. raripes* from this region. They had 7–9 pairs of free, ventrolateral tubefeet, and (judging from the illustrated specimen) about 6 pairs included in the posterior brim. In number and distribution of the tubefeet the specimens thus agreed with those from the eastern Pacific and the North Atlantic. The deposits had dissolved.

Kurile-Kamchatka Trench. *Nectothuria translucida* Belyaev & Vinogradov is known from one pelagic specimen taken in a closing-net at 4940–5930 m. It was 3.2 cm long, transparent, with a long unpaired appendage inserted at the posterior end of the body, and the tubefeet fused into a continuous brim round the body. The deposits were rather similar to those of the equally small juvenile specimen from *Galathea* St. 663, consisting dorsally of spinous crosses with up to 0.5 mm long arms, and ventrally of crosses with 0.12–0.25 mm long arms. The *Galathea* specimen, which was not transparent, might just have settled after a pelagic life.

Variation:

Colour varying from a uniformly yellow to dark violet. Many specimens are yellow on the dorsal side and violet on the ventral. Apart from the uniformly yellow specimens, all others are darker ventrally than dorsally.

The whole range of variation in colour is present in each of the following regions: The North Atlantic, the Indian Ocean, the Kermadec Trench, the Southern Ocean, and the eastern Pacific. Although the body colour does not exhibit geographic variation, a narrow local variation may occur, as indicated by the differences in body colour between the specimens from Sts. 663 and 664 in the Kermadec Trench.

Tentacles 18, with almost no exception.

The variation in number of tubefeet and papillae is shown in Table 16.

Anterior brim usually with conspicuous, radial elevations on the dorsal side. They are absent in the specimens from the Indian Ocean and in three specimens from St. 664 in the Kermadec Trench. Besides, they are usually absent in the smallest specimens in all localities.

Table 16. *Psychropotes longicauda.* Number of pairs of ambulacral appendages.

	Dorsal papillae	Tubefeet of anterior brim	Free, ventrolateral tubefeet	Tubefeet of posterior brim
North Atlantic	3–7	c. 14	8–10	5–6
Western Indian Ocean	–	–	c. 11–14	6–9
Southern Ocean	2–7	7–15	(8) 18–32	5–9
Tasman Sea	–5	12–14	14–15	2–3
Kermadec Trench	2–6	10–13	7–21	2–4
Eastern Pacific	5–7	9–24	7–12	5–7
Japan	4–8	12–14	7–9	–

Geographic differences in the number of tubefeet included in the anterior brim can scarcely be demonstrated. The highest numbers (16–24 pairs) were found in the eastern Pacific *Galathea* specimens; however, the type specimen of *P. raripes* from the same region had only 9 or 10 pairs.

Free, ventrolateral tubefeet apparently showing a geographic variation. The number is low in specimens from the North Atlantic, eastern Pacific, and off Japan, whereas it is usually high in Antarctic specimens. In the smallest specimens the bases of the tubefeet may be enclosed in a low fold of the skin.

Posterior brim. The tubefeet number included in the posterior brim is remarkably low in the Tasman Sea and the Kermadec Trench where most specimens have 2 or 3 pairs of tubefeet in the brim. In other localities at least five pairs are included in the brim.

In specimens from the western Indian Ocean the transition between free and fused tubefeet is rather gradual, and the anterior and posterior brims occupy a larger part of the body side than is usual in the species.

Dorsal papillae minute. A geographic variation in number cannot be demonstrated.

Unpaired dorsal appendage placed close to posterior end of body. No variation is found in its position. The length varies from one-fifth to the same length as the body. The variation is a purely individual one, with no correlation to the size of the specimens, or to locality.

Deposits. A geographic variation is present in the shape of the dorsal crosses. The North Atlantic specimens have dorsal crosses with high, vertical, and smooth spines, of which the proximal one on each arm is often the only large spine present. The deposits which differ most from this type are found in the eastern Pacific specimens; the crosses here are strongly spinous, the spines being covered with secondary spines; one large, bipartite spine is usually present on each arm, but otherwise the spines are irregularly shaped and arranged.

The specimens from the Southern Ocean and the Kermadec Trench have greatly varying deposits which bridge the gap between the North Atlantic and the eastern Pacific types.

The specimens formerly referred to the species *P. brucei* and *P. laticauda* (Weddell Sea and southernmost part of the Atlantic) apparently have more than four arms in some of the crosses.

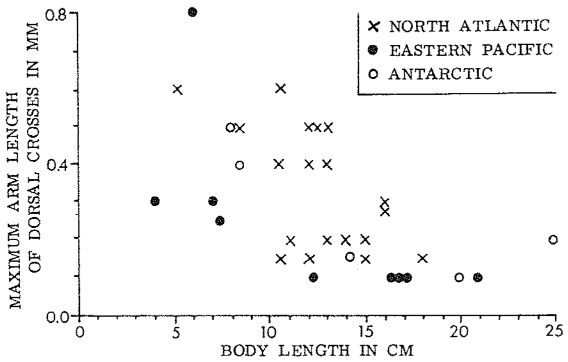


Fig. 54. *Psychropotes longicauda.* Maximum arm length of dorsal crosses in relation to body length.

This may represent a geographic or local variation; deposits with more than four arms have not otherwise been found in *P. longicauda.*

The ventral deposits probably show no geographic variation. In the Kermadec Trench the variation in shape comprised the whole variation found in the species.

An age variation is present in the size of the crosses. In the specimens from the North Atlantic, the Antarctic, the Kermadec Trench, and the eastern Pacific the maximum arm length of the dorsal crosses decreases on an average with the size of the specimens (Fig. 54).

The ventral crosses belong to two size groups. Crosses with arms smaller than 0.1 mm are abundant in all the specimens, and are usually the only deposits present. (One specimen from St. 664 in the Kermadec Trench, however, had only rod-shaped deposits in the ventrum). Large scattered crosses, with arm lengths of 0.2–0.3 mm, are found mainly in smaller specimens.

Conclusion. A *geographic variation* is shown by the shape of the dorsal crosses, by the number of free ventrolateral and fused posterior tubefeet, and by the presence or absence of radial elevations on the head. The variation in each feature is largely independent. A division of the species into geographic subspecies cannot be made on the basis of our present knowledge.

A *local variation* in body colour was found between specimens from two *Galathea* stations in the Kermadec Trench.

An *age variation* is shown by the presence of large, juvenile crosses both in dorsum and ventrum, and by the fact that the tubefeet in specimens up to 5–6 cm in length are fused to form a continuous brim. A number of 12 tentacles was present in the 3.2 cm long specimen from St. 663; already at a body length of 5–6 cm the full number of 18 tentacles is attained.

Relationships: A large unpaired dorsal appendage placed close to the posterior end of the body is found also in *P. loveni* which possibly represents a juvenile stage of *P. longicauda.* No other species can be pointed out as being particularly close to *P. longicauda.*

Distribution: Cosmopolitan, 2210–5173 m.

Type: BM, labelled "Type".
Type locality: *Challenger* St. 157 (53°55'S, 108°35'E).

Psychropotes loveni Théel, 1882

Fig. 55

Théel 1882, p. 100, pls. XXVII: 2–4, XXXV: 1–3.

Diagnosis: Tentacles 10–12. Dorsal papillae minute. Unpaired dorsal appendage large and placed close to posterior end of body; base of appendage as broad as the body. Brim continuous round the body. Dorsal deposits with a high and smooth central apophysis; arms up to 0.5 mm long, and usually with only one large spine on each arm. Ventral deposits with a low and spinous central apophysis, or with no apophysis; arms up to 0.2 mm long, with small spines only.

Material:
St. 668, Kermadec Trench (36°23'S, 177°41'W), 2640 m. – 2 specimens.

Description: The two specimens are 2.5 and 2.0 cm long, and very defective. The unpaired appendage as well as large parts of the skin are lacking.

Skin whitish and soft.

Tentacles 12 in both specimens. Discs with about 20 marginal knobs. On all the tentacles most or all of the knobs are retracted.

Brim (preserved in patches only) continuous round the body.

Midventral tubefeet very small but present throughout length of ventral sole.

Deposits (Fig. 55). Dorsal crosses very uniform in appearance, with a high and smooth central

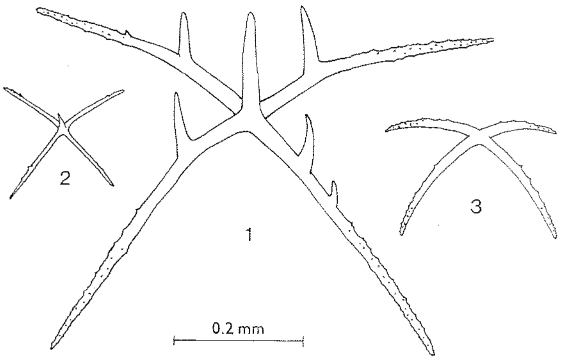


Fig. 55. *Psychropotes loveni*. Deposits. St. 668. 1–2, dorsum; 3, ventrum.

apophysis, and four high and smooth arm spines; additional spines rarely present. Arms up to 0.5 mm long. Ventral crosses (preserved in one of the specimens only) with regularly curved and tapered arms which are up to 0.2 mm long; central apophysis absent; arm spines very small.

Remarks: The reference to *Psychropotes loveni* is based primarily on the dorsal crosses which are of the same characteristic shape (although almost twice as large) as those in the *Challenger* specimen (the type). The ventral crosses differ by the complete absence of a central apophysis.

The small size of the specimens and the low number of tentacles (the type is about 5 cm long and has 10 tentacles) suggest that all the known specimens of *P. loveni* are juveniles.

In external features the specimens resemble the 3.2 cm long juvenile of *P. longicauda* from St. 663. However, the deposits in *P. loveni* are outside the known variation of *P. longicauda*.

Distribution: Southwestern Indian Ocean, 2514 m. Kermadec Trench, 2640 m.

Psychropotes sp.

St. 217. One specimen, 7.5 cm long and 1.5 cm broad. Tentacles 18. Brim continuous round the body. Unpaired appendage 0.5 cm long, close to posterior end of body. Skin gelatinous, light violet, ventral side of head dark violet. Deposits strongly corroded.

Family **ELPIDIIDAE** Théel, 1879

Diagnosis: Tentacles 10–12. Ventrolateral tubefeet large, well spaced, and usually few. Midventral tubefeet absent. Calcareous ring consisting of five star-shaped pieces.

Taxonomy: The taxonomic position of the family is considered in the General Part (pp. 206–207), where the view is advanced that the family represents a paedomorphic trend of evolution.

In the present section only the subdivision of the family is discussed. The question of the correct basis of this subdivision has been subject to divergent opinions by earlier authors. This was partly due to the fact that divisions based on the external characters were difficult to reconcile with divisions based on the deposits, and partly to different opinions regarding the phylogeny of the deposits.

The views presented here with regard to the phylogeny of the deposits (pp. 183–185) and the calcareous ring (pp. 187–189) in the Elpidiidae lead to a new evaluation of the interrelationship of the genera.

1. – Earlier systems of the Elpidiidae. Théel (1882), who established the original system for the family, based the genera mainly on external characters. *Peniagone* was defined by the large velum (an anterior, dorsal appendage composed of two or three pairs of fused papillae); *Parelpidia* by the elongated, *Synapta*-shaped body and the reduced dorsal papillae; *Scotoanassa* by the depressed body form; and *Achlyonice* by the number of 12 tentacles.

Théel regarded the deposits as less important taxonomically. *Peniagone* included species with four-armed deposits and one species *(Amperima naresi)* with three-armed deposits. Other species with four-armed deposits were referred to *Elpidia,* despite the fact that the type species of this genus *(E. glacialis)* had completely different deposits.

The genera *Kolga* and *Irpa* were separated by an anatomical feature, the stone canal in *Kolga* opening to the exterior, in *Irpa* to the body cavity.

The genus *Enypniastes* was characterized by the large anterior brim composed of both dorsal and ventrolateral papillae, and by the presence of 20 tentacles.

R. Perrier (1902) primarily based his system on the deposits and thereby attained a more natural grouping of the species. He reserved the genus *Elpidia* for the species *E. glacialis* which possesses spicules of a type otherwise unknown in the holothurians. He defined *Scotoplanes* by the presence of rods in addition to C-shaped spicules, and united species simultaneously possessing C-shaped and tripartite spicules into a new genus, *Periamma*. (Pawson (1965a) pointed out that the name *Periamma* was preoccupied and changed it to *Amperima*). The genera *Scotoplanes* and *Periamma (=Amperima)* together embraced all Elpidiidae with C-shaped spicules.

Species with four-armed spicules were by Perrier collected into four closely related genera, distinguished by the shape of the body, and by the presence or absence of a velum. Of these genera, *Parelpidia* and *Scotoanassa* were defined in accordance with Théel, whereas *Peniagone* was given another content – being no longer defined by the presence of a particularly large velum. In Perrier's system this genus included species with four-armed spicules, an elongatedly oval body, and a velum (whether or not the latter was large), while species having a similar body form, but with separate dorsal papillae, were referred to a new genus, *Elpidiogone*.

Hérouard (1902) proposed a system based exclusively on external characters. This constituted no improvement of Théel's system and needs no comment – particularly since Hérouard himself later replaced it by another system which, similar to that of Perrier, was primarily based on the deposits.

In his new system, Hérouard (1923) adopted most of Perrier's generic definitions. However, the presence or absence of a velum was discarded as a generic character. The genus *Elpidiogone* was accordingly regarded as a synonym of *Peniagone*. On the other hand, the genus *Scotoplanes* was restricted to species possessing both anterior and posterior dorsal papillae, whereas species in which all the papillae were anteriorly placed (whether or not the papillae were fused into a velum) were referred to a new genus, *Ellipinion*.

The genus *Rhipidothuria* Hérouard, 1901, with the single species *R. racowitzai*, was regarded as closely related to *Peniagone* – differing only in having small papillae throughout the length of the dorsal radii.

Enypniastes Théel, 1882, and *Euriplastes* Koehler & Vaney, 1905, together with *Pelagothuria* Ludwig, 1894, were united to form the family Cyclioninae. As pointed out by Ekman (1926) the correct name of this family is Pelagothuriidae Ludwig, 1894. The family is not included in the present work.

Although Hérouard's revised division of the family into genera did not differ essentially from that of Perrier, he did advance an entirely new idea concerning the generic interrelationship. Based on theoretical considerations on the phylogeny of the deposits, the genera were regarded as belonging to two evolutionary trends – one comprising the genera with four-armed deposits, the other all the remaining genera, the deposits of the latter being derived from a single, "trinary" type.

Ekman (1926) replaced Hérouard's theory by yet another, contending that some holothurian deposits are derivatives of a primary cross, while others are derived directly from a primary rod. Based on this theory, he divided the Elpidiidae into two subfamilies, Elpidiinae and Peniagoninae. Although based on completely different theoretical considerations, these subfamilies were identical to the two evolutionary trends assumed by Hérouard.

The Elpidiinae (comprising the genera *Elpidia, Kolga, Irpa, Scotoplanes, Ellipinion, Amperima,* and *Achlyonice)* were characterized by the absence of primary cross derivatives (apart from the occasional presence of wheel-shaped deposits in some species).

The Peniagoninae (comprising the genera *Peniagone, Parelpidia, Scotoanassa, Elpidiogone, Psychrelpidia,* and, with some doubt, *Rhipidothuria)* were characterized by the presence of both primary cross and primary rod derivatives.

Ekman's theory, along with Hérouard's, is contradicted in the present investigation (pp. 183–185). No support was found of the idea that the genera of the Elpidiidae represent two evolutionary lines.

2. – Taxonomic characters. The shape of the body, used to characterize the genera *Parelpidia* and *Scotoanassa,* would appear to be unfit for generic distinctions. In actual fact, these genera merely represent two extremes in the variation of the genus *Peniagone,* being interconnected with typical representatives of the latter genus by species intermediate in shape. Accordingly, *Parelpidia* and *Scotoanassa* are regarded here as synonyms of *Peniagone*.

The following features provide information on the interrelationship of the genera:

(1) *The deposits.* The finding (p. 184) that the tripartite and rod-shaped spicules are reductional stages of primary crosses, and not representing a separate line of evolution, reduces the taxonomic importance of the different types of spicule. However, although the deposits do not justify a division of the family into two subfamilies, they remain of primary importance in characterizing the genera and also provide information on intergeneric relationships.

Psychrelpidia, Rhipidothuria, and *Peniagone* possess primary crosses (or crosses with reduced stem). Also in other respects they occupy an original position within the family.

Achlyonice and *Amperima* have tripartite spicules, while *Ellipinion* and *Scotoplanes* have rods. The three latter genera have in common the presence of C-es, a spicule type related to the curved rods found in *Kolga* and *Irpa.*

Among the spicules occurring in the family, those of *Elpidia* are the most deviating, representing a specialized development from rod-shaped spicules.

Wheel-shaped deposits occur scatteredly in a few, mutually unrelated species of the family (pp. 185–186; Fig. 93).

(2) *The calcareous ring* (Fig. 95). The view that the Elpidiidae represent a paedomorphic trend of evolution is based, in particular, on a study of the calcareous ring. However, the unique development which has taken place in the calcareous ring within this family not only supplies information on the derivation of the family as a whole but also provides a means of distinguishing between primitive and specialized genera, analogous to the conditions found in the deposits. The genera of the Elpidiidae may be divided into three groups of relationship according to the structure of the calcareous ring (pp. 187–189).

(3) *The velum* is in all probability an original feature in the family (p. 190).

(4) *The tentacles.* Deviations from the number of 10 tentacles are found in the genus *Achlyonice* (10–12) and in *Peniagone islandica* (8).

Differences in the shape of the tentacle discs may characterize genera and species (p. 192).

(5) *The gonads.* The presence of paired gonads is one of the primitive features of *Psychrelpidia* and *Peniagone.* Differences in the external morphology of the gonads are of little taxonomic importance in the family (pp. 194–195).

(6) *The rectal caecum.* The absence in the primitive genera *Psychrelpidia* and *Peniagone* of a rectal caecum indicates that the latter is an organ developed within this particular family (p. 192).

3. – Interrelationship of the genera. The above considerations on the taxonomic characters within the family lead to a reduction in the number of genera from 13 to 10.

(1) *Psychrelpidia* Hérouard forms a link between the three families which are united here to form the suborder Psychropotina (pp. 206–207).

(2) *Rhipidothuria* Hérouard, with the single species *R. racowitzai,* has four-armed deposits, a similarity to *Psychrelpidia* and *Peniagone.* Papillae are present throughout the length of the dorsal radii. The two anteriormost pairs, which are placed close together on an elevation of the skin, apparently represent a velum. The difference between *Rhipidothuria* and *Peniagone* thus consists in presence or absence of papillae on the posterior part of the dorsum. The structure of the calcareous ring is unknown.

(3) *Peniagone* Théel includes *Parelpidia* Théel, *Scotoanassa* Théel, and *Elpidiogone* R. Perrier as synonyms. These genera were distinguished from *Peniagone* by external features which show a gradual transition to those of *Peniagone.*

Four-armed spicules are common to all the genera synonymized. Among these spicules, those having an unreduced primary rod (the primary crosses) are the most primitive – representing the prototype of spicule within the suborder Psychropotina.

The calcareous ring resembles the embryonic ring of other holothurians, and represents a type from which the rings of the other genera may be derived. The paired gonads and probably also the absence of a rectal caecum (both features shared with *Psychrelpidia)* are further primitive features.

(4) *Achlyonice* Théel resembles *Amperima* in the presence of tripartite spicules, and *Peniagone* in the structure of the calcareous ring. The absence of C-shaped spicules represents a difference from *Amperima,* to which *Achlyonice* is probably not closely related. The presence of tripartite spicules in both genera may be due to convergence.

(5) *Amperima* Pawson (=*Periamma* R. Perrier) is closely related to *Ellipinion* and *Scotoplanes* as indicated by the presence of C-shaped spicules in all species of the three genera. A less close

relationship is shown to *Kolga* and *Irpa,* both of which possess curved rods which are reminiscent of C-es. C-shaped spicules are otherwise absent in the Elasipoda.

The calcareous ring is similar in *Amperima, Ellipinion,* and *Scotoplanes,* as the pieces are isolated from each other and each one has four pairs of arms. This type of ring is here regarded as a derivative of the type found in *Elpidia* and *Irpa.*

The three genera differ in the arrangement of the dorsal papillae and in the type of spicule. *Amperima* and *Ellipinion* possess a velum, whereas in *Scotoplanes* the second and third pairs of papillae are placed on the posterior part of the dorsum. On the other hand, *Ellipinion* and *Scotoplanes* both possess rod-shaped spicules, whereas the spicules are tripartite in *Amperima.*

In the report on the hadal specimens (Hansen 1956) the genus *Ellipinion* was considered a synonym of *Scotoplanes.* The latter genus was defined according to R. Perrier (1902), who regarded the presence of rod-shaped spicules as being more significant than the different position of the dorsal papillae. In accordance with the generic distinctions presented here, the species *Scotoplanes galatheae* Hansen, 1956, is transferred to the genus *Ellipinion.*

(6) *Ellipinion* Hérouard is discussed under *Amperima.*

(7) *Scotoplanes* Théel comprises *S. globosa* and *S. clarki.* The genus is discussed under *Amperima.*

(8) *Kolga* Danielssen & Koren, with the single species *K. hyalina,* resembles *Irpa* in the shape of the tentacles, the external morphology of the gonads, and the presence of curved rods and irregularly ramified deposits. The curved rods indicate a relationship to *Amperima, Ellipinion,* and *Scotoplanes. Kolga* differs from all four genera by the structure of the calcareous ring which has some similarity to the *Peniagone* type.

(9) *Irpa* Danielssen & Koren comprises *I. abyssicola* and *I. ludwigi,* the latter being transferred from *Kolga.* The calcareous ring is similar to that of *Elpidia.* In other features the genus is closest to *Kolga* (q. v.).

(10) *Elpidia* Théel occupies an isolated position within the family. It has a spicule type which is unique in all holothurians, and has lost every trace of a velum. The calcareous ring is highly specialized and similar to that of *Irpa.*

Key to the genera of Elpidiidae

1.	Deposits four-armed	2	
1.	Deposits not four-armed	4	
2.	Anterior brim present, composed of dorsal and ventrolateral papillae	*Psychrelpidia*	(p. 131)
2.	Anterior brim absent, or represented by a velum, which consists of dorsal papillae only	3	
3.	Papillae present throughout length of dorsal radii	*Rhipidothuria*	(p. 131)
3.	Papillae confined to anterior part of dorsal radii and usually forming a velum	*Peniagone*	(p. 131)
4.	Deposits rod-shaped, with two pairs of obliquely placed, horizontal arms and two vertical apophyses	*Elpidia*	(p. 172)
4.	Deposits not so	5	
5.	C-shaped deposits or irregularly curved rods with a middle enlargement present (except, possibly, in *Amperima furcata* and *Irpa ludwigi*). Tentacles 10	6	
5.	Neither C-shaped deposits nor irregularly curved rods with a middle enlargement. (Deposits entirely absent in *A. tui*). Tentacles 10–12	*Achlyonice*	(p. 155)
6.	Deposits tripartite or rod-shaped, besides true C-es	7	
6.	Deposits irregularly rod-shaped or branched; curved rods with a middle enlargement present, but true C-es absent	9	
7.	Deposits tripartite	*Amperima*	(p. 158)
7.	Deposits rod-shaped	8	
8.	Dorsal papillae separated into one pair of large papillae, placed anteriorly, and		

one large and one small pair, placed close together on the middle or posterior part of the body .... *Scotoplanes* (p. 166)

8. Dorsal papillae placed close together anteriorly, usually forming a velum .... *Ellipinion* (p. 162)
9. Pieces of calcareous ring sturdy, firmly joined to each other, each with four pairs of arms, two pairs of which may possess irregular processes .... *Irpa* (p. 171)
9. Pieces of calcareous ring delicate, meeting (at the most) at their periphery, each with five pairs of arms (a number of which may be subdivided) .... *Kolga* (p. 170)

Genus ***Psychrelpidia*** Hérouard, 1923
Fig. 118

Hérouard 1923, pp. 75–76. – Type species: *Peniagone discrepans* Sluiter, 1901, by monotypy.

Diagnosis: Anterior brim present, composed of dorsal and ventrolateral papillae. Ventrolateral tubefeet numerous, slender, almost forming a brim. Deposits cross-shaped. Calcareous ring consisting of five isolated pieces, each probably with a varying number of arms.

Psychrelpidia discrepans (Sluiter, 1901)

Peniagone discrepans Sluiter, 1901a, pp. 27–28; Sluiter 1901b, pp. 75–76, pl. X: 3–4.

Record: Celebes Sea, 2035 m. One specimen.

Remarks: Sluiter pointed out that the species has features in common both with the Elpidiidae (the number of ten tentacles, the structure of the calcareous ring, and the absence of midventral tubefeet) and the Psychropotidae (the anterior brim, the numerous ventrolateral tubefeet, and the long and free dorsal papillae). Re-examination of the specimen (in ZMA) revealed two additional psychropotid features: The tentacles were partly retracted into their stalks (a similarity to *Benthodytes)* and the body was violet in colour. This colour is the usual one in the Psychropotidae, but rarely found in the Elpidiidae.

The specimen is 6 cm long.

Genus ***Rhipidothuria*** Hérouard, 1901
Fig. 118

Hérouard 1901, pp. 41–42. – Type species: *Rhipidothuria racowitzai* Hérouard, 1901, by monotypy.

Diagnosis: Papillae present throughout length of dorsal radii, the anterior two pairs placed close together. Deposits cross-shaped. (Structure of calcareous ring unknown).

Rhipidothuria racowitzai Hérouard, 1901

Hérouard 1901, pp. 41–42; Hérouard 1906, pp. 7–8, pl. I: 1–3.

Record: Antarctic, c. 450 m. Two specimens.

Genus ***Peniagone*** Théel, 1882
Figs. 119–120

Peniagone Théel, 1882, p. 42. – Type species, designated by Deichmann (1930): *Peniagone wyvillii* Théel, 1882.
Parelpidia Théel, 1882, p. 15.
Scotoanassa Théel, 1882, p. 55.
Elpidiogone R. Perrier, 1902, pp. 424–425.

Diagnosis: Dorsal papillae anteriorly placed, usually forming a velum. Deposits primary crosses, or cross-shaped. Calcareous ring consisting of five isolated pieces, each having a varying number of arms.

Remarks: The most primitive species of the genus are probably those having an ovoid body form, with tubefeet throughout the length of the ventral sole. Species with a similar body form are found in almost all the other genera of the family.

A specialized body form is found in the species formerly referred to *Parelpidia* and *Scotoanassa* – the former having a very elongated body and a reduced velum, the latter a broad and flattened body, a posteriorly directed oral tube, and the tubefeet confined to the hind edge of the body. The occurrence of intermediary forms made it inadvisable to retain the two genera.

Peniagone ecalcarea Sluiter, 1901, which lacks deposits and possesses an anterior brim composed of dorsal and ventrolateral papillae, has later been transferred to the genus *Euriplastes* Koehler & Vaney, 1905 (family Pelagothuriidae).

The species of *Peniagone* are delicate creatures which are often extensively damaged during capture. The following species, based on poorly preserved specimens, are omitted from the present survey:

Peniagone horrifer Théel, 1882. Known from one Antarctic specimen. The external characters could not be made out with any certainty during re-examination. The longitudinal arrangement of the velum, supposed to be characteristic of the species, appeared to be caused by a distortion of the body.

Peniagone atrox Théel, 1882. One specimen taken south of Australia. The specimen was found on re-examination to be very defective, and the external characters of the species uncertain.

Peniagone vexillum R. Perrier, 1896. One specimen taken in the North Atlantic. The specimen was extensively damaged and only provisionally erected as a new species. Heding (1940), with some hesitation, referred to the same species an Antarctic specimen, also in poor condition.

Scotoanassa incerta Sluiter, 1901(a,b). Known from four Indonesian specimens; they were found to be so defective that neither the shape of the body nor the arrangement of the tubefeet could be made out.

Peniagone stabilis Koehler & Vaney, 1905. One specimen taken in the Bay of Bengal. The species was characterized by the posterior lobated border of fused tubefeet and the triangular velum, consisting of one large and two small papillae. This latter structure, however, is incompatible with that of a velum.

Peniagone obscura Koehler & Vaney, 1905. One specimen, taken at the same station as *P. stabilis*. The specimen was apparently too defective to allow an illustration, and little can be concluded from the description.

Peniagone piriei Vaney, 1908. Known from one Antarctic specimen. As the deposits had totally dissolved, the specimen is not even referable to genus.

Peniagone bispiculata H. L. Clark, 1920. Known from three eastern Pacific specimens. The description was not illustrated. The external features could not be made out during re-examination of the specimens (in USNM). The deposits, as noted by Clark, consist of slender primary crosses of two size groups, the majority with 0.10–0.12 mm long arms and a smaller number with 0.15–0.17 mm long arms. Clark failed to observe that the deposits possess a central apophysis in addition to the four apophyses on the arms. The deposits differ in shape from those of all other species of *Peniagone*. However, due to the uncertainty concerning the external features, the species is omitted from the present work.

Parelpidia anamesa H. L. Clark, 1920. Known from one specimen taken off Peru. The specimen was in a poor state of preservation. The number, size and arrangement of the tubefeet and papillae could not be made out.

Peniagone mus D'yakonov, 1952a, is known from three specimens taken southeast of Kamchatka. The specimen illustrated lacked tentacles, velum, and all the tubefeet, except one.

Key to the species of *Peniagone*

1. Papillae not fused into a velum (although their bases may be enclosed in a right and left elevation of the skin) 2
1. Papillae fused into a velum 7
2. Papillae 4–5 pairs, at least the anteriormost pair long and slender 3
2. Papillae 1–3 pairs, all rudimentary 5
3. Tubefeet 8–9 pairs. Deposits primary crosses with 4 apophyses ...... *papillata* (p. 145)
3. Tubefeet 10–12 pairs. Deposits primary crosses, sometimes with reduced stem; apophyses reduced in number on some or all of the deposits 4
4. Papillae separated into an anterior group of 3 pairs which on each side are fused at their bases, and 1 pair placed more posteriorly. All papillae long (although the first pair is longest) .... *dubia* (p. 144)
4. Papillae consisting of 2 pairs of long and 2 pairs of reduced papillae, all closely placed, although completely separated .... *incondita* (p. 145)
5. Tubefeet about 10 pairs, bordering the entire ventral sole .... *incerta* (p. 143)

5. Tubefeet 8–9 pairs, bordering the posterior $^2/_3$ of the ventral sole 6
6. Body very elongated, *Synapta*-like. Arms of crosses about 0.12 mm long. *elongata* (p. 147)
6. Body short and broad. Arms of crosses about 0.60 mm long .... *verrucosa* (p. 147)
7. Body flattened 8
7. Body ovoid or elongate 13
8. Velar papillae with a long and slender, free part .... *purpurea* (p. 151)
8. Velar papillae to the greater part of their length enclosed in the velum 9
9. Tubefeet present both laterally and posteriorly 10
9. Tubefeet present only along hind edge of the body 12
10. Tubefeet consisting of 3 pairs of free, lateral tubefeet and 4 pairs which form two fan-shaped clusters at posterior end of body .... *intermedia* (p. 152)
10. Tubefeet decreasing evenly in size in posterior direction, and not separated into a lateral and a posterior group 11
11. Deposits cross-shaped, with 5 apophyses .... *foliacea* (p. 152)
11. Deposits nearly cross-shaped, with 4 apophyses .... *expansa* (p. 152)
12. Tentacle discs with a pair of large, digitiform processes .... *diaphana* (p. 153)
12. Tentacle discs devoid of large processes .... *gracilis* (p. 155)
13. Body ovoid (less than three times as long as broad) 14
13. Body elongate (at least three times as long as broad) 22
14. Deposits with a well-developed stem 15
14. Deposits cross-shaped, or nearly so 19
15. Velum very large 16
15. Velum small 17
16. Tubefeet bordering almost the entire ventral sole, regularly decreasing in size posteriorly .... *wyvillii* (p. 150)
16. Tubefeet bordering the posterior $^2/_3$ of the ventral sole, all of them large (with the possible exception of the one or two hindmost pairs) .... *ferruginea* (p. 151)
17. Deposits with 4 apophyses .... *porcella* (p. 134)
17. Deposits with 2–0 apophyses 18
18. Deposits with 2 apophyses. Rod-shaped deposits absent from body wall. *mossmani* (p. 134)
18. Deposits with 1–0 apophyses. Rod-shaped deposits present in body wall, interspersed among the primary crosses .... *wiltoni* (p. 134)
19. Deposits with a central apophysis 20
19. Deposits lacking a central apophysis 21
20. Apophyses absent from arms of deposits .... *humilis* (p. 138)
20. Apophyses present on arms of at least the dorsal deposits .... *rigida* (p. 136)
21. Tubefeet 5 pairs, all of them large .... *obsoleta* (p. 134)
21. Tubefeet 6–8 pairs, the posterior pairs reduced .... *convexa* (p. 135)
22. Tubefeet bordering the entire ventral sole 23
22. Tubefeet bordering the posterior $^1/_3$–$^2/_3$ of the ventral sole 25
23. Posterior tubefeet separated by a median incision into a right and left group. Dorsal deposits usually almost cross-shaped and with one apophysis .. *willemoesi* (p. 144)
23. No posterior, median incision of body. Dorsal deposits usually with a distinct stem, and with 2–4 apophyses 24
24. Posterior tubefeet well developed and partly fused into a brim. Dorsal deposits with up to 0.3 mm long arms and up to 0.4 mm long apophyses .... *affinis* (p. 142)
24. Posterior tubefeet small. Dorsal deposits usually with up to 0.15 mm long arms and 0.10 mm long apophyses .... *azorica* (p. 138)
25. Tubefeet bordering the posterior $^1/_3$–$^1/_2$ of the ventral sole. Apophyses of dorsal deposits usually longer than the arms 26
25. Tubefeet bordering the posterior $^1/_2$–$^2/_3$ of the ventral sole. Apophyses of dorsal deposits shorter than the arms 27

26. Tentacles 10 .... *vitrea* (p. 148)
26. Tentacles 8 .... *islandica* (p. 150)
27. Body about five times as long as broad .... *challengeri* (p. 146)
27. Body about three times as long as broad 28
28. Velum small .... *vignoni* (p. 146)
28. Velum well developed 29
29. Velar papillae completely fused. Body colour dark violet .... *lugubris* (p. 148)
29. Velar papillae with free distal parts. Body colour whitish .... *japonica* (p. 147)

Peniagone porcella R. Perrier, 1896

Peniagone porcellus R. Perrier, 1896, p. 901; R. Perrier 1902, pp. 426–429, pls. XIII: 7–9, XIX: 13–23; Madsen 1953, pp. 155–156, fig. 4.

Diagnosis: Body ovoid. Tubefeet about 9 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Dorsal papillae 3 pairs, short, the 2 anterior pairs fused at their base to form a low velum. Deposits rather robust and spinous primary crosses with four apophyses.

Records: Off the Azores, 4060 m. Numerous specimens, taken by the *Talisman.* – Off the West Indies, 5033–5044 m. One specimen, taken by the Swedish Deep-Sea Expedition.

Relationships: *Peniagone porcella* appears to be most closely related to the Antarctic species *P. mossmani* and *P. wiltoni.* They differ by the number of apophyses on the deposits: *P. porcella* has four apophyses, *P. mossmani* two, and *P. wiltoni* one or none at all. *P. wiltoni* possesses, in addition, rod-shaped spicules interspersed among the crosses all over the body wall. In external appearance the three species are probably indistinguishable.

The fact that in *P. azorica* a reduced number of apophyses on the spicules may characterize local populations, or represent a geographic variation within the species, suggests that *P. mossmani* and *P. wiltoni* might together form a local or geographic form of *P. porcella.*

Peniagone mossmani Vaney, 1908

Vaney 1908, p. 411, pls. I: 10–11, II: 19, III: 32–33.

Known from one specimen, taken in the Antarctic at 4789 m, simultaneously with the specimen of *P. wiltoni.* Both species are discussed under *P. porcella.*

Peniagone wiltoni Vaney, 1908

Vaney 1908, pp. 413–414, pls. I: 6–7, III: 29–31.

Known from one specimen, taken in the Antarctic at 4789 m, simultaneously with the specimen of *P. mossmani.* Both species are discussed under *P. porcella.*

Peniagone obsoleta (Hérouard, 1899)

Fig. 56

Kolga obsoleta Hérouard, 1899, p. 170, fig. 1; Hérouard 1902, pp. 41–42, pls. VI: 11–15, VIII: 16, 18.
Peniagone nybelini Madsen, 1953, pp. 157–158, fig. 5.

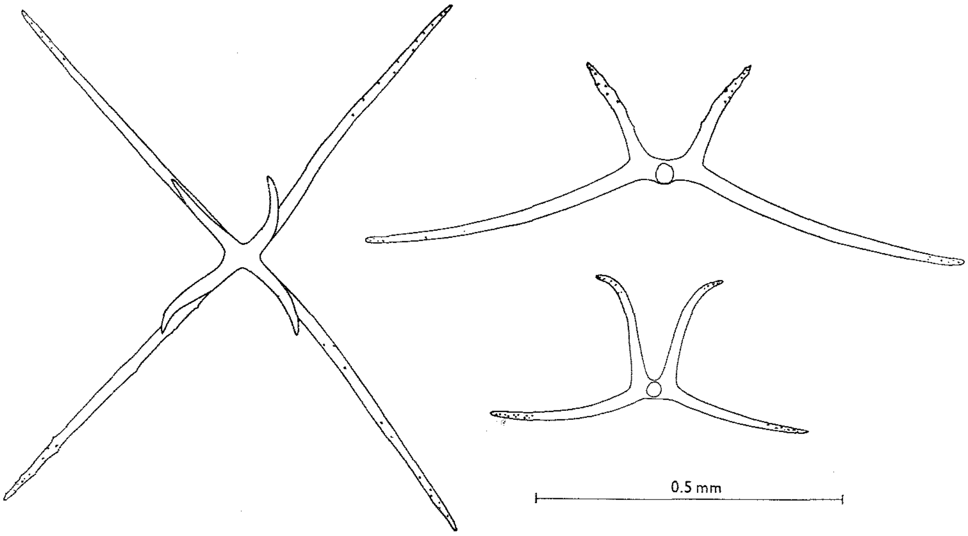
Diagnosis: Body ovoid. Tubefeet 5 pairs, bordering the entire ventral sole, all of them large and placed at equal intervals. Velum small. Deposits almost cross-shaped, with rather horizontal, slender arms and four long, slender, pointed, usually somewhat outwardly curved apophyses placed near the centre of the cross.

Records: East of the Azores, 4360 m. Six specimens. – Mid-Atlantic near the equator, 5250–5300 m. One specimen *(P. nybelini).*

Remarks: The proposed synonymy between *P. obsoleta* and *P. nybelini* is, in particular, based on the similarity shown by the deposits and by the size, number, and arrangement of the tubefeet.

Skin preparations made during re-examination of five of Hérouard's six specimens of *P. obsoleta* were compared to those made by Madsen from *P. nybelini.* While Madsen's illustration makes clear the variation of the deposits, the three deposits shown by Hérouard are not representative. In actual fact, the deposits of the two species differ in minor details only, e. g., the some-

Fig. 56.
Peniagone obsoleta.
Monaco St. 753.
Dorsal deposits.



what enlarged arm ends in many of the *nybelini* deposits – details which represent hardly more than individual or local variations.

The presence of five pairs of large tubefeet, and apparently no small ones, is, within the genus *Peniagone*, unique to *P. obsoleta* and *P. nybelini*. (The presence of six tubefeet in the right side of the *nybelini* specimen forms no exception, as, according to Madsen, the extra tubefoot was formed through an abnormal duplication of a single one).

P. obsoleta is most closely related to *P. convexa* (q. v.).

Peniagone convexa n. sp.

Figs. 57–58, 95: 1, pl. X: 4–5

Diagnosis: Body ovoid. Tentacles with broad, soft discs with a thin, indented and pliable margin. Tubefeet 6–8 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the posterior 2–3 pairs rudimentary. Velum placed anteriorly, the body wall between the velum and the tentacle crown vertical. Deposits almost cross-shaped; their arms rather horizontally placed, with the ends curved slightly upwards; the four apophyses placed near the centre of the cross, their bases joined, and their distal parts pointed and usually curved outwards; arms and apophyses smooth, except at the tips.

Material:
St. 234, Madagascar–Mombasa (5°25'S, 47°09'E), 4820 m. – 1 specimen.
St. 282, Seychelles–Ceylon (5°32'N, 78°41'E), 4040 m. – 1 specimen.

Description:
St. 282. – The type specimen (Fig. 57) is 6 cm long and has a 2 cm broad ventral sole. Body strongly vaulted, reaching a height of 3.5 cm somewhat posterior to the velum. The posterior part of the body decreases abruptly in height – a feature which may, however, be due to contraction. The body wall anterior to the velum is vertical.

Tentacles 10 (Pl. X: 4). The stalks are short and thick; the discs are broad, soft, and slightly concave, with a thin, pliable and indented margin.

Tubefeet 7–8 pairs, bordering the entire ventral sole. The anterior 5 pairs are large, with Nos. 4

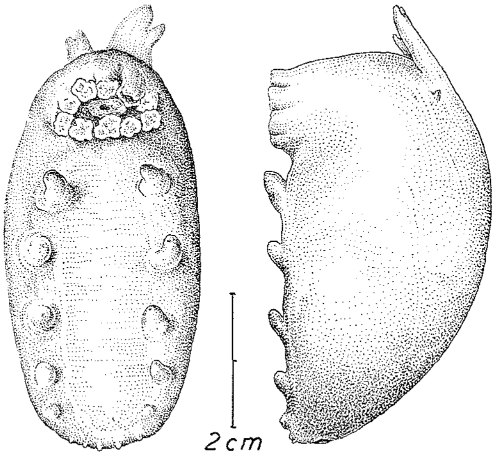


Fig. 57. *Peniagone convexa.* St. 282. Type specimen. PHW.

and 5 only slightly decreasing in size. There is an abrupt transition to the extremely reduced posterior 2–3 pairs. The ends of the tubefeet are rounded, usually with a minute groove, indicating a retracted sucking-disc.

Velum composed of two pairs of papillae, the two on the left considerably longer than those on the right – an indication that the size of the velum is of little importance as a species character. Behind the velum is a pair of minute, free papillae.

Skin white and thin, although rather tough.

Deposits similar to those of the specimen from St. 234, although somewhat corroded by the formalin.

St. 234. – The specimen is 6 cm long and rather defective. The dorsal skin is torn, and the intestines are absent.

Tentacles (Pl. X: 5) resembling those of the type specimen. (The two tentacles illustrated for the species are both within the variation at each station).

Tubefeet probably agreeing with those of the type, both in number and arrangement.

Velum completely separated into a right and left lobe, which are both contracted. Each lobe is composed of two fused papillae and is followed by a minute, free papilla.

Deposits (Fig. 58) almost cross-shaped. The arms are rather horizontally placed, with the ends curving slightly upwards. The four apophyses are placed near the centre of the cross. Their bases merge into each other, giving the deposit, when seen from above, the appearance of being superimposed by another and smaller cross. The apophyses are pointed and outwardly curved. The deposits are almost completely devoid of spines, except at the tips of the arms and the apophyses.

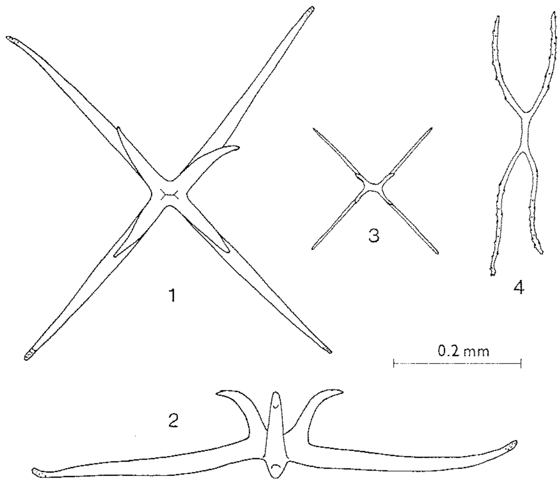


Fig. 58. *Peniagone convexa*. St. 234. Deposits. 1–3, dorsum; 4, gonad.

The deposits vary greatly in size (the deposits figured show their size variation). The dorsal deposits are usually larger than the ventral ones. There are very few rod-shaped deposits, even in the tentacles and tubefeet. Walls of gonads dense with irregular, slender primary crosses which lack apophyses.

Calcareous ring (Fig. 95: 1) belonging to the usual type in *Peniagone*. Two ring pieces examined each possessed 7 pairs of arms.

Polian vesicle single, 2 cm long, and placed in the left ventral interradius.

Relationships: The deposits indicate a close relationship to *P. obsoleta*. The two species differ primarily in the development of the tubefeet – *P. obsoleta* possessing only five pairs, which are all large and placed at equal intervals.

Peniagone rigida (Théel, 1882)

Figs. 59–60

Elpidia rigida Théel, 1882, pp. 20–21, pl. XXXII: 18–20.

Diagnosis: Body ovoid. Tubefeet 8–9 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the posteriormost 4–5 pairs rudimentary. Velum placed anteriorly, the body wall between the velum and the tentacle crown vertical. Deposits cross-shaped, the dorsal crosses with five apophyses, the ventral crosses with one.

Material:
St. 282, Seychelles–Ceylon (5°32'N, 78°41'E), 4040 m. – 1 specimen.

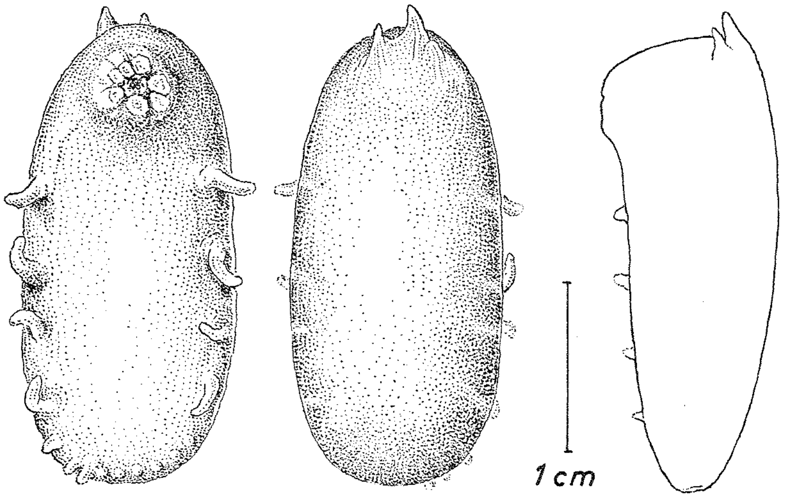
Description: The specimen (Fig. 59) is 28 mm long; ventral sole 10 mm broad.

Tentacles 10, with short stalks. Discs with papillae on the surface; no conspicuous marginal incisions are visible.

Tubefeet 8–9 pairs, the posterior 4–5 pairs rudimentary.

Velum placed anteriorly, the body wall between the velum and the tentacle crown vertical.

Fig. 59. *Peniagone rigida*. St. 282. PHW.



Skin white, thick, and rather soft. The outer, deposit-containing layer almost completely intact.

Deposits (Fig. 60) cross-shaped. The dorsal crosses (1) have very slender, slightly curved and slightly spinous arms which attain a length of 0.5 mm. The five high and slender apophyses are strongly spinous. The ventral crosses (2) are generally more robust. The arms are straight, spinous, often with blunt ends, and few attain a length of 0.3 mm. A strongly spinous central apophysis is present, but there are no apophyses on the arms.

A few curved rods surround the end-discs of the tubefeet, but no end-plates are present. The tentacle discs contain a few rods.

Remarks: The single previously known specimen, taken by the *Challenger* in the northwestern Pacific, was re-examined. Agreement with the *Galathea* specimen included the ovoid body form, the number and placing of the tubefeet, and the shape of the dorsal deposits (ventral deposits not examined).

The skin was, according to Théel, thin, brittle, and rough. However, on re-examination the skin appeared to be similar to that found in most species of *Peniagone,* i. e. rather soft under the outer deposit-containing layer.

Relationships: Most closely related to *P. humilis* (q. v.).

Distribution: Northwestern Pacific, 4204 m. Western Indian Ocean, 4040 m.

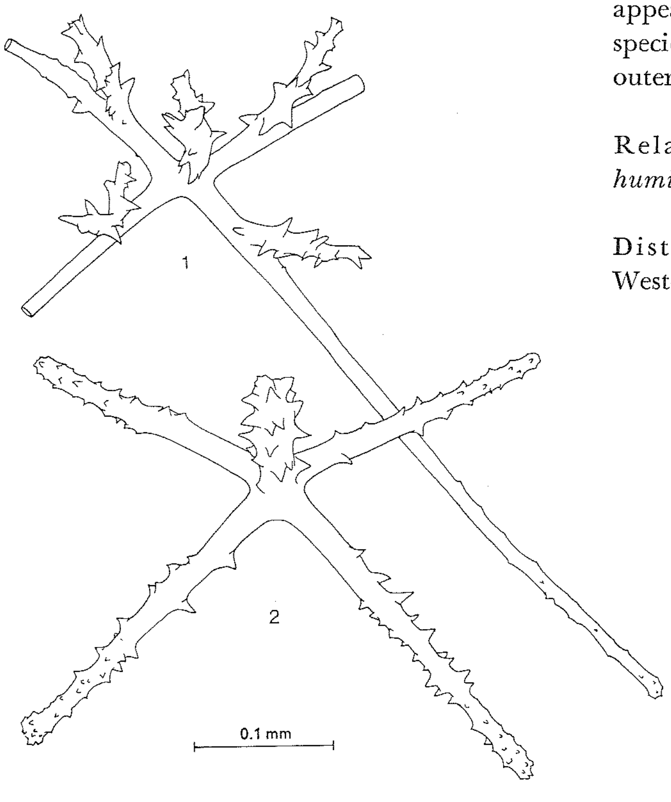


Fig. 60. *Peniagone rigida*. St. 282. Deposits. 1, dorsum; 2, ventrum.

Peniagone humilis n. sp.

Figs. 61–62

Diagnosis: Body ovoid. Ventral sole slightly increasing in breadth posteriorly. Tentacles with firm and vaulted discs with an almost smooth surface and an only feebly indented margin. Tubefeet 10 pairs, bordering the entire ventral sole, posteriorly of smaller size and partially enclosed in a low brim. Velum low, placed near the mouth, and composed of two pairs of completely fused papillae. Deposits cross-shaped, with a single, central apophysis; arms with upwardly curved ends.

Material:

St. 663, Kermadec Trench (36°31'S, 178°38'E), 4410 m. – 1 specimen.

Description: The specimen (Fig. 61) is about 20 mm long and 10 mm broad. The ventral skin is ruptured, and the body is somewhat distorted and contracted; the proportions of the body, as shown in the figure, should therefore be regarded with some reservation – although the species evidently belongs to the broad and strongly vaulted forms of the genus.

Ventral sole broadest posteriorly, its hind edge forming a large, semicircular curve.

Tentacles 10, short. Discs of a firm consistency, vaulted, with an almost smooth surface and an almost un-indented margin.

Tubefeet 10 pairs, bordering the entire ventral sole, and decreasing evenly in size in posterior direction. The anteriormost 4–5 pairs are separate, while the bases of the remaining tubefeet are enclosed in a low brim.

Velum low, but distinct, placed near the mouth. Its four papillae are almost equally large and completely fused. On the right side, two minute, free papillae are seen.

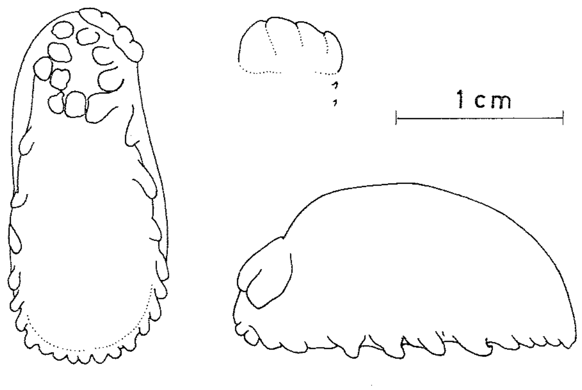


Fig. 61. *Peniagone humilis.* St. 663.

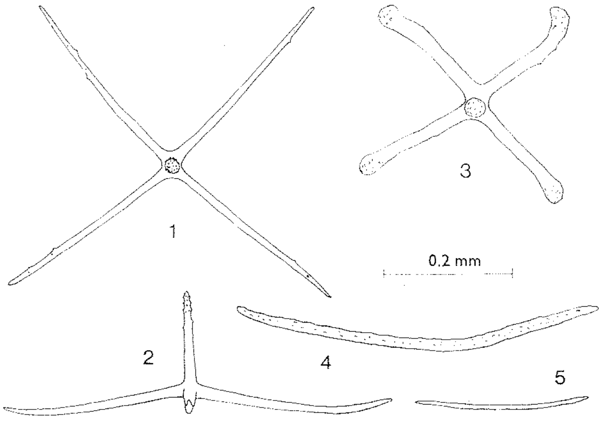


Fig. 62. *Peniagone humilis.* St. 663. Deposits. **1–2, dorsum;** 3, ventrum; 4–5, tentacle.

Skin whitish and soft.

Deposits (Fig. 62) cross-shaped with upwardly curved arms and a single, central apophysis. The deposits are smooth, except at the tips of the arms and apophyses. The ventral deposits are more robust than the dorsal ones. Rods present in tentacles and tubefeet. End-plate absent from tubefeet.

Relationships: In external features and deposits somewhat similar to *P. rigida,* but differs in the velum being positioned near the mouth, in the shape of the ventral sole, in the posterior tubefeet forming a low brim, and in the absence of apophyses on the arms of both the dorsal and ventral crosses.

Peniagone azorica von Marenzeller, 1893

Fig. 63, pl. X: 1–3

Peniagone azorica von Marenzeller, 1893a, pp. 12–13, pls. I: 4, II: 5; Hérouard 1902, pp. 42–43, pl. VI: 21–26; Hérouard 1923, pp. 87–88; Grieg 1921, p. 8, fig. 4; Heding 1942, p. 20.

Peniagone vedeli Hansen, 1956, pp. 42–44, figs. 12–13.

Peniagone willemoesi (Théel), Hansen 1967, pp. 495–498, fig. 12.

Diagnosis: Body elongate, somewhat flattened posteriorly. Tentacles with rather long stalks; discs with a papillate surface and a pair of retractile marginal lobes. Tubefeet 9–11 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Velum usually bipartite in the greater part of its length. Dorsal deposits extremely varying; the usual type with a well-developed stem, arms curving strongly downwards, and four high, slender apophyses; length of arms usually less than 0.15 mm; deposits with reduced stem and fewer apophyses, or deposits which are similar to the usual ventral type, occur as local or geographic variants. Ventral deposits nearly always with a well-developed stem, slightly curved arms, and four low apophyses.

Material:

St. 649, Kermadec Trench (35°16'S, 178°40'W), 8210–8300 m. – 160 specimens.
St. 650, Kermadec Trench (32°20'S, 176°54'W), 6620–6730 m. – 260 specimens.
St. 651, Kermadec Trench (32°10'S, 177°14'W), 6960–7000 m. – 6 specimens.
St. 653, Kermadec Trench (32°09'S, 176°35'W), 6180 m. – 1 specimen.
St. 654, Kermadec Trench (32°10'S, 175°54'W), 5850–5900 m. – 11 specimens.
St. 658, Kermadec Trench (35°51'S, 178°31'W), 6660–6770 m. – 600 specimens.
St. 661, Kermadec Trench (36°07'S, 178°32'W), 5230–5340 m. – 60 specimens.
St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 267 specimens.
St. 664, Kermadec Trench (36°34'S, 178°57'W), 4540 m. – 179 specimens.
St. 668, Kermadec Trench (36°23'S, 177°41'E), 2640 m. – 5 specimens.

Description: The specimens from the hadal part of the Kermadec Trench were previously (Hansen 1956) described as a new species, *Peniagone vedeli,* considered to be a close relative of the Atlantic species *P. azorica.* Examination of specimens from abyssal depths proved that the variation in the trench comprised the features of *P. azorica,* and that also the Antarctic species *P. willemoesi, P. incerta,* and *P. affinis* are possible synonyms. Hansen (1967), believing in the synonymy, regarded the Kermadec Trench specimens as belonging to *P. willemoesi.*

The following description deals, in particular, with the specimens taken at the five abyssal Kermadec stations.

Skin soft and mucous. The species belongs to the most watery members of the benthic Elasipoda, and almost no specimens are preserved intact. The thickness of the skin varies rather much from one specimen to another – a variation which cannot be explained simply by a different state of preservation, as specimens preserved in the same vial could differ greatly in this respect.

No correlation was present between the development of the mucous layer and the size of the specimens. The mucous specimens are apparently not juveniles.

Tentacles (Pl. X: 1–3) with rather long and slender stalks. Discs broad, covered with papillae, and with marginal indentations. In the fully extended state a deep aboral incision is present, separating two lobes which taper into a distal, finger-like part. In the contracted discs the lobes are broader or have completely disappeared. (The three tentacles illustrated are all from one specimen).

Tubefeet 9–11 pairs, bordering the entire ventral sole, and gradually decreasing in size posteriorly.

Velum usually bipartite in at least half its length. The specimen illustrated (Hansen 1956, fig. 12) had an only feebly bipartite velum.

A few specimens possess a pair of minute papillae in front of the velum.

Some specimens show an abrupt downward bend of the body part anterior to the velum, brought about by a strong contraction of the ventral, longitudinal muscles. This bend of the anterior part of the body has been regarded as characteristic of some other species of *Peniagone.* However, the fact that this feature does not necessarily represent the natural shape of the body is notable, although in some species (e. g. *P. diaphana* and *P. gracilis)* the bend is a constant feature.

Calcareous ring with about 10–12 pairs of irregularly shaped arms on each of the five pieces. In some specimens some pieces, or even the whole ring, seem to be absent.

Deposits (Fig. 63). Due to the mucous consistency of the skin, the outer, deposit-containing layer is completely worn off in most of the specimens.

Hansen (1956) emphasized the great variability of the deposits of the hadal specimens. The abyssal specimens from the trench added even further to this variation and also revealed a marked local variation of the deposits. In the following, the deposits are described separately for each station, arranged according to depth.

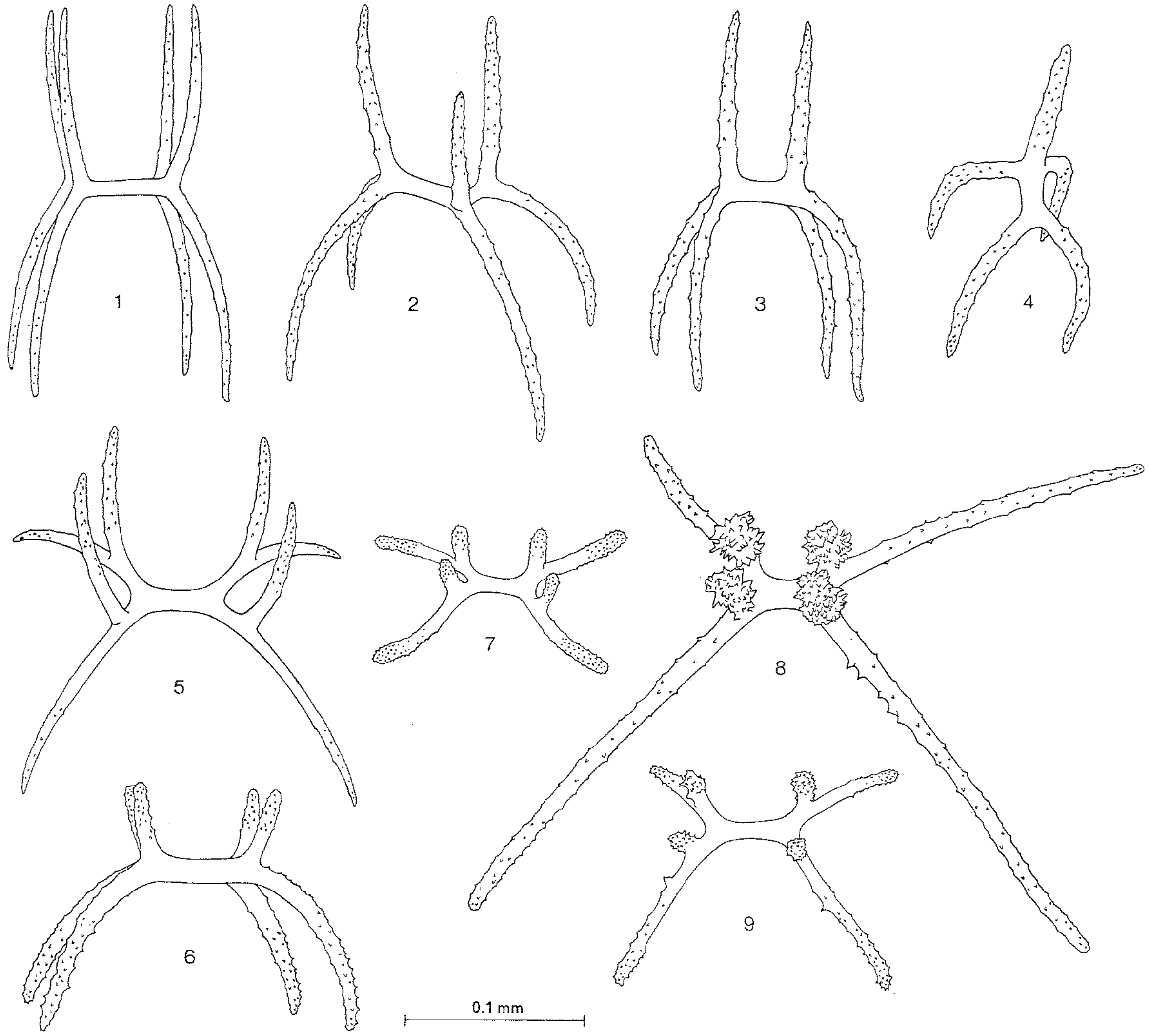


Fig. 63. *Peniagone azorica.* Deposits. 1–4, dorsum (St. 663); 5, dorsum (St. 668); 6, dorsum (St. 661); 7, dorsum (St. 649); 8, ventrum (St. 663); 9, ventrum (St. 668).

St. 668 (2640 m). The 11 fragments, which probably belonged to five specimens, were all examined by means of skin preparations. Three preparations could be determined as belonging to the dorsal side, and two to the ventral side; in the remaining the actual body position could not be determined.

The three pieces of dorsal skin possessed deposits with four high, curved apophyses. Most deposits were similar to the one shown as Fig. 63: 5; but some had longer arms and apophyses or arms which were placed almost vertically. The latter type was represented also at Sts. 661 and 663 (cf. Fig. 63: 1).

The two pieces of ventral skin had deposits with slightly curved arms and low apophyses (Fig. 63: 9). These deposits were similar to those of the hadal specimens.

Of the seven remaining pieces of skin, six possessed deposits similar to those found in the dorsal pieces, and one to those of the ventral pieces. Since none of the preparations had deposits intermediate in shape between these two distinct types, a clear separation between a dorsal and a ventral type apparently exists. A similar separation was found in specimens examined from the abyssal stations 661 and 663, whereas in the hadal specimens the dorsal deposits were similar to the ventral ones.

St. 663 (4410 m). Parts of the outer deposit-containing layer are preserved in only five of the numerous specimens from this station. The dorsal deposits (Fig. 63: 1–4) are in all five specimens characteristically developed, with strongly curved arms and high apophyses. Usually, two apophyses are present, placed at the ends of the stem. A few deposits possess one, three or four apophyses. The size of the deposits varies a great deal: While most are of the size represented in the figure, many reach double that size.

Most of the ventral deposits are similar, both in size and appearance, to those from St. 668, although larger deposits prevailed in one preparation (Fig. 63: 8). In a few of the ventral deposits the apophyses were reduced to three or two; when two in number they were placed at the ends of the stem. Similarly, in deposits with four apophyses, the latter had a somewhat asymmetric position, one or two of them being placed near the ends of the stem.

St. 661 (5230–5340 m). Among the 60 specimens, 12 are preserved with parts of the outer deposit-containing layer. Dorsal deposits were present in two of them only. One specimen had dorsal deposits (Fig. 63: 6) with the strongly curved arms usually found in the abyssal specimens, but the apophyses were only of moderate height. Some of the dorsal deposits possessed only three or two apophyses.

The other specimen had only the dorsal deposits preserved. These were similar to the deposit from St. 663 shown in Fig. 63: 1.

The ventral deposits in all the specimens agreed with those from the other stations – having a well-developed stem and four, low apophyses.

No outer deposits were preserved in the specimens from Sts. 654 and 664.

Synonymy: *Peniagone azorica* has been reported from many stations in the northeastern Atlantic at depths of 2320–4020 m. Most of the known material was re-examined, and also a number of hitherto unrecorded specimens from two Monaco stations off the Azores, at smaller depths than previously recorded: St. 553, 1385 m: 1 specimen (in MNHN). St. 673, 2252 m: 34 specimens (30 in MOM, 2 in ZMUC, and 2 in MNHN).

The N. E. Atlantic specimens in external appearance were similar to the specimens from the Kermadec Trench. As in the latter, the mucous layer of the skin varied greatly in development. The velum was almost completely divided into a right and left section. Some specimens showed an abrupt, downward bend of the anterior part of the body, similar to that found in some of the Kermadec specimens.

The deposits were examined in 12 specimens, five from Monaco St. 673 (off the Azores), three from Monaco St. 2990 (Bay of Biscay), one from *Ingolf* St. 11 (west of Iceland), and three from *Ingolf* St. 41 (south of Iceland).

The dorsal deposits in all the preparations resembled the type found at *Galathea* St. 668 (Fig. 63: 5). Usually, however, the deposits attained a larger size, being often twice as large, but deposits of that size were also present in the Kermadec specimens.

The ventral deposits were in some of the examined specimens similar to the ventral deposits of the Kermadec specimens. In other Atlantic specimens the ventral deposits were indistinguishable from the dorsal ones of the same specimens, possessing curved arms and high apophyses. The occurrence of these two types of ventral deposits is apparently not geographically determined within the Atlantic, as both types occurred at the two Monaco stations and at *Ingolf* St. 41. Deposits with curved arms and high apophyses were not found in the ventrum of any of the Kermadec specimens.

Deposits with less than four apophyses were not found in the examined Atlantic specimens.

Variation: An extensive individual variation is shown by several features: The development of the mucous layer of the skin, the shape of the velum, the size and arrangement of the posterior tubefeet, and the deposits. In addition, the state of preservation and the degree of contraction may influence such characters as the shape of the tentacle discs, the size of the velum, and the degree of the downward bend of the anterior part of the body which depends on the amount of contraction in the ventral, longitudinal muscles.

The *dorsal deposits* show several interesting features in their variation. In addition to an often considerable individual variation, a local variation (and probably also a geographic variation) can be demonstrated with regard to the number and height of the apophyses, the curvature of the arms, and the degree of reduction of the stem.

The North Atlantic specimens all had dorsal deposits with a rather well-developed stem, four high apophyses, and downwardly-curved arms. Similar deposits were present in the Kermadec specimens from *Galathea* St. 668.

The populations from the Kermadec Trench show a pronounced local variation in the dorsal deposits. In addition, there seems to be a consistent difference between the abyssal and the hadal specimens. All the examined abyssal specimens from the trench, like those from the Atlantic, had dorsal deposits with strongly curved arms and high, slender apophyses. But the hadal specimens had dorsal deposits with rather horizontally placed arms and low, spinous apophyses, agreeing with the usual ventral type in the species. Examination of 51 specimens from four hadal stations suggested that the similarity is not accidental. It may indicate that the hadal trench populations are in closer contact with each other than with the abyssal populations (p. 243).

The *ventral deposits* do not show a variation comparable to that of the dorsal ones, being nearly always provided with rather horizontally placed arms and four, low apophyses. However, in three Atlantic specimens the ventral deposits were found to be similar to the usual dorsal type, with strongly curved arms and high apophyses. These specimens were all taken simultaneously with specimens possessing normal, ventral deposits.

Relationships: *Peniagone azorica* is closely related to the three Antarctic species *P. incerta, P. affinis,* and *P. willemoesi.* The dorsal deposits of *P. incerta* and *P. affinis* are in their shape within the variation of *P. azorica* at St. 663. Those of *P. affinis* are larger than in the Kermadec specimens, but not appreciably larger than in Atlantic specimens of *P. azorica.* The dorsal deposits of *P. willemoesi* are almost cross-shaped, usually with one apophysis, and somewhat smaller than those of *P. azorica.*

The tubefeet in the three Antarctic species seem to decrease less in size posteriorly than in *P. azorica.*

The features distinguishing the four species may actually represent geographic or local variations of one species.

The ventral deposits are similar in the four species.

Distribution: Northeastern Atlantic, 1385–4020 m. Kermadec Trench, 2640–8210 (8300) m.

The occurrence of *Peniagone azorica* in the Romanche Trench (00°16'S, 18°35'W, depth 7100–7300 m) is indicated by a deep-sea photograph (Heezen *et al.* 1964, fig. 9). The specimen has five pairs of large and well spaced lateral tubefeet, three pairs of small and closely placed tubefeet along the hind end, and a velum which is cleft almost to the base. The authors report that, according to Dr. E. Deichmann, the species "appears to be closest to *Peniagone incerta* Théel". *P. incerta* in external appearance resembles *P. azorica,* but has a more feebly developed velum than *P. azorica* and the specimen photographed.

Deep-sea photographs from the PROA Expedition 1962 (Lemche *et al.* in press) suggest that *Peniagone azorica* occurs also in the New Britain Trench (depth 6790–7665 m) and the Solomon Trench (depth 7850–8625 m).

Peniagone affinis Théel, 1882

Fig. 64

Théel 1882, pp. 52–54, pls. VIII: 4–5, XXXIV: 12–13.

Diagnosis: Body elongate, somewhat flattened posteriorly. Tubefeet about 11 pairs, bordering the entire ventral sole, only slightly decreasing in size posteriorly; the anterior 5 pairs are placed with decreasing intervals, while the posterior 6 pairs are closely set and partly fused into a brim. Velum low, composed of two pairs of papillae of which the median pair is largest and free in about half the length of the papillae. Dorsal deposits with a short stem, strongly curved arms, and 2 or 3 (occasionally 1 or 4) high apophyses; length of arms up to 0.3 mm. Ventral deposits about half as large, with a well-developed stem, slightly curved arms, and 4 low apophyses.

Record: Off the Crozet Islands (southern Indian Ocean), 2924 m. Numerous specimens.

Remarks: Ten specimens (in BM) were re-examined, all by means of skin preparations.

In external appearance the specimens agree well with Théel's illustration, especially in the arrangement of the tubefeet, of which the posterior ones are well developed, closely placed, and partly fused into a brim. Velum feebly developed; only one had a velum of the size shown in Théel's drawing.

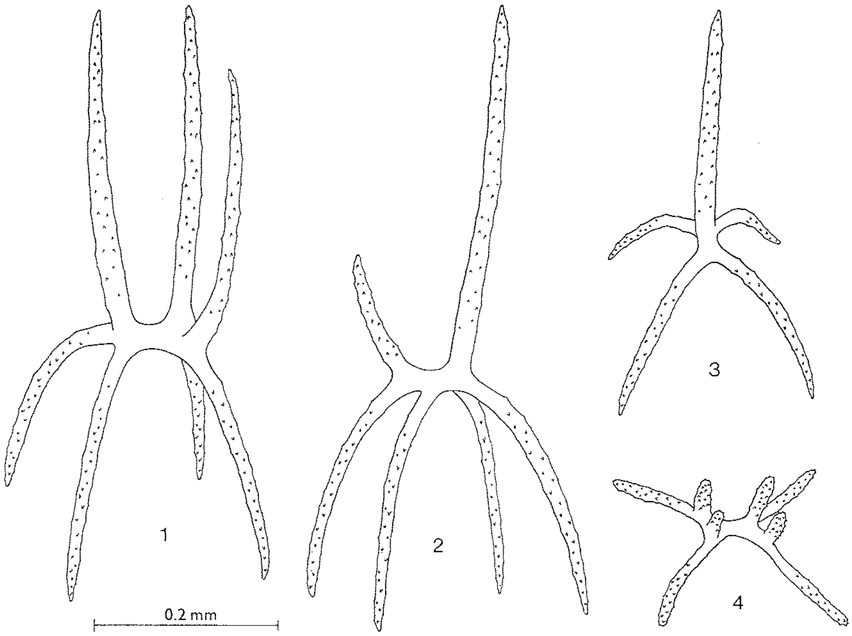


Fig. 64. *Peniagone affinis.* Deposits. *Challenger* St. 147. 1–3, dorsum; 4, ventrum.

Deposits (Fig. 64) dorsally with strongly curved arms and 2 or 3 (occasionally 1 or 4) apophyses; the arms are up to 0.3 mm long; the apophyses are up to 0.4 mm and often of unequal length in the same deposit. The stem is rather short or almost absent, especially in deposits with only one apophysis. The ventral deposits are only half as large as the dorsal ones; they have a well-developed stem, slightly curved arms, and four low apophyses.

As noted by Théel, the dorsal deposits are rather similar to those of *P. vitrea.* In external appearance the two species are very different, as *P. vitrea* has the tubefeet confined to the posterior third of the ventral sole.

P. affinis resembles *P. incerta* in external appearance and in shape of the deposits which, however, are twice as large as in *P. incerta.*

Peniagone incerta (Théel, 1882)
Fig. 65

Elpidia incerta Théel, 1882, pp. 26–27, pls. VIII: 1, XXXIII: 3–4.

Diagnosis: Body elongate, somewhat flattened posteriorly. Tubefeet about 10 pairs, bordering the entire ventral sole, slightly decreasing in size posteriorly; the posterior 5 or 6 pairs partly fused. Velum very small, or absent. Dorsal deposits with strongly curved arms, 2 (occasionally 3 or 4) apophyses and a well-developed stem. Ventral deposits with slightly curved arms, 4 low apophyses, and a well-developed stem.

Record: Antarctic Ocean, 2293 m. Four specimens.

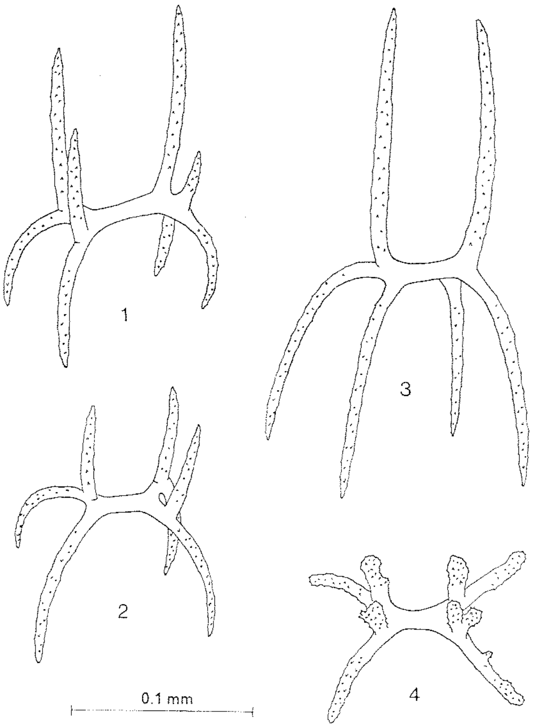


Fig. 65. *Peniagone incerta.* Deposits. *Challenger* St. 152. 1–3, dorsum; 4, ventrum.

Remarks: The four specimens known (two in BM and two in ZMA) were re-examined, all by means of skin preparations.

The species in external appearance resembles *P. affinis;* the posterior tubefeet are, as in the latter species, rather large and partially fused. Velum not present (or not preserved), its place being occupied by a pair of inconspicuous knobs.

Deposits (Fig. 65) dorsally with strongly curved arms and two high apophyses, placed at the ends of the stem. Occasionally, three or four apophyses are present. Arms as well as apophyses 0.10–0.15 mm long. The ventral deposits agree with those of *P. affinis* and *P. azorica,* having slightly curved arms and four low apophyses. Arm length c. 0.07 mm. One of the four specimens, however, had ventral deposits similar to the dorsal type.

The species is closest related to *P. affinis* and *P. azorica.*

Peniagone willemoesi (Théel, 1882)
Fig. 66

Elpidia willemoesi Théel, 1882, pp. 24–26, pls. VIII: 2–3, XXXIII: 10–12, XXXVII: 1.

non *Peniagone willemoesi* (Théel), Hansen 1967, pp. 495–498, fig. 12 (= *P. azorica).*

Diagnosis: Body elongate, posteriorly flattened. Tubefeet about 10 pairs, bordering the entire ventral sole, the hindmost pairs slightly smaller, slightly fused, and separated by a median incision into a right and left group. Velum composed of two pairs of papillae. Dorsal deposits with strongly curved arms, an almost completely reduced stem, and 1 (occasionally 2–4) high apophysis. Ventral deposits with slightly curved arms, a well-developed stem, and 4 (sometimes 3) low apophyses which are often somewhat asymmetric in position.

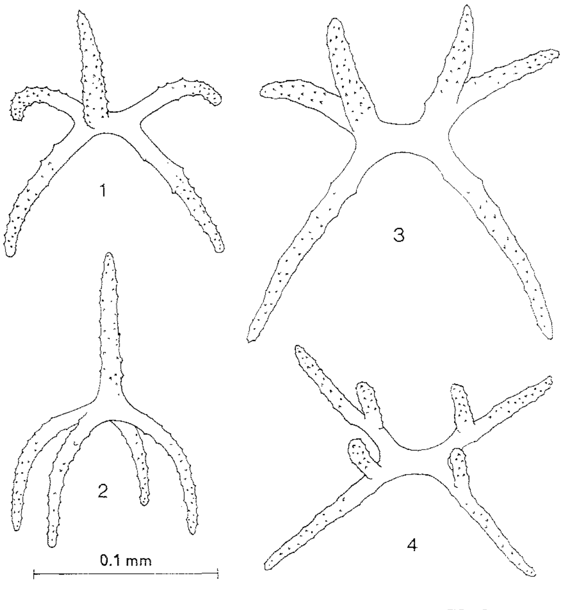


Fig. 66. *Peniagone willemoesi.* Deposits. *Challenger* St. 156 (the specimen in BM). 1–3, dorsum; 4, ventrum.

Record: Antarctic Ocean, 3609 m. Four specimens.

Remarks: One specimen (in BM) and one lacking the tentacular crown and the velum (in ZMUC) were re-examined.

The specimen in BM was illustrated in the Challenger Report. The drawing shows two conspicuous features, viz. a velum consisting of three triangular lobes and a posterior median incision of the body, separating the posterior tubefeet into a right and left group. The re-examination showed that the median lobe of the velum was composed of two papillae – the velum consisting, as usual, of two pairs of papillae. The posterior median incision of the body was verified in the specimen in BM, but not in the more defective specimen in ZMUC.

Deposits (Fig. 66) dorsally with strongly curved arms, almost no stem, and practically all of them with only one, subcentral apophysis. However, deposits with 2–4 apophyses and a well-developed stem occur scatteredly among the other deposits. The arms are c. 0.10 mm long. The ventral deposits have slightly curved arms, a well-developed stem, and 4 (occasionally 3 or 5) low apophyses which are often somewhat asymmetric in position.

The species is closest related to *P. affinis, P. incerta,* and *P. azorica* (q. v.).

Peniagone dubia (D'yakonov & Savel'eva, 1958)

Elpidiogone dubia D'yakonov & Savel'eva, 1958 (in D'yakonov, Baranova & Savel'eva 1958, pp. 361–363, figs. 2–4).

Diagnosis: Body elongate. Tubefeet about 12 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Dorsal papillae 4 pairs, all long and slender, the first pair being longest;

anteriormost 3 pairs of papillae fused at their bases, while the last pair is separate and placed more posteriorly. Deposits primary crosses with a well-developed stem and 2 or 4 high apophyses.

Record: Southern part of the Okhotsk Sea, 2850 m. Six incomplete specimens.

Relationships: The long and almost entirely free papillae represent a similarity to *P. incondita* and *P. papillata,* while the separation of the papillae into an anterior group and a more posteriorly placed pair is unique to *P. dubia.* The deposits are different in the three species.

Peniagone incondita Agatep, 1967

Agatep 1967b, pp. 51–53, pl. II: 1–14.

Diagnosis: Body elongate. Tubefeet 10–11 pairs, bordering almost the entire ventral sole, decreasing in size posteriorly. Dorsal papillae 4 pairs, of which the anteriormost 2 pairs are long and slender; all papillae separate even at their base. Deposits, dorsally large crosses with reduced stem and 1 (occasionally 2) apophysis; ventrally primary crosses with 2 apophyses.

Records: Antarctic, 3537–5435 m. Four *Eltanin* stations with 115 specimens.

Relationships: The species is closest related to *P. papillata,* but differs in the number and position of the tubefeet, the entirely free papillae, the shape of the deposits, and the violet body colour.

Peniagone papillata n. sp.
Figs. 67–68

Diagnosis: Body elongate. Tubefeet 8–9 pairs, placed along the posterior $^2/_3$ of the ventral sole, decreasing in size posteriorly. Dorsal papillae 4–5 pairs, the 1–2 anteriormost pairs long, slender, and free in almost their whole length, the others rudimentary; the small papillae and the bases of the large papillae enclosed in a pair of low elevations which are either separate throughout, or slightly fused anteriorly – a true velum being absent. Deposits primary crosses with a well-developed stem and four low, spinous apophyses.

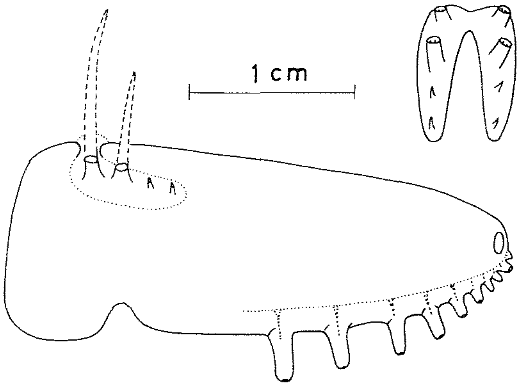


Fig. 67. *Peniagone papillata.* St. 716.

Material:
St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – 41 specimens.

Description: The specimens are all rather defective. They are 2–5 cm long, and the body form is similar to that of *P. azorica,* being elongated, and usually possessing a downwardly bent anterior part.

Tentacles 10. Only one tentacle preserved, the shape of which could not be determined.

Tubefeet 7–8 pairs, placed along the posterior two-thirds of the ventral sole. They decrease in size and distance from one another posteriorly, the posteriormost rudimentary and placed without intervals. Each tubefoot possesses a minute sucking-disc.

Dorsal papillae 4–5 pairs. In most specimens two pairs of conspicuous holes are present in the dorsal skin. These are scar-markings left by the two first pairs of dorsal papillae. In some specimens the basal parts of these papillae are preserved, but only one specimen has a complete papilla. It is 9 mm long (body length 30 mm) and very slender and pointed. This, apparently, represents the size and shape of the first two pairs of papillae – the scar-markings from the second pair of papillae usually being as large as those from the first pair. However, in some specimens the scar-markings from the second pair (and even from one of the papillae of the first pair) are small.

The small papillae and the bases of the large papillae are enclosed in a low, gelatinous pillow. The two pillows are either completely separate, or adjoin each other anteriorly.

Skin soft, mucous, and white-transparent.

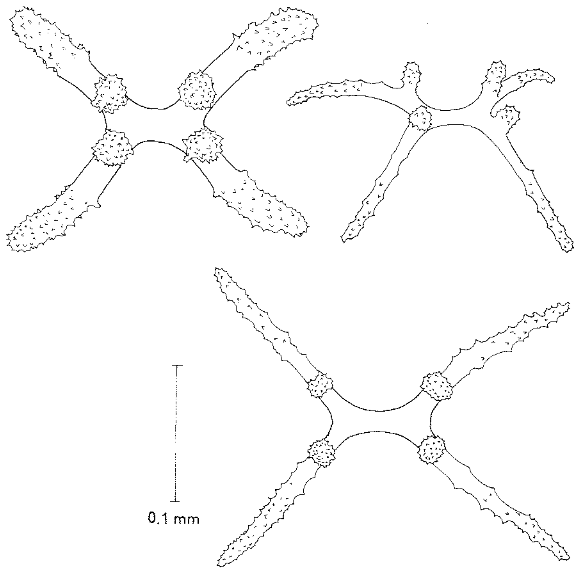


Fig. 68. *Peniagone papillata.* St. 716. Deposits.

Deposits (Fig. 68) examined in 16 specimens. They are rather uniformly developed – those illustrated representing the whole variation. No difference is found between the dorsal and ventral deposits. The small sucking-discs of the tubefeet are framed by rods, but no end-plates are present. The gonads contain slender primary crosses. No deposits were found in the wall of the intestine or in the muscles.

Calcareous ring consisting of five, isolated pieces, which have somewhat irregularly formed arms with flattened ends. The ring was examined in two specimens. The number of arms on the pieces varied from 7 to 9 on each side.

Polian vesicles two.

Type specimen: 3.5 cm long. The tentacles are all absent, but the tubefeet are better preserved than in any other specimen, all being preserved on the left side. The first two pairs of dorsal papillae are broken off near the base. In Fig. 67 the probable appearance of the papillae is shown by dotted lines, the reconstruction being based on the presence of one long, whiplash-like papilla in one of the other specimens.

Relationships: Most closely related to *Peniagone incondita* (q. v.).

Peniagone challengeri Théel, 1882

Théel 1882, pp. 49–50, pls. IX: 6–8, XXXIII: 16.

Diagnosis: Body very elongated, about 5 times as long as broad, somewhat flattened posteriorly. Tubefeet 8–9 pairs, approximately bordering the posterior half of the ventral sole, slightly decreasing in size posteriorly; posterior 3–4 pairs of tubefeet placed without intervals. Velum large, leaf-like, distally bipartite. Deposits with a well-developed stem and arms of varying length, with four, low apophyses; both arms and apophyses strongly spinous.

Record: South of Australia, 3276 m. Two specimens.

Remarks: The two specimens (both in BM) were re-examined. One was finely preserved, the other very defective.

The absence of tubefeet on the anterior part of the ventral sole was verified on the complete specimen, in which the skin was wholly intact on one side, between the tentacle crown and the anteriormost tubefoot. The posterior 3–4 pairs of tubefeet were separate and rather well developed. A median incision, separating the posterior tubefeet into a right and left group (as seen in Théel's illustration) could not be distinguished.

The velum is bipartite, with a broad, leaf-like basis – as illustrated by Théel. The velum probably varies to a lesser degree in preservation than usually in species of *Peniagone,* as it is covered with a tough skin.

The deposits (examined only ventrally) agreed perfectly with those described and illustrated by Théel.

Relationships: The species is possibly closest related to *P. azorica,* from which it differs by the elongated body form, the large and leaf-like velum, and the absence of tubefeet on the anterior part of the ventrum.

Peniagone vignoni Hérouard, 1901

Peniagone vignoni Hérouard, 1901, p. 42; Hérouard 1906, pp. 8–9, pls. I: 4–5, II: 13–23.

Peniagone theeli Ekman, 1925, pp. 13–20, fig. 1.

Diagnosis: Body elongate, flattened posteriorly. Tubefeet 8–9 pairs, bordering the posterior half of the ventral sole, decreasing in size posteriorly. Velum very low, with almost free papillae. Deposits primary crosses with four low apophyses.

Records: *P. vignoni* (3 specimens) and *P. theeli* (10 specimens), both Antarctic. Depth 400 m (stated for *P. theeli* only).

Remarks: The proposed synonymy between *P. theeli* and *P. vignoni* is based on an examination of four specimens kept in ZMUC and hitherto unrecorded. The specimens were taken in the Ross Sea by the *Discovery* (St. 1658, 76°09'S, 168°40'E, 520 m).

P. theeli was regarded as being different from *P. vignoni* in the following respects: (1) *P. theeli* has a low velum, while *P. vignoni* has four small separate dorsal papillae. (2) A lateral brim is present above the tubefeet in *P. theeli*, absent in *P. vignoni*. (3) The tubefeet are more posteriorly placed in *P. theeli*. (4) Deposits are present in the body wall in *P. theeli*, but confined to the tentacles and tubefeet in *P. vignoni*.

The examined specimens have a feebly developed velum with almost free papillae. The rather flattened body shows in places a lateral edge which might well be due to a collapse of the body. The external, deposit-containing layer of the skin is almost entirely worn off, apparently due to a mucous consistency of the subcutaneous tissue. The deposits are best preserved in the tubefeet and tentacles in which the mucous, subcutaneous tissue is less well developed. In shape the deposits agree with those of both species. The tubefeet number 8–9 pairs. In their arrangement they bridge the difference between the two species.

The tentacles are well developed, with a long stalk and an enlarged disc, which in the extended state has two aboral lobes, similar to those found in *P. azorica*.

The species is closest related to *P. japonica* (q. v.).

Peniagone japonica Ohshima, 1915

Ohshima 1915, pp. 240–241, pl. IX: 10; Ohshima 1916–1919, with four figures.

Diagnosis: Body elongate, flattened posteriorly. Tubefeet about 8 pairs, bordering the posterior half of the ventral sole, decreasing in size posteriorly. Velum well developed, composed of two pairs of large and two pairs of small papillae, and gradually passing into a lateral brim which is present above the tubefeet throughout the length of the body. Deposits primary crosses with downwardly bent arms and four rather high apophyses.

Records: Off Japan, 1135–1669 m. 11 specimens.

Remarks: The species differs from *P. vignoni* by its larger velum which passes gradually into a marked lateral brim of the body, and by the shape of the primary crosses which have downwardly bent arms with rather high apophyses.

Peniagone elongata (Théel, 1879)

Parelpidia elongata Théel, 1879, p. 17, figs. 34–35; Théel 1882, pp. 15–16, pls. I: 3–4, XXXII: 16–17, XXXVII: 2.

Parelpidia cylindrica Théel, 1882, pp. 16–17, pl. I: 1–2.

Diagnosis: Body very elongated, about six times as long as broad. Tubefeet 8–9 pairs, bordering the posterior $^2/_3$ of the ventral sole, the posterior 3–4 pairs closely placed, but not reduced in size. Dorsal papillae 2–3 pairs, rudimentary, not forming a velum. Deposits cross-shaped, with strongly curved, c. 0.12 mm long arms, and a single, high, central apophysis.

Records: The two species here synonymized are known from one specimen each, taken at two adjacent *Challenger* stations off Chile: *P. elongata* at 4065 m, and *P. cylindrica* at 3947 m.

Remarks: The specimens (both in BM) were re-examined and found to be similar in all essential features.

P. elongata is closest related to *P. verrucosa* (q. v.).

Peniagone verrucosa (Théel, 1879)

Elpidia verrucosa Théel, 1879, p. 15, figs. 26–28; Théel 1882, pp. 19–20, pls. III: 1–2, XXXIV: 3–4, XXXIX: 2.

Diagnosis: Body ovoid. Tubefeet 9 pairs, bordering the posterior $^2/_3$ of the ventral sole, decreasing in size posteriorly. Dorsal papillae 2 pairs, rudimentary, not forming a velum. Deposits cross-shaped, with strongly curved c. 0.6 mm long arms, and a single, high, central apophysis. Interspersed among the normal type are crosses with a short stem bearing an apophysis at either end. Small primary crosses with four apophyses occur in tubefeet.

Record: Off Chile, 4065 m. One specimen, taken simultaneously with *P. elongata*.

Remarks: The specimen of *P. verrucosa* may be a strongly contracted *P. elongata*. The two species are retained as separate species because they also differ in the size of deposits and in the presence in *P. verrucosa* of primary crosses with two or four apophyses in addition to the normal type.

Peniagone lugubris Théel, 1882
Fig. 69

Théel 1882, pp. 44–45, pl. X: 1.

Diagnosis: Body elongate. Tubefeet bordering the posterior $^2/_3$ of the ventral sole, numbering 5 pairs (plus, possibly, 2–3 pairs of rudimentary tubefeet at the posterior tip of the body). The anteriormost 3 pairs of tubefeet separated by wide gaps. Velum very large, composed of two pairs of completely fused papillae. Deposits primary crosses with four apophyses.

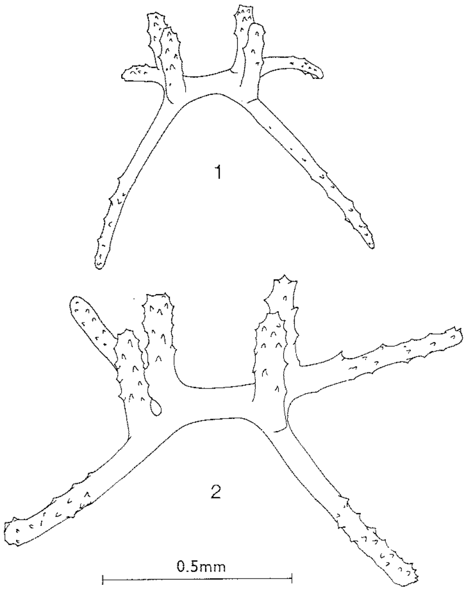


Fig. 69. *Peniagone lugubris*. Deposits from type specimen (*Challenger* St. 104). 1, dorsum; 2, ventrum.

Record: Mid-Atlantic, 4545 m. One specimen.

Remarks: The specimen (in BM) was reexamined and found to agree well with Théel's illustration. The skin was dark violet, tough and with a rather hard surface. The specimen might therefore have preserved its natural shape better than is usual in species of this genus. The posterior tip of the body was slightly torn; a few pairs of rudimentary tubefeet could have been present in this place, as in most species of the genus. One tentacle preserved, with a long stalk and an enlarged disc with a papillate surface.

The deposits (Fig. 69), not illustrated by Théel, were densely crowded both in the dorsal and ventral skin. They consisted of primary crosses with a well-developed stem and four low or moderately high apophyses; the arms were slightly curved. The dorsal crosses measured about 0.7 mm across (occasionally up to 1.0 mm), the ventral crosses 1.0–1.5 mm.

The five specimens which Madsen (1953) referred to this species are here re-determined to *P. ferruginea*.

Peniagone vitrea Théel, 1882
Fig. 70

Peniagone vitrea Théel, 1882, pp. 50–52, pls. VII: 7–9, XXXIV: 17–18, XLIV: 10; Clark 1920, p. 136; Ekman 1927, pp. 368–370, fig. 4; non Sluiter 1901b, p. 74.
Peniagone vitrea Théel var. *setosa* Ludwig, 1894, pp. 105–108.
Peniagone setosa Clark, 1920, p. 136.

Diagnosis: Body elongate, the part anterior to the broad velum being ventrally or posteriorly directed. Tubefeet 6–9 pairs, bordering the posterior third of the ventral sole, closely placed, slightly decreasing in size posteriorly. Deposits primary crosses with a short stem, strongly downwardly bent arms, and 1–4 spinous, pointed apophyses, which are usually longer than the arms.

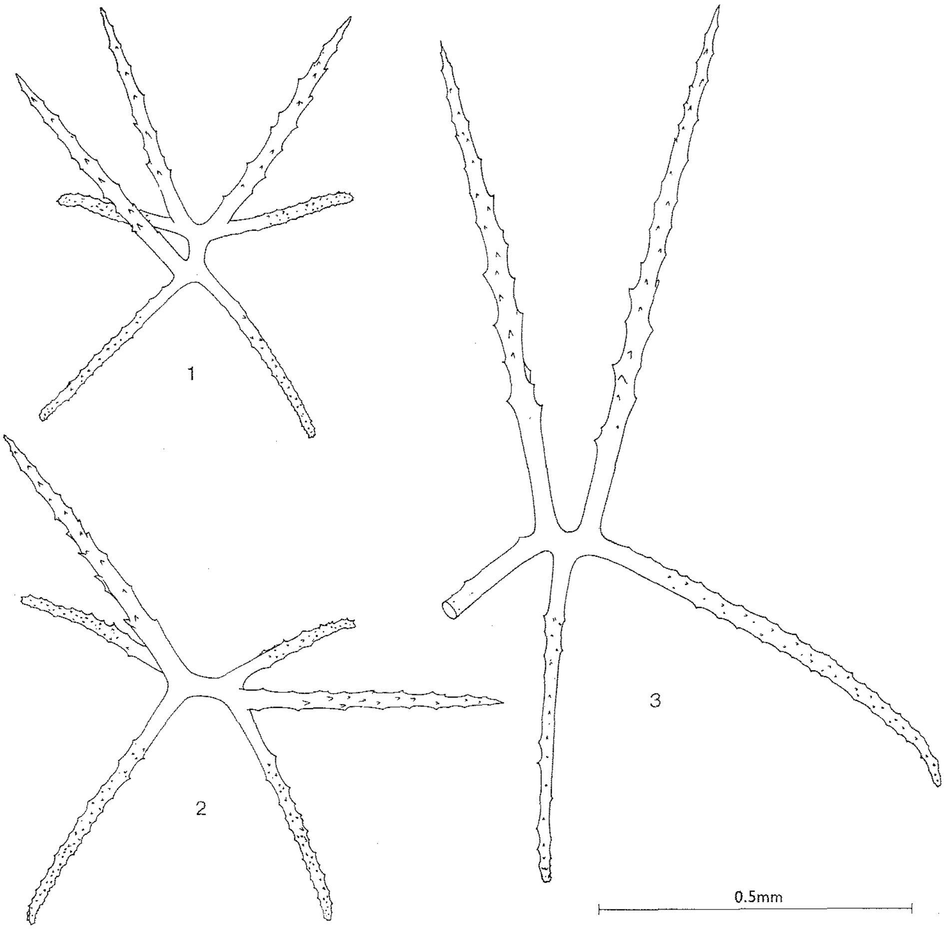


Fig. 70. *Peniagone vitrea.* Dorsal deposits. 1–2, *Challenger* St. 302 (the specimen in BM); 3, *Albatross* St. 3400 (var. *setosa).*

Material:
St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – 1 specimen.

Description: The specimen is c. 3 cm long and very defective. The deposits, however, are those typical of the species – primary crosses with a rather short stem, slender arms c. 0.4 mm in length, and two, occasionally three, high apophyses with distally directed spines.

Previous records: Off southern Chile, 2654 m. Several specimens of *P. vitrea* taken by the *Challenger* (Théel 1882). – Gulf of Panama, 1790–4337 m. 38 specimens of *P. vitrea* var. *setosa* (Ludwig 1894) and one of *P. setosa* (Clark 1920). – Central Pacific, 4507 m. One specimen of *P. vitrea* (Clark 1920). – Antarctic Ocean, 3423 m. One specimen of *P. vitrea* (Ekman 1927).

After an examination of his own Antarctic and the *Challenger* specimens, Ekman found that the features of *P. setosa* were included in the variation of *P. vitrea.*

The present re-examination of two of the *Challenger* specimens of *P. vitrea* (in BM), eight of Ludwigs' specimens of *P. vitrea* var. *setosa* (in USNM), and Clark's specimens of *P. vitrea* and *P. setosa* (in USNM), confirmed that all are one species, although differences in the deposits may represent a geographic variation.

The two *Challenger* specimens had dorsal deposits (Fig. 70: 1–2) with arm lengths of 0.2–0.4 and 0.3–0.6 mm, respectively. The latter had ventral deposits with arm lengths of 0.3–0.5 mm. In both specimens the deposits were larger than found by Théel (arm length "0.16 mm or sometimes more").

The nine specimens from the Gulf of Panama had deposits (3) with arm lengths of 0.4–0.7 mm (very few exceeding 0.6 mm).

The deposits of the Antarctic specimen, according to Ekman, measured up to 0.4 mm in arm length.

The deposits were remarkably similar in shape in the specimens from the three localities. The stem was short, and the apophyses very high (usually exceeding the arms in length), with pointed ends and distally directed spines. (Few apophyses were as short as those illustrated by Théel). The apophyses were usually two in number both in the specimens from off Chile and from the Gulf of Panama; deposits with three apophyses were not uncommon, while the number of four was very rare. Ekman did not state the number of apophyses in his Antarctic specimen; the deposit illustrated has four apophyses.

The deposits of the Central Pacific specimen of *P. vitrea* reported by Clark (1920) were found to resemble, both in shape and size, those illustrated by Théel for the *Challenger* specimens. The external morphology of the specimen could not be made out.

The tentacles have small discs. In the two re-examined *Challenger* specimens all the tentacles had the discs inwardly turned, agreeing with Théel's drawing. Two of the specimens re-examined from the Gulf of Panama (both from Ludwig's material) had similarly shaped tentacles, but one (from Clark's material) had only one tentacle like this, while the others had discs vertical to the axis of the stalk.

P. vitrea has been erroneously recorded from an Indonesian station of the *Siboga* (Sluiter 1901b). Re-examination of the single specimen taken (in ZMA) revealed that the deposits were tripartite. As C-shaped deposits were not present in the preparations, the specimen seems to belong to the genus *Achlyonice*.

Relationships: *Peniagone vitrea* agrees with *P. islandica* in the shape of the velum and the tentacles, and partly in the number and arrangement of the tubefeet.

The deposits of *P. islandica* are similar to those of the Antarctic specimen of *P. vitrea*, described by Ekman. The presence of eight tentacles, and possibly also the absence of the abrupt, downward bend of the anterior part of the body, separates *P. islandica* from *P. vitrea*. However, the degree of the bend may depend on the contraction of the ventral, longitudinal muscles – the two species possibly not differing in this respect.

Peniagone islandica Deichmann, 1930

Peniagone islandicus Deichmann, 1930, p. 137; Heding 1942, pp. 20–21, fig. 19.

Diagnosis: Body elongate. Tentacles 8. Tubefeet 9 pairs, bordering the posterior $^1/_3$–$^1/_2$ of the ventral sole, the anterior 5 pairs large and free (although closely set), whereas the posterior 4 pairs are minute and fused into a brim along the hindmost edge of the body. Velum broad. Deposits primary crosses with a short stem, strongly curved arms and four spinous, pointed apophyses, which are longer than the arms.

Record: Southwest of Iceland, 2137 m. Two specimens, taken by the *Ingolf*.

Remarks: Deichmann (1930) gave a diagnosis of the species which was later described in detail by Heding (1942).

Both specimens were re-examined and found to agree well with Heding's description. The tentacles were so well preserved that their number in both specimens could be stated to be eight with certainty. The tentacles resembled those of *P. vitrea*, as illustrated by Théel (1882, pl. XLIV: 10).

The species is most closely related to *P. vitrea* (q. v.).

Peniagone wyvillii Théel, 1882

Théel 1882, pp. 42–44, pls. X: 3–4, XXXVII: 6, XLIV: 5, 7; Grieg 1921, pp. 6–7, figs. 1–2, pl. III: 3–5.

Diagnosis: Body twice as long as broad. Tubefeet about 8 pairs, bordering almost the entire ventral sole, decreasing in size posteriorly. Velum very large, composed of two pairs of partially free papillae. Deposits, primary crosses with curved arms and four apophyses.

Records: The type specimen was taken in the Central Pacific at 4413 m. The five specimens reported by Grieg were taken in the North Atlantic at 2615–2865 m.

Remarks: The type specimen (in BM) was found on re-examination to be in a poor state of preservation and nothing could be added to the description given by Théel. The deposits (not re-examined) were stated to be similar to those of *P. lugubris.*

Grieg (1921) determined his North Atlantic specimens to *P. wyvillii* because of their close similarity in external appearance to the type specimen, as illustrated by Théel. The deposits apparently differed by the absence of some or all of the apophyses. However, it seems doubtful whether the deposits illustrated by Grieg represent the fully developed deposits of the outer layer of the skin.

P. wyvillii is most closely related to *P. ferruginea,* from which it differs by the tubefeet, which are more spaced in position, occupy a larger part of the ventral sole, and diminish more regularly in size posteriorly. The light violet colour of the body and the shape of the deposits are more doubtful differences.

Peniagone ferruginea Grieg, 1921

Peniagone ferruginea Grieg, 1921, pp. 7–8, fig. 3, pl. I: 4–6.

Peniagone lugubris Théel, Madsen 1953, pp. 153–155, figs. 2–3.

Diagnosis: Body two and a half times as long as broad. Tubefeet about 7 pairs, bordering the posterior $^1/_2$–$^2/_3$ of the ventral sole, closely placed and almost equally large, apart from the one or two posteriormost pairs which may be rudimentary. Velum very large, composed of two pairs of partially free papillae. Deposits, primary crosses with four, usually high apophyses.

Records: The type specimen was taken off the Canary Islands at 2800–3000 m. The five specimens reported by Madsen were taken in the mid-Atlantic at 5600–5610 m.

Remarks: Madsen referred his specimens to *P. lugubris* which, according to Théel, had exclusively large-sized tubefeet. The type specimen of *P. ferruginea* possessed in addition to the large tubefeet a rudimentary hindmost pair.

Re-examination of a 3.0 cm long specimen (in ZMUC) from Madsen's material revealed, in addition to the six pairs of large tubefeet, a rudimentary posterior one on the left side (the right side was not sufficiently well preserved to permit the demonstration of a right rudimentary tubefoot). The specimen illustrated by Madsen (1953, fig. 2) had seven pairs of equally large tubefeet, with no space for a rudimentary pair. Apparently, the presence of a rudimentary posterior pair of tubefeet is not a constant feature in the species.

The similarity between Madsen's specimens and the type specimen of *P. ferruginea* also applied to the deposits, and to the dark colour of the body. (The type specimen was "greyish rusty-brown", with the tentacles and the oral disc dark violet. Madsen's specimens were when alive reddish-violet, in alcohol blackish-violet).

Re-examination of the type specimen of *P. lugubris* (q. v.) showed difference from *P. ferruginea* both in external features and (less distinct) in the deposits.

P. ferruginea seems to be most closely related to *P. wyvillii* (q. v.).

Peniagone purpurea (Théel, 1882)

Elpidia purpurea Théel, 1882, pp. 21–23, pls. VII: 4–6, XXXIII: 13–14, XLIV: 6.

Elpidia ambigua Théel, 1882, pp. 27–28, pl. XXXIII: 6.

Peniagone lacinora Agatep, 1967b, pp. 53–55, pl. III: 1–9.

Diagnosis: Body flattened. Tentacles with bilobed discs. Tubefeet 7–9 pairs, the first two pairs being separate and ventral in position, while the remaining 5–7 pairs are closely placed and partly fused. Velum consisting of two pairs of very long and slender papillae, which are fused only at their bases. Edge of velum proceeding along the body side as a brim above the tubefeet. Deposits, primary crosses with a well-developed stem and four long apophyses.

Records: The three species synonymized were all taken in the Antarctic Ocean, at 2934–4789 m.

Remarks: Théel regarded *Elpidia ambigua* as a close relative of *E. purpurea,* differing only by its lighter violet colour, the more densely crowded deposits, and by the presence of a few wheel-shaped deposits. None of these differences can be attributed a taxonomic significance. Re-examination of one specimen of each species (both in BM) confirmed that they agree in all essential features, including the shape of the velum (although in the *ambigua* specimen only one of the papillae was preserved in its full length).

Agatep stated that *P. lacinora* differs from the two above-mentioned species in the size and position of the first two pairs of tubefeet. In *P. purpurea* and *P. ambigua* all the tubefeet were small and closely placed along the border of the ventral sole. In *P. lacinora* the tubefeet of the first two pairs were large, separated from each other and from the remaining tubefeet, and placed beneath the lateral edge of the body. This apparently conspicuous difference is probably due to a different state of preservation. Contraction of the body in the specimens of *P. purpurea* and *P. ambigua* might explain the fact that the first two pairs of tubefeet were small and placed more closely to the remaining tubefeet, and that a body brim was absent above them.

P. lacinora agrees with *P. purpurea* and *P. ambigua* in the violet colour of the body, the peculiarly shaped velum, the thin and soft skin, the merging of the bases of the posterior tubefeet to form a brim, the shape of the deposits, and the bi-lobed tentacle discs.

Deep-sea photographs (Lemche *et al.* in press) reveal the common occurrence of *P. purpurea* (or a closely related, undescribed species) at a depth of 8030 m in the Palau Trench.

Relationships: The species is most closely related to *P. foliacea* and *P. expansa*. It differs from both in the long free velar papillae, the violet body colour, and the deposits being primary crosses. *P. foliacea* and *P. expansa* have cross-shaped deposits without stem.

Peniagone foliacea (Hérouard, 1912)

Kolga foliacea Hérouard, 1912, pp. 5–6, figs. 3–4.
Peniagone foliacea (Hérouard), Hérouard 1923, pp. 86–87, pls. I: 31, IX: 1–2.

Diagnosis: Body flattened. Tubefeet 7 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Velum very large, as broad as the body, forwardly directed, its lateral edges continuing into a brim along the anterior half of the body. Deposits almost cross-shaped, with four apophyses placed near the centre of the cross, their bases joined.

Record: Between the Azores and Portugal, 4275 m. One specimen.

Remarks: In external features the species is most similar to *P. expansa,* although it has a much smaller velum. The deposits resemble those of *P. obsoleta* and *P. convexa,* in particular in the position and shape of the apophyses.

Peniagone expansa Koehler & Vaney, 1905

Koehler & Vaney 1905, pp. 68–69, pls. IV: 10, XII: 27–28.

Diagnosis: Body flattened. Tubefeet about 8 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Velum large, as broad as the body, forwardly directed. Deposits cross-shaped with five apophyses.

Record: Bay of Bengal, 3194 m. One specimen.

Remarks: In external features the species is reminiscent of *P. foliacea.* The deposits (both ventral and dorsal) resemble the dorsal deposits of *P. rigida.*

Peniagone intermedia Ludwig, 1894

Ludwig 1894, pp. 108–110, pl. XII: 1–6.

Diagnosis: Body flattened. Mouth posteriorly directed. Tubefeet, 3 free lateral pairs and 4 pairs which are fused into two fan-shaped clusters at the posterior end of the body. Velum large, as broad as the body, forwardly directed, its lateral edges continuing into a brim along the anterior half of the body. Deposits spinous primary crosses with four apophyses.

Records: The type specimen was taken at *Albatross* St. 3400 at 2406 m between the Galapagos Islands and South America. The other specimens from Ludwig's material, as well as those recorded by Clark (1920), were too poorly preserved to allow a correct identification.

Relationships: Probably most closely related to *P. diaphana* and *P. gracilis,* both of which were formerly referred to *Scotoanassa.* The similarities include the flattened body, the velum which forms the anterior margin of the body, the hindmost tubefeet being fused into a brim, the posteriorly directed mouth, and the deposits, which possess a well-developed stem. However, the presence of three pairs of free, lateral tubefeet clearly distinguishes *P. intermedia* from both species.

A large velum which forms the anterior margin of the body is found also in *P. purpurea, P. foliacea,* and *P. expansa.* From these species *P. intermedia* primarily differs by the clear separation between the free lateral and the fused posterior tubefeet.

Peniagone diaphana (Théel, 1882)
Fig. 71, pl. X: 7–8

Scotoanassa diaphana Théel, 1882, pp. 55–56, pls. IX: 3–5, XXXV: 18, XLIV: 9.

Scotoanassa translucida Hérouard, 1899, pp. 71–72, fig. 3; Hérouard 1902, pp. 43–45, pls. III: 4–6, VI: 17–20; Hérouard 1923, pp. 88–90, pls. III: 7–8, IV: 4; Madsen 1953, pp. 158–159, fig. 6.

Diagnosis: Body flattened. Mouth placed on a posteriorly directed, retractile tube. Tentacles with two conspicuous, digitiform processes on the discs, the latter obliquely placed to the axis of the stalk; discs covered with conspicuous, slightly ramified papillae. Tubefeet 4–5 pairs, enclosed in a brim bordering the hind edge of the body. Velum broad, forwardly directed, forming the anterior continuation of the dorsal surface; the four papillae composing the velum project only slightly from the anterior edge. Deposits with a well-developed stem and four apophyses.

Material:

St. 52, San Tomé–Cameroon (1°42'N, 7°51'E), 2550 m. – One complete and two fragmentary specimens.

St. 63, off Gabon (2°00'N, 9°14'E), 1520 m. – 1 specimen.

St. 574, Tasman Sea (39°45'S, 159°39'E), 4670 m. – 2 specimens and 6 isolated tentacles from a larger specimen.

Description:

St. 52. – The complete specimen is 7.5 cm long and 3.5 cm broad. The anterior edge of the flattened body, although identical with the velum, does not appear to be composed of papillae in external view. The posterior brim is composed of four pairs of fused tubefeet, the tips of which project slightly from the edge of the brim. The anterior and posterior brims continue directly into the lateral edge of the body, but a true lateral brim is not present. Mouth placed 2.5 cm from anterior edge of body at the end of a posteriorly directed tube, which is, however, almost completely retracted.

Tentacles not preserved.

Skin whitish, with a faint reddish-purple tinge. The outer layer hard and rough, caused by the crowding of the deposits, and easily separated from the soft connective tissue.

Deposits (Fig. 71: 1) slenderly built primary crosses with long arms and a well-developed stem. Dorsal and ventral deposits similar.

The two fragmentary specimens possess deposits similar to those of the complete specimen.

Calcareous ring of the usual type in the genus. The five isolated pieces each possesses at least seven pairs of slender, often distally branched arms.

St. 63. – The specimen is 2.2 cm long and 0.7 cm broad. Although in a poor state of preservation it shows the external features characteristic of the species. The velum consists of two pairs of papillae and forms the anterior margin of the body. Three pairs of tubefeet on the posterior margin of the body. The body is flattened, with the edge of the velum proceeding into the lateral edge of the body. The mouth is placed on a ventrally directed tube. (Tentacles not preserved).

The outer, deposit-containing layer of the skin is completely lost on the dorsum, and partly on the ventrum. The ventral crosses (Fig. 71: 4–5) show large variation: Anteriorly with short and pointed arms (5), posteriorly much larger crosses with high apophyses (4).

St. 574. – Both specimens are 10.5 cm long and 5.5 cm broad. The anterior edge of the body is somewhat defective, and the papillae composing the velum are not visible in external view. The posterior brim in both specimens consists of four pairs of papillae and a single unpaired, median papilla. The posterior brim continues directly into the lateral edge of the body, although it is clearly distinguishable from it. Mouth placed at the end of a posteriorly directed tube.

Tentacles. Only one tentacle is preserved. However, at the same station six isolated, much larger tentacles were taken (Pl. X: 7–8), being similar in shape to the small one. The tentacle discs, including the two processes, are covered with conspic-

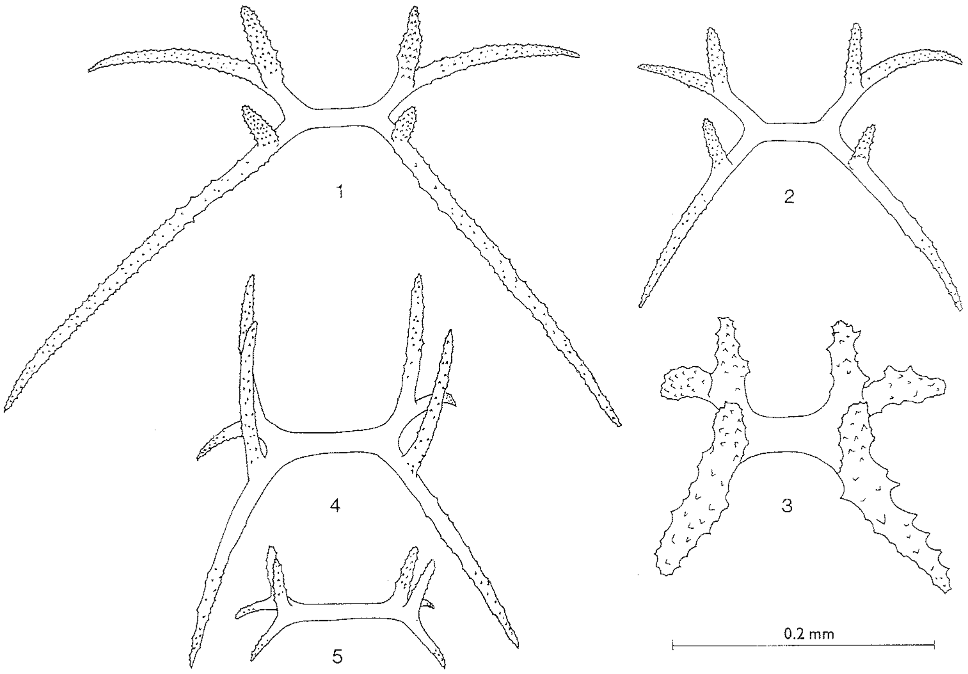


Fig. 71. ***Peniagone diaphana.*** Deposits. 1, St. 52, ventrum; 2, St. 574, dorsum; 3, St. 574, ventrum; 4–5, St. 63, posterior and anterior part of ventrum.

uous, slightly ramified papillae. The size (10–14 mm) compared with that of the small tentacle (5 mm) suggests that they belonged to a very large specimen of *P. diaphana.*

Skin whitish, and similar in structure to that of the Atlantic specimens.

Deposits similar in the two specimens and dorsally (2) resembling those of the Atlantic specimens (1), but with shorter and slightly more curved arms. Ventral deposits (3) very sturdy, only few approaching the dorsal ones in slenderness.

Calcareous ring absent (one specimen examined). Hérouard (1902) similarly noted the absence of a ring in some Atlantic specimens examined. Apparently, the ring is resorbed with advancing age.

Synonymy and variation: *Scotoanassa translucida* Hérouard was believed to differ from *S. diaphana* by the somewhat differently shaped posterior brim and the more robust deposits. However, the posterior brim in the *Galathea* specimens from the Tasman Sea (taken comparatively near the type locality of *P. diaphana* in the Great Australian Bight) is similar to that of the Atlantic species *S. translucida,* as illustrated by Hérouard.

The differences reported between the deposits of the two species cannot be regarded as taxonomically significant, in view of the subsequently acquired knowledge of the variation in this character. The ventral deposits of the *Galathea* specimens from the Tasman Sea are remarkably different from those of the type specimens of both *P. diaphana* and *P. translucida,* but resemble those of the Atlantic specimens described by Madsen. Apparently, the differences found represent local rather than geographic variations.

S. diaphana and *S. translucida* agree in a number of features, including the shape of the body, the mouth being placed at the end of a posteriorly directed tube, the shape of the velum, the inclusion of 4–5 pairs of tubefeet in the posterior brim, and the presence of a pair of digitiform processes on the tentacle discs.

Relationships: Closely related to *P. gracilis* (q. v.) and more distantly to *P. intermedia.*

Biology: The Atlantic material reported by Hérouard (1923) included specimens from four pelagic stations. They were considered to be larval or to have just completed their larval stage. Two of them were described – one 5 mm long, almost spherical, and supposed to have only five tentacles, the other 10 mm long and having 10 tentacles (the shape of the body was not mentioned).

During re-examination of Hérouard's specimens, the external characters of the two larval specimens could no longer be ascertained. However, in addition to the larval specimens, a 3 cm long specimen, having the normal appearance of the species, was found to originate from the pelagic Station 3001, proving that the ability to lead a pelagic life is not confined to the larval stage. The depths (actually, the wire lengths) of the four pelagic stations were stated to be 0–4200, 0–4500, 0–4800, and 0–4900 m.

Distribution: Atlantic, 2550–5600 m. Great Australian Bight, Tasman Sea, 4670–4732 m.

Peniagone gracilis (Ludwig, 1894)

Scotoanassa gracilis Ludwig, 1894, pp. 111–113, pl. XII: 7–8.

Diagnostic features: The species differs from *P. diaphana* by the shape of the primary crosses which have strongly curved arms with very high apophyses, and possibly also by the absence of the two large, digitiform processes on the tentacle discs.

Record: Off the Galapagos Islands, 2475 m. Four specimens.

Relationships: Re-examination of the *Albatross* material in USNM revealed only some fragments which gave no additional information to the original description.

The alleged absence of the pair of digitiform processes on the tentacle discs remains to be verified on well-preserved specimens. In *P. diaphana* the processes, when placed close together, are easily overlooked.

The deposits fall outside the known variation in *P. diaphana*. On the other hand, the differences are not greater than can be found as local or geographic variations within a single species.

Ludwig supposed that *P. gracilis* differed from *P. diaphana* also by the tubefeet being placed below the brim (and not on the edge of it), and by the prolongation of the brim into a posteriorly directed, median prong. But the specimens were so defective that the exact shape of the body could not be determined with certainty.

Peniagone spp.

Specimens representing several species are left undescribed.

Sts. 231 and 232. Fragments of four specimens.

St. 466. Eight specimens which have lost their deposits.

St. 495. Fragments of a dark brown specimen, probably belonging to a new species.

St. 626. Four juvenile specimens, ovoid in shape and 9–10 mm long. Tubefeet in one specimen numbering 6–7 pairs, placed around the posterior half of the ventral sole. However, tubefeet might have been present also along the anterior half of the ventral sole. Spicules slender primary crosses with four high apophyses.

St. 658. One dark violet specimen resembling *P. purpurea;* deposits lacking, possibly dissolved.

Genus ***Achlyonice*** Théel, 1879

Fig. 121

Théel 1879, p. 13. – Type species: *Achlyonice ecalcarea* Théel, 1879, by monotypy.

Diagnosis: Tentacles 10–12. Deposits tripartite, rod-shaped, or absent. Calcareous ring consisting of five isolated pieces, each having a varying number of arms.

Remarks: *Scotoplanes gilpinbrowni* Pawson, 1965a, known from one incomplete specimen taken at 1782 m depth north of New Zealand, should probably be transferred to the genus *Achlyonice*. C-shaped spicules were absent, the deposits consisting exclusively of slender rods with spinous ends, resembling those found in *A. monactinica*. The two species also agree in the number (11 pairs) and arrangement of the tubefeet. However, since neither tentacles nor velum were preserved, the specimen cannot be identified with certainty.

Key to the species of *Achlyonice*

1.	Deposits absent. Dorsal papillae not forming a velum	*tui*	(p. 158)
1.	Deposits present. Dorsal papillae forming a velum	2	
2.	Body ovoid. Tubefeet with large sucking-discs, all closely placed, not notably decreasing in size posteriorly. Deposits regularly tripartite, usually with an apophysis on each arm; in addition, rod-shaped deposits occur	*ecalcarea*	(p. 156)
2.	Body elongate. Tubefeet with minute sucking-discs, spaced in position anteriorly, closely placed and reduced in size posteriorly. Deposits rod-shaped, sometimes with a side-branch, but never regularly tripartite	*monactinica*	(p. 157)

Achlyonice ecalcarea Théel, 1879
Figs. 72–73, 93: 1, pl. X: 9

Achlyonice ecalcarea Théel, 1879, p. 13, fig. 8. Non Clark 1913, p. 230.

Achlyonice paradoxa Théel, 1882, pp. 57–59, pls. V: 1–2, XXXIX: 3, 7, XLI: 5.

Achlyonice lactea Théel, 1882, pp. 59–60, pl. XXXII: 21–23.

Diagnosis: Body ovoid. Tentacles 12. Ventral sole increasing in breadth posteriorly. Tubefeet 10–14 pairs, with large sucking-discs, all closely placed, bordering the entire ventral sole, not notably decreasing in size posteriorly. Velum composed of three pairs of almost completely fused papillae. Deposits tripartite, usually with a spinous, bipartite apophysis on each arm; in addition, rod-shaped deposits are present.

Material:

Galathea St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 1 specimen.

Dr. Th. Mortensen's Java–South Africa Exp. St. 78, St. Helena (8 miles W. by N. of Sugarloaf), 2400–2780 m. – 1 specimen.

Description:

1. – Specimen from the Kermadec Trench (Fig. 72: 1–2). Length 21 mm. Ventral sole 6 mm broad anteriorly, increasing in breadth posteriorly to 9 mm.

Tentacles 12, similar in shape to those of the specimen from St. Helena, although less well preserved.

Tubefeet 12–13 pairs, bordering the entire ventral sole. The tubefeet are all closely placed and almost equal in size. The sucking-discs are very large on all the tubefeet, their diameter almost equal to that of the tubefeet.

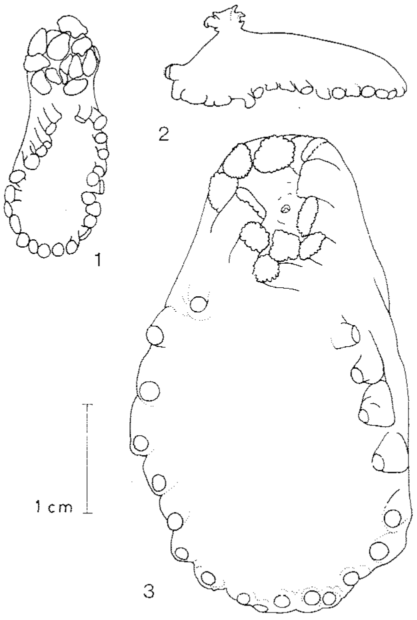


Fig. 72. *Achlyonice ecalcarea.* 1–2, *Galathea* St. 663; 3, Java-South Africa Exp. St. 78.

Velum composed of three pairs of almost completely fused papillae.

Skin white and soft, although rather firm.

Deposits (Fig. 73) tripartite, nearly all with a spinous, often bifurcate, apophysis on each arm. Similar apophyses are present on many of the rod-shaped deposits. Dorsal and ventral deposits similar. Wheels (Fig. 93: 1) occur scatteredly in the dorsal and ventral skin.

The tentacles possess numerous sturdy rods and irregular deposits, all of them lacking apophyses. The discs of the tubefeet are bordered by sturdy, smooth, curved rods, but end-plates are absent.

2. – Specimen from off St. Helena (Fig. 72: 3). Length 44 mm. Ventral sole reaching a breadth of 23 mm.

Tentacles 12, the discs (Pl. X: 9) with a papillate surface and indented marginal processes; the fully extended discs show a deep incision on the aboral margin, separating two particularly large processes.

Tubefeet 10 pairs, the hindmost ones slightly smaller than the others. They are somewhat conical in shape, mutually converging at their base, and are all provided with a large sucking-disc.

Velum similar in shape to that of the *Galathea* specimen.

Deposits similar to those of the *Galathea* specimen; the similarity even includes the presence of scattered wheels.

Synonymy: *A. ecalcarea,* taken in two specimens by the *Challenger* at 4204 m in the northwestern Pacific, was erected in the preliminary report on the *Challenger* holothurians. Théel at that time found no deposits in the specimens. On later examination of the specimens he discovered traces of dissolved tripartite deposits, and, therefore, in the final report changed the name to *A. paradoxa.* This change of name, as noted by Clark (1913), is not valid.

Both specimens (one in BM, the other in ZMA) were re-examined. They agreed in external features with the two specimens described above. The rather small size of the discs of the tubefeet in the specimen illustrated by Théel (in BM) was found to be due to contraction; a few fully extended discs were equal in diameter to the tubefeet.

A. lactea was taken in four specimens by the *Challenger* at 2928 m west of the Crozet Islands (southern Indian Ocean). Two specimens (both in BM) were re-examined and found to agree with the specimens described above in the shape of the ventral sole, the arrangement and shape of the tubefeet, the shape of the tentacles, and the type of deposits. Wheels were present in both specimens.

The specimens described by Clark (1913) from Baja California (depth 1598 m) were referred to *A. ecalcarea* because they lacked deposits, despite the fact that the absence of deposits in the *Challenger* specimens of *A. ecalcarea* was due to dissolution. Re-examination of one of Clark's specimens (in MCZ) threw doubt on his determination. It has 12 pairs of tubefeet which border only the posterior two-thirds of the ventral sole, and only the posteriormost tubefeet are placed without intervals. Eleven tentacles could be counted in the specimen (but 12 tentacles might have been present). The superficial layer of the skin is worn off, which may explain the absence of deposits.

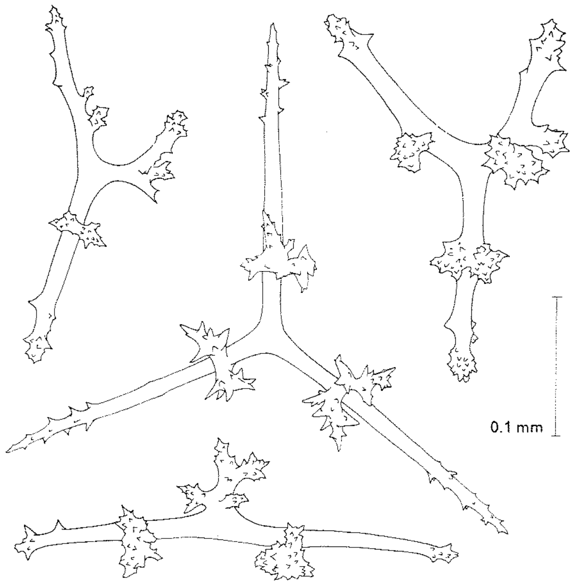


Fig. 73. *Achlyonice ecalcarea.* Deposits. *Galathea* St. 663.

Distribution: Probably cosmopolitan. Depth 2780–4924 m.

Achlyonice monactinica Ohshima, 1915

Ohshima 1915, pp. 241–242, pl. IX: 11; Ohshima 1916–1919, with four figures.

Diagnosis: Body ovoid to elongate. Tentacles 12, connected with one another by a membranaceous fold of skin, which leaves only the four posteriormost tentacles free. Tubefeet 10–13 pairs, with minute sucking-discs, bordering almost the entire ventral sole, decreasing in size and placed with decreasing intervals posteriorly. Velum low but with long free, filiform parts of papillae. Deposits rod-shaped, occasionally with a side-branch but not regularly tripartite.

Records: Off Japan, 1645–1669 m. 17 specimens.

Remarks: The species is characterized primarily by the rod-shaped deposits, the membranaceous fold of skin which encloses the stalks of the tentacles, and the long free, filiform parts of the velar papillae. Although only the second pair of velar papillae was seen to project into a long filiform part, the first pair has probably the same structure.

Achlyonice tui (Pawson, 1965)

Amperima tui Pawson, 1965a, pp. 216–217, pl. IV: 1–3.

Diagnosis: Body ovoid to elongate. Tentacles 10–12. Tubefeet 12 pairs, bordering the posterior $^2/_3$ of the ventral sole, all rather closely placed; the posterior 6 pairs inconspicuous. Dorsal papillae consisting of two pairs of closely placed but separate papillae arranged in a transverse row, and two small pairs behind the row. Deposits absent.

Record: North of New Zealand, 1170 m. 16 specimens.

Remarks: Because of the complete lack of calcareous deposits the reference to *Achlyonice* is uncertain. It is motivated by the number of tentacles which in no other elpidiid genus is known to exceed 10.

Genus *Amperima* Pawson, 1965
Fig. 121

Periamma R. Perrier, 1896, p. 901.
Amperima Pawson, 1965a, pp. 215–216. – Type species: *Periamma roseum* Perrier, 1896.

Diagnosis: Dorsal papillae anteriorly placed, usually forming a velum. Deposits consisting of tripartite spicules and C-es. Calcareous ring consisting of five isolated pieces, each with four pairs of arms.

Remarks: The species of *Amperima* are more easily defined than those of the related genus *Ellipinion*, primarily because of the more clearly differentiated deposits. Materials of all previously known species, except *A. velacula*, has been examined.

Key to the species of *Amperima*

1\. Posterior tubefeet large, forming two fan-shaped clusters .... *insignis* (p. 162)
1\. Posterior tubefeet small, not forming two fan-shaped clusters 2
2\. Tubefeet absent from anterior part of ventral sole .... *robusta* (p. 161)
2\. Tubefeet bordering the entire ventral sole 3
3\. Deposits, all regularly tripartite. An apophysis present on each arm 4
3\. Deposits, tripartite interspersed with irregularly rod-shaped, quadripartite, and pentapartite. Apophyses absent, or placed without regularity 5
4\. Apophyses undivided .... *rosea* (p. 158)
4\. Apophyses bifurcate .... *furcata* (p. 159)
5\. Large tripartite deposits with a smooth proximal arm part. Smaller deposits robust and strongly spinous .... *velacula* (p. 161)
5\. Deposits, all of the same type, although greatly varying in size; arms slender and spinous throughout their length .... *naresi* (p. 159)

Amperima rosea (Perrier, 1896)
Fig. 74, 93: 2

Periamma roseum R. Perrier, 1896, p. 901; R. Perrier 1902, pp. 419–423, pls. XIII: 10–12, XX: 1–11; Hérouard 1923, pp. 91–94.

Diagnosis: Body ovoid. Tubefeet 9–10 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the hindmost pairs rudimentary. Velum well developed, composed of two pairs of papillae. Deposits regularly tripartite, with an undivided, spinous apophysis on each arm.

Records: Between the Azores and Portugal, 4060–5005 m. Numerous specimens.

Remarks: Five of Perrier's specimens and three of Hérouard's were re-examined by means of skin preparations. The deposits (Fig. 74) all

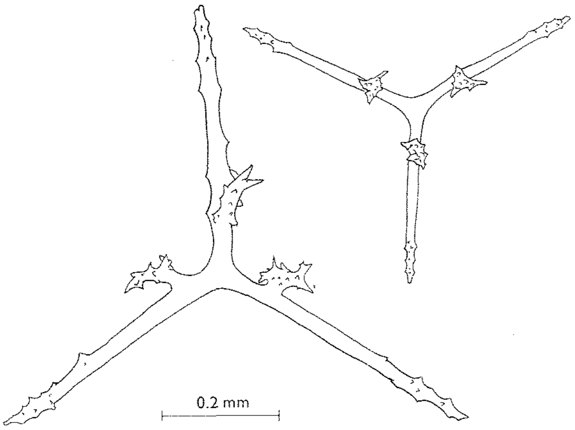


Fig. 74. *Amperima rosea.* Deposits. *Talisman* St. 137.

possessed a single, undivided apophysis on each arm. Wheels (Fig. 93: 2) were found in three of Perrier's and two of Hérouard's specimens. C-es few in number (absent in some of the preparations).

Amperima furcata (Hérouard, 1899)

Fig. 75

Kolga furcata Hérouard, 1899, p. 171, fig. 2; Hérouard 1902, pp. 40–41, pls. III: 7, VI: 4–10, VIII: 17.

Periamma furcata (Hérouard), Hérouard 1923, p. 91.

Diagnostic features: In external features probably similar to *A. rosea,* but the deposits have bipartite apophyses.

Records: Vicinity of the Azores and in the Bay of Biscay, 1846–2320 m. (Number of specimens not stated).

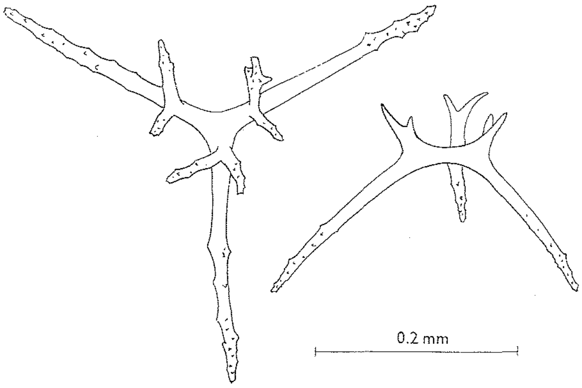


Fig. 75. *Amperima furcata.* Deposits. Monaco St. 698.

Remarks: Two specimens from Monaco St. 698 were re-examined. Their external features could no longer be made out, but the deposits (Fig. 75) were finely preserved. They were regularly tripartite and all possessed a bifurcate apophysis on each arm, this feature being apparently a reliable species character. C-shaped deposits were not found, nor was their presence mentioned by Hérouard. This suggests that the species actually belongs to the genus *Achlyonice.* On the other hand, C-shaped spicules may be very rare in the species of *Amperima* (cf. *A. rosea*). A correct identification to genus requires an examination of the calcareous ring.

Amperima naresi (Théel, 1882)

Fig. 76, pl. X: 6

Peniagone naresi Théel, 1882, pp. 47–49, pls. IX: 1–2, XXXIII: 15.

Periamma naresi (Théel), Hansen 1956, pp. 38–40, figs. 7–9; Belyaev & Vinogradova 1961, p. 129.

Periamma tetramerum H. L. Clark, 1920, p. 134, pl. II: 4; D'yakonov, Baranova & Savel'eva 1958, pp. 363–365, figs. 5–7.

Amperima naresi (Théel), Agatep 1967a, pp. 57–61, figs. 2–3.

Diagnosis: Body ovoid. Tubefeet 8–10 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the hindmost pairs rudimentary. Velum well developed, composed of two pairs of papillae. Deposits slenderly built, of varying and often irregular shape, being tri-, quadri-, pentapartite, and rod-shaped; arms irregularly spinous; apophyses, if present, placed without regularity.

Material:

St. 466, Sunda Trench (10°21'S, 110°12'E),
7160 m. – 114 specimens.

Description: The specimens were described previously (Hansen 1956), and only a few supplementary remarks are made here.

Tentacles 10. Discs (Pl. X: 6) with rather few, large, retractile papillae on the surface, and an indented margin. Some of the discs possess a pair of small aboral lobes.

Deposits (Fig. 76) examined in 25 specimens, including five previously examined. Dorsal and ventral deposits similar. In the previous report

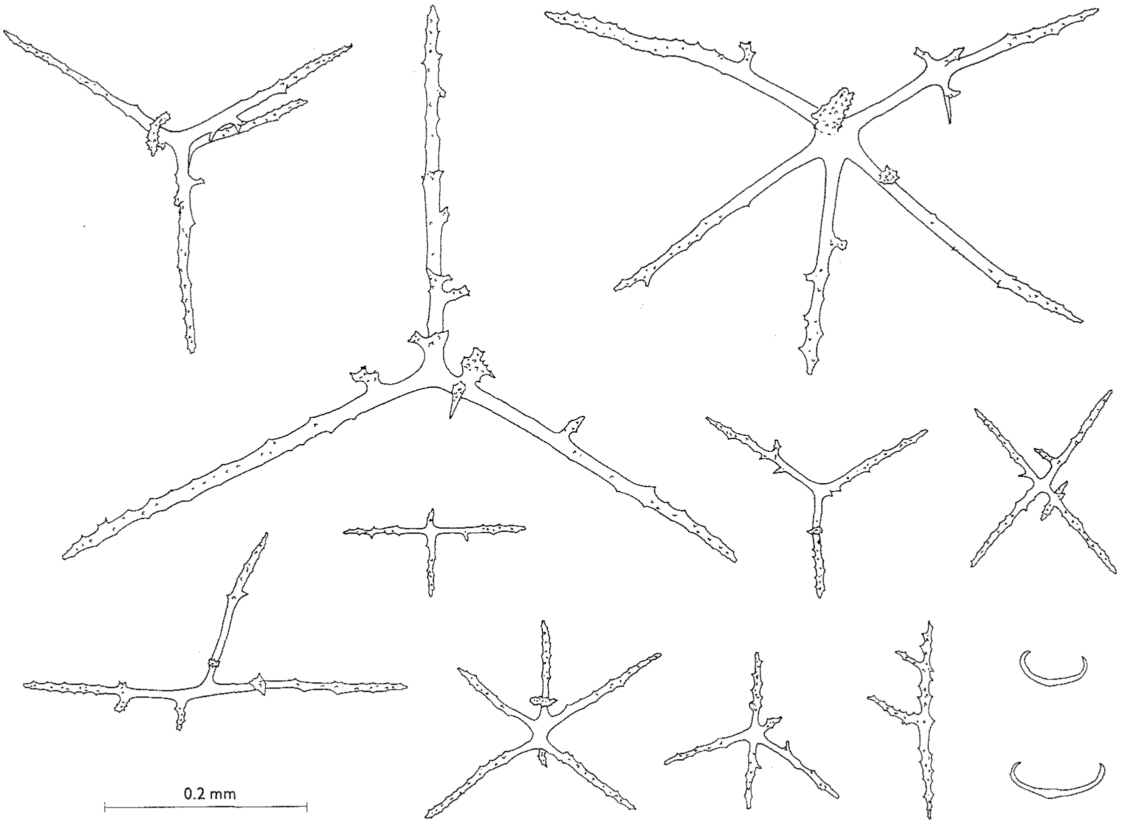


Fig. 76. *Amperima naresi*. Deposits. St. 466.

it was stated that the tripartite deposits, as reported by Théel, could be divided into two size groups; most of the deposits had arm lengths of about 0.11 mm, whereas a smaller number had arms twice as long. The examination of additional specimens showed that these size groups cannot always be distinguished. Deposits of intermediate size were often found; the size of the deposits sometimes varied considerably from one specimen to another. In some preparations nearly all had arms longer than 0.2 mm, a few even attaining a length of 0.8 mm.

Interspersed among the tripartite deposits are found rods (usually with side-branches), and quadri- and pentapartite deposits. (In two preparations the quadripartite deposits were as numerous as the tripartite ones). A few wheels were present in some of the preparations. The wheels were similar both in shape and size to those of *A. rosea* (Fig. 93: 2).

End-plates absent from tubefeet.

Calcareous ring absent in five specimens examined.

Synonymy: The type specimen, taken by the *Challenger* between Australia and the Antarctic, was re-examined. The presence of a very large velum, as seen on Théel's figure, could be verified – indeed, the velum was larger than that found in any of the *Galathea* specimens. However, agreement with the *Galathea* specimens in other features, including the characteristically shaped deposits, makes it improbable that the *Challenger* and *Galathea* specimens are different species.

The numerous Antarctic specimens taken by the *Eltanin* (Agatep 1967a) agreed with the *Galathea* specimens both in external features (including the greatly varying velum) and deposits.

Periamma tetramerum Clark, known from six specimens taken at 5835 m off Peru, was distinguished from *A. naresi* by the predominance of quadripartite deposits. As these are rather common also in the *Galathea* specimens, there seems no reason to keep the two species apart.

D'yakonov, Baranova & Savel'eva (1958) reported six specimens of *Periamma tetramerum* from 2850 m depth in the southern Okhotsk Sea. The specimens were held to agree perfectly with Clark's description, which was confirmed by the figures of the deposits.

Relationships: Appears to be most closely related to *A. velacula* (q. v.).

Distribution: Antarctic and Indo-Pacific, 2010–7130 m.

Amperima velacula Agatep, 1967

Agatep 1967a, pp. 61–68, figs. 4–6.

Diagnosis: Body ovoid. Tubefeet 9–10 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the hindmost pairs rudimentary. Velum small. Deposits consisting of scattered large tripartite spicules with a smooth proximal arm part, and smaller, very robust and spinous spicules which are tripartite, quadripartite, or irregularly shaped.

Records: Seven Antarctic stations of the *Eltanin*. Depth 2837–4850 m, except one station at the South Shetland Islands with a depth of only 131 m.

Remarks: The irregular shape of the deposits indicates a relationship with *A. naresi*, but the large tripartite deposits differ by the smooth proximal part of the arms and the smaller deposits by their great robustness and spinousness. Wheels occurred scatteredly in the ventral skin of most of the specimens. They had a tripartite centre, and were apparently similar in shape to those of *A. rosea* and *A. naresi*. Agatep did not mention whether wheels were also present in his specimens of *A. naresi*.

In external appearance the species is probably indistinguishable from *A. naresi*. The velum is not smaller than in many specimens of this species.

Amperima robusta (Théel, 1882)
Figs. 77–78

Scotoplanes robusta Théel, 1882, pp. 35–36, pls. VI, XXXIV: 6–7, XXXVII: 9.
Amperima robustum (Théel), Agatep 1967a, pp. 56–57.

Diagnosis: Body elongate. Tubefeet about 11 pairs, bordering the posterior $^{2}/_{3}$ of the ventral sole, decreasing in size posteriorly. Velum well developed, composed of two pairs of papillae. Deposits tripartite, dorsally with three apophyses and distal arm spines; ventrally smaller, more robust, and without apophyses.

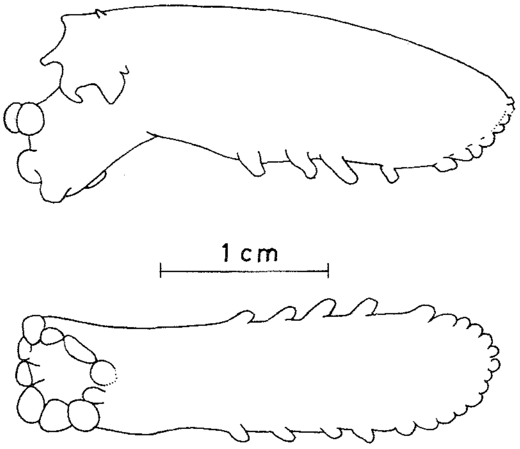


Fig. 77. *Amperima robusta*. St. 668.

Material:
St. 668, Kermadec Trench (36°23'S, 177°41'E), 2640 m. – 1 specimen.

Description: The specimen (Fig. 77) is 30 mm long and 8 mm broad.

Tentacles 10; obliquely forwardly directed; discs convex with a smooth surface and a smooth, non-lobated margin.

Tubefeet 11 pairs, bordering the posterior two-thirds of the ventral sole. Anteriormost 4–5 pairs rather long, with rounded ends, and separated by gaps equal to the width of a tubefoot. Remaining tubefeet closely placed and decreasing in size posteriorly.

Velum consisting of two pairs of fused papillae, followed by a pair of small, free papillae.

Deposits (Fig. 78) tripartite, with conspicuous spines confined to the distal part of the arms. The dorsal deposits have on each arm a small apophysis (sometimes represented by a few spines only). The ventral deposits are smaller, more robust, often less regularly shaped, and the arms are destitute of apophyses. Rods are found occasionally. C-shaped deposits present both in dorsal and ventral skin.

Remarks: Previously recorded from the Antarctic at 2010–4240 m, one specimen being taken by the *Challenger* and 51 by the *Eltanin*. The well-preserved *Challenger* specimen (in BM) was re-

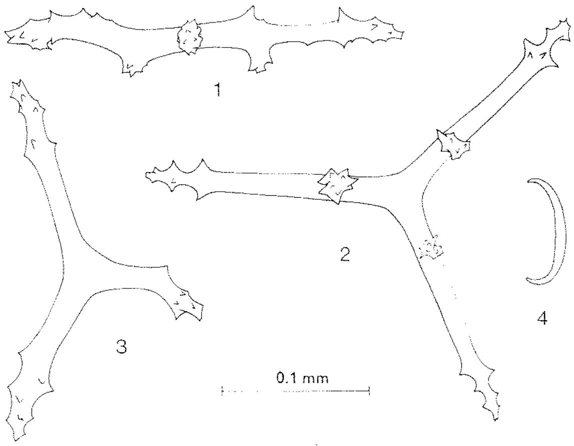


Fig. 78. *Amperima robusta.* Deposits. St. 668. 1–2, dorsum; 3, ventrum; 4, C-shaped spicule.

examined. The absence of tubefeet on the anterior part of the ventral sole was verified. Théel mentioned two processes on the outer margin of the tentacle discs; they were found to be scarcely visible. The tripartite deposit figured by Théel is similar to the dorsal deposits in the *Galathea* specimen. (Deposits were not re-examined).

Relationships: Differs from the other species of the genus by the absence of tubefeet on the anterior part of the ventral sole, and by its small and robust ventral spicules which are destitute of apophyses.

Distribution: Antarctic, 2010–4240 m. Kermadec Trench, 2640 m.

Amperima insignis (Théel, 1882)

Scotoplanes insignis Théel, 1882, pp. 36–38, pls. VII: 1–3, XXXIII: 7.

Diagnosis: Body flattened posteriorly. Tubefeet 11 pairs, 6 pairs of which are free and border the lateral edge of the ventral sole, while the posterior 5 pairs are fused into two conspicuous, fan-shaped clusters. Dorsal papillae 3 pairs, small, not fused into a velum. Deposits tripartite, spinous, and devoid of apophyses.

Record: Antarctic, 3594 m. One specimen.

Remarks: The specimen (in BM) was re-examined. As Théel remarked, the body is so strongly contracted that its natural shape cannot be deduced with any certainty. However, the species is well characterized by the posterior tubefeet being fused into a pair of fan-shaped clusters. The dorsal papillae are small and do not form a velum. Théel reported three dorsal papillae, followed by a pair of minute papillae, but on re-examination two pairs of larger and one pair of smaller papillae were found; hence, the papillae corresponded, both in number and arrangement, to those of a normal velum.

The deposits, according to Théel, very much resemble those of *A. robusta.*

Genus ***Ellipinion*** Hérouard, 1923
Fig. 122

Hérouard 1923, p. 82. – Type species: *Scotoplanes delagei* Hérouard, 1896.

Diagnosis: Dorsal papillae anteriorly placed, usually forming a velum. Deposits consisting of rods and C-es. Calcareous ring consisting of five isolated pieces, each with four pairs of arms. (In *E. kumai* an additional, unpaired arm is present on each piece).

Remarks: The species of *Ellipinion* are difficult to evaluate taxonomically as they are rather uniform in external appearance and their deposits are only feebly differentiated. The two species erected here are based on questionable taxonomic characters. Additional material may prove that they are identical with species previously known.

The species *Scotoplanes albida* Théel, 1882, which, according to definition, should be transferred to *Ellipinion,* is omitted from the present survey as it is based on one, insufficiently preserved specimen. The specimen was not illustrated, and a re-examination did not reveal anything of importance regarding its external appearance.

Key to the species of *Ellipinion*

1. Tubefeet 5 pairs, all large. Tentacle crown straight forwardly directed *galatheae* (p. 165)
1. Tubefeet 7–12 pairs. Tentacle crown ventrally or obliquely forwardly directed . 2
2. Skin with vesicular warts 3
2. Skin smooth 4

3. Tentacle discs possessing two large, rounded lobes .... *molle* (p. 165)
3. Tentacle discs devoid of large lobes .... *papillosum* (p. 165)
4. Tubefeet 7–10 pairs, the anteriormost pairs spaced in position 5
4. Tubefeet 11–12 pairs, all closely placed 6
5. Deposits confined to tips of papillae. Velum not very high and slender .. *kumai* (p. 166)
5. Deposits present all over the body wall. Velum very high and slender, composed of two pairs of equally long and almost completely fused papillae ....*facetum* (p. 166)
6. Tubefeet rather slender, and placed with small intervals. Ventral sole broadest posteriorly .... *delagei* (p. 163)
6. Tubefeet broad, adjoining each other. Ventral sole broadest anteriorly 7
7. Tentacle crown very large, obliquely forwardly directed. Velum placed above the third tubefeet pair .... *bucephalum* (p. 163)
7. Tentacle crown of usual size, ventrally turned. Velum anterior to the first tubefeet pair .... *solidum* (p. 164)

Ellipinion delagei (Hérouard, 1896)

Scotoplanes delagei Hérouard, 1896, pp. 167–168, fig. 3; Hérouard 1902, pp. 39–40, pls. VI: 1–3, VIII: 8–9.

Ellipinion delagei (Hérouard), Hérouard 1923, pp. 90–91.

Diagnosis: Ventral sole increasing in breadth posteriorly. Tubefeet 11–12 pairs, bordering the entire ventral sole, the first pair close to the tentacle crown; all rather closely placed and, with the exception of the somewhat reduced posteriormost two pairs, all of the same size. Velum small, composed of three pairs of almost equally large and partially free papillae.

Records: North Atlantic, 1165–2478 m. Several specimens.

Remarks: The specimens (in MOM) were reexamined, and two (both from Monaco St. 553) were found to be in a fine state of preservation. The characteristic shape of the ventral sole was verified, while the shape of the velum could no longer be made out. The C-shaped deposits, according to Hérouard, possessed an outwardly directed spine rising from the middle enlargement of the C, which thus becomes tripartite. Similar variations from the C-es are found also in other species of the genus, but not as a dominant type.

E. delagei is closest related to *E. bucephalum* and *E. solidum* but differs from both in the C-es being transformed into tripartite spicules, in the shape of the ventral sole, and in the less closely placed tubefeet. Besides, it differs from *E. bucephalum* by the smaller size of the tentacle crown.

Ellipinion bucephalum n. sp.

Figs. 79–80

Diagnosis: Tentacle crown large and obliquely forwardly directed. Tubefeet 11–12 pairs, bordering the entire ventral sole, the first pair close to the tentacle crown; the tubefeet are broad and even the anteriormost ones are closely placed. Velum placed above the third tubefeet pair, composed of two pairs of stout and one pair of small papillae, all fused almost in their whole length.

Material:
St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 1 specimen.

Description: The specimen (Fig. 79) is 2.4 cm long and 0.9 cm broad.

Tentacle crown very large, and obliquely forwardly directed.

Tentacles 10, with short stalks; discs broad, vaulted, with a smooth margin and an almost smooth surface.

Tubefeet 11–12 pairs, bordering the entire ventral sole, posteriormost 2 pairs probably reduced (hind edge of body defective). The tubefeet are

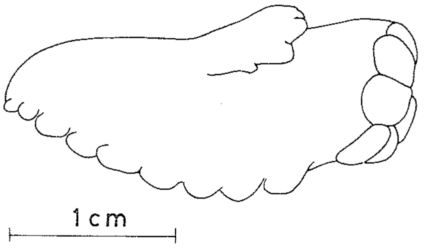


Fig. 79. *Ellipinion bucephalum*. St. 663.

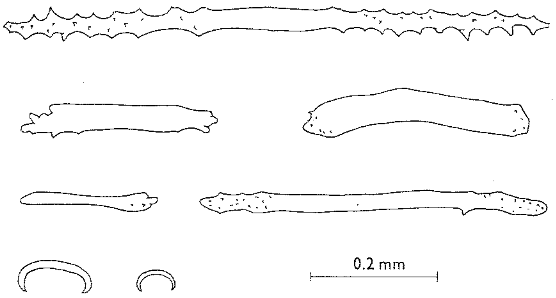


Fig. 80. *Ellipinion bucephalum.* Deposits. St. 663.

broad and even the anteriormost ones adjoin each other at their bases. Sucking-discs well developed.

Velum composed of three pairs of almost completely fused papillae.

Skin whitish and rather firm.

Deposits (Fig. 80) consisting of scattered rods of varying shape and size, and a superficial layer of crowded C-es. Tentacles and tubefeet with short rods. End-plates absent from tubefeet.

Relationships: *E. bucephalum* resembles *E. solidum* in number, size, and arrangement of the tubefeet, but differs by the large size of the tentacle crown and by the more posterior position of the velum.

Ellipinion solidum n. sp.
Figs. 81–82

Diagnosis: Tubefeet about 12 pairs, bordering the entire ventral sole, all of them closely placed. Velum anterior to first tubefeet pair, composed of two pairs of stout and one pair of small papillae, all fused almost in their whole length.

Material:

St. 231, Madagascar–Mombasa (8°52'S, 49°25'E), 5020 m. – 1 specimen.

St. 232, Madagascar–Mombasa (9°03'S, 49°22'E), 4930 m. – 1 specimen.

Description:

1. – The type specimen (Fig. 81), from St. 232, is 5.5 cm long, 2.5 cm high, and 2.3 cm broad.

Tentacles 10, discs not preserved.

Tubefeet 12 pairs, bordering the entire ventral sole. They decrease somewhat in size posteriorly, although less than in other species of the genus (not counting *E. galatheae,* with its five pairs of almost equally large tubefeet). The sucking-discs are conspicuous, although somewhat retracted. No gaps present between the tubefeet, not even between the anteriormost ones.

Velum consisting of two pairs of stout and one pair of small papillae, all of them fused throughout almost their whole length; the velum is rather firm and probably less changeable in shape than in most other velum-bearing species.

Skin whitish and rather firm.

Deposits (Fig. 82) almost entirely absent, consisting of extremely scattered C-es in body wall and tubefeet, the latter in addition with a few rods, but no end-plate. No deposits were found in the gonads or in the intestinal wall.

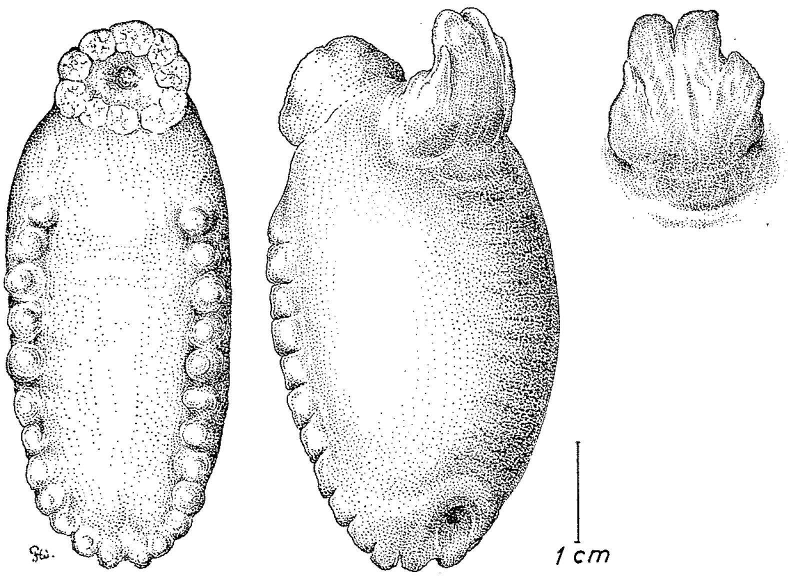


Fig. 81. *Ellipinion solium.* St. 232. Type specimen (lacking tentacle discs). PHW.

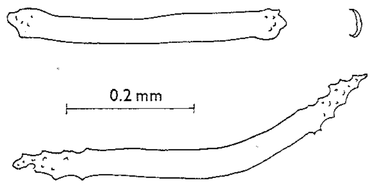


Fig. 82. *Ellipinion solidum.* St. 232. Deposits from a tubefoot.

2. – The specimen from St. 231 is somewhat torn, but nevertheless, some additional information can be gained. It is 6.5 cm long, and the ventral sole is 2.5 cm broad.

Tentacles (only two are preserved) with short stalks and slightly vaulted discs covered with small papillae; margin slightly indented.

Tubefeet lacking at the posterior end of the body. The preserved tubefeet (5 left and 9 right) are well developed and unretracted, cylindrical and with broad sucking-discs. The anteriormost tubefeet are about 4 mm long and 2 mm broad. The tubefeet were probably similar, both in arrangement and number, to those of the type specimen.

Velum defective, but apparently similar in shape to that of the type.

Deposits absent in a preparation from the body wall. Rods present in tentacles and tubefeet; a few C-es present in the tubefeet; end-plate absent.

Calcareous ring absent.

Relationships: Closest related to *E. bucephalum* (q. v.).

Ellipinion galatheae (Hansen, 1956)
Pl. X: 10

Scotoplanes galatheae Hansen, 1956, pp. 41–42, figs. 10–11.

Diagnosis: Body flattened. Tentacle crown large and forwardly directed. Tentacle discs with about 10 conical, retractile marginal knobs. Tubefeet 5 pairs, bordering almost the entire ventral sole, all of them large, although the hindmost pair is somewhat smaller.

Material:
St. 435. Philippine Trench (10°20'N, 126°41'E), 9820–10.000 m. – 1 specimen.

Remarks: The specimen, 17 mm long, was described previously (Hansen 1956) and referred to *Scotoplanes* because of its rod-shaped deposits. However, in accordance with the generic definitions adopted in the present work, the species should be referred to *Ellipinion*.

The species occupies an isolated position within the genus, being characterized by the large and forwardly directed tentacle crown, and by the presence of only five pairs of tubefeet. The tubefeet of the fifth pair are closely placed, leaving no room for reduced posterior tubefeet.

The tentacles (Pl. X: 10) are characteristic in shape, the enlarged discs having about ten conical, retractile knobs on the margin.

Velum, or velar papillae, not preserved.

Ellipinion molle (Théel, 1879)

Elpidia mollis Théel, 1879, p. 14, figs. 29–30.

Scotoplanes mollis (Théel), Théel 1882, pp. 31–32, pls. II: 1–2, XXXIII: 17, XLIV: 2.

Ellipinion mollis (Théel), Hérouard 1923, p. 82.

Diagnosis: Body ovoid. Skin covered with vesicular warts. Tentacle discs with two large, rounded marginal lobes. Tubefeet 7 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the hindmost pairs rudimentary. Velum almost completely bipartite, each side consisting of two fused papillae of which the first is very large. Post-velar papillae absent.

Record: South of Australia, 4732 m. One specimen.

Remarks: Re-examination of the specimen (in BM) confirmed the presence of vesicular warts on the skin (called "papillae" by Théel), the characteristic shape of the velum, and the presence of a pair of rounded lobes on all the tentacle discs. But contrary to the six pairs of almost equally large tubefeet shown in Théel's figure, seven pairs of tubefeet were, in actual fact, present; as usual in the genus they decreased in size posteriorly, the hindmost pair being very small.

The species is closest related to *E. papillosum* (q. v.).

Ellipinion papillosum (Théel, 1879)

Elpidia papillosa Théel, 1879, pp. 16–17, fig. 31–33.

Scotoplanes papillosa (Théel), Théel 1882, pp. 32–33, pls. II: 5–6, XXXVII: 12; D'yakonov, Baranova & Savel'eva 1958, p. 361, fig. 1.

Ellipinion papillosa (Théel), Hérouard 1923, p. 82.

Scotoplanes angelicus Agatep, 1967b, pp. 59–61, pl. VI: 1–21.

Diagnosis: Similar to *E. molle,* differing by the absence of marginal lobes on the tentacle discs, and by the presence of a pair of free, post-velar papillae.

Records: The type specimen was taken by the *Challenger* at 4823 m in the South Atlantic. D'yakonov, Baranova & Savel'eva (1958) reported the species from 700 m in the southern part of the Okhotsk Sea. *Scotoplanes angelicus,* here considered a synonym of *E. papillosum,* was taken in three specimens at 4731 m in the Antarctic part of the South East Pacific Basin.

Remarks: Re-examination of the type specimen (in BM) revealed agreement with *E. molle* in the presence of vesicular warts on the skin, in body shape, and in number and distribution of the tubefeet. The small size of the tubefeet, as seen in Théel's figure, was found to be due to contraction. The velum was somewhat defective and apparently contracted; possibly, it was not different from that of *E. molle.*

Two rather doubtful features remain to distinguish *E.papillosum* from *E. molle,* viz. the presence of a pair of post-velar papillae and the absence of a pair of marginal lobes on the tentacle discs. (In *Scotoplanes globosa* such lobes were clearly visible in specimens preserved in formalin but difficult or even impossible to distinguish in alcohol-preserved specimens).

Scotoplanes angelicus agrees in both the above-mentioned features with *E. papillosum.* The presence in *S. angelicus* of a large number of irregular C-es is hardly taxonomically significant.

Ellipinion kumai (Mitsukuri, 1912)

Periamma kumai Mitsukuri, 1912, pp. 213–214, fig. 39, pl. VI: 56–58.

Diagnosis: Body ovoid. Tubefeet 8–10 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Velum well developed, composed of two pairs of papillae. Deposits confined to ambulacral appendages.

Records: Sagami Sea (Japan), c. 500 m.

Remarks: Mitsukuri referred the species to *Periamma (= Amperima)* because tripartite deposits were present in the gonadal wall. These deposits, however, are different from the tripartite deposits of *Amperima,* and appear to be rods with an occasional side-branch.

Ellipinion facetum (Agatep, 1967)

Scotoplanes facetus Agatep, 1967b, pp. 57–59, pl. V: 1–14.

Diagnosis: Body somewhat elongate, 2.5 times as long as broad. Velum high and slender, composed of two pairs of equally long and almost completely fused papillae. Tubefeet 10 pairs, bordering the entire ventral sole, decreasing in size posteriorly.

Record: The Antarctic part of the South East Pacific Basin, 4789 m. One specimen.

Remarks: Differs from the other species of the genus by the peculiarly shaped velum.

Ellipinion sp.

Three fragmentary specimens resembling *E. molle* and *E. papillosum* were taken at St. 661.

Genus ***Scotoplanes*** Théel, 1882

Fig. 123

Scotoplanes Théel, 1882, p. 29 (partim). – Type species: *Scotoplanes globosa* Théel, 1882.

Diagnosis: Dorsal papillae separated into one pair of large anterior papillae, and one large and one small pair placed close together on the middle or posterior part of the body. Tentacle discs with a few, large papillae on the surface and a knobbed margin divided into a pair of large, aboral, retractile lobes. Deposits consisting of rods and C-es. Calcareous ring consisting of five isolated pieces, each with four pairs of arms.

Key to the species of *Scotoplanes*

1. Skin smooth. Dorsal papillae rather sturdy .... *globosa* (p. 167)
1. Skin covered with vesicular warts. Dorsal papillae in the extended state slender and pointed .... *clarki* (p. 169)

Scotoplanes globosa (Théel, 1879)
Fig. 83, 95: 4, pl. IX: 9

Elpidia globosa Théel, 1879, pp. 14–15, figs. 17–19.
Scotoplanes globosa (Théel), Théel 1882, pp. 29–31, pls. IV, V: 3, XXXIV: 8–9, XXXVI: 5–6, XLIV: 12; Vaney 1908, pp. 409–410, pl. III: 25–28; Hansen 1956, pp. 40–41; D'yakonov, Baranova & Savel'eva 1958, p. 360; Agatep 1967b, pp. 55–57, pl. IV: 1–13.
Elpidia murrayi Théel, 1879, p. 16, figs. 23–25.
Scotoplanes murrayi (Théel), Théel 1882, p. 34, pls. III: 3–4, XXXIV: 2, XLIV: 4; Savel'eva 1966, p. 295, pl. LXIV: 7.
Scotoplanes theeli Ohshima, 1915, pp. 242–243; Ohshima 1916–1919, with three figures.

Diagnosis: Skin smooth. Dorsal papillae rather sturdy.

Material:
St. 32, Monrovia–Takoradi (4°05'N, 2°13'W), 2100 m. – 37 specimens.
St. 650, Kermadec Trench (32°20'S, 176°54'W), 6620–6730 m. – 31 specimens.
St. 653, Kermadec Trench (32°09'S, 176°35'W), 6180 m. – 1 specimen.
St. 654, Kermadec Trench (32°10'S, 175°54'W), 5850–5900 m. – 16 specimens.
St. 658, Kermadec Trench (35°51'S, 178°31'W), 6660–6770 m. – 17 specimens.
St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 5 specimens.
St. 665, Kermadec Trench (36°38'S, 178°21'E), 2470 m. – 1 specimen.
St. 668, Kermadec Trench (36°23'S, 177°41'E), 2640 m. – 66 specimens.

Description: The hadal material of *Scotoplanes globosa* was described previously (Hansen 1956). The following description deals especially with the variation in the taxonomic characters, as revealed by the examination of the abyssal specimens.

Length 4–9 cm at St. 32, and 2–9 cm in the Kermadec Trench.

Tentacles 10 (Pl. IX: 9). Discs with few and large papillae on the surface and conspicuous knobs on the margin. In many specimens (especially those preserved in formalin) the discs are seen to possess a pair of lobes on the margin. The discs are similar in shape in the West African and the Kermadec specimens.

Tubefeet 5–7 pairs. In the Kermadec Trench a correlation is suggested between number of tubefeet and depth (Table 17). The number of tubefeet is independent of the size of the specimens.

Table 17. *Scotoplanes globosa*. Number of tubefeet pairs in 110 specimens from the *Galathea*.

Number of tubefeet pairs		5	6	7
St. 32	2100 m	–	15	6
– 668	2640 m	1	15	25
– 663	4410 m	–	1	2
– 654	5850–5900 m	5	–	–
– 650	6620–6730 m	12	14	–
– 658	6660–6770 m	2	12	–

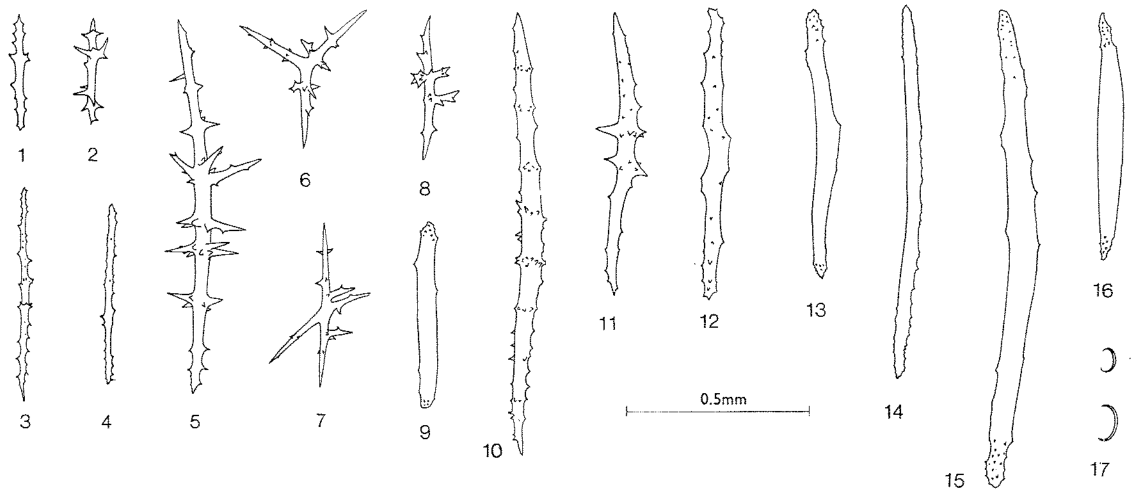


Fig. 83. *Scotoplanes globosa*. Deposits. 1–4, St. 32; 5–8, St. 650; 9–12, St. 663; 13–15, St. 668; 16, St. 665; 17, C-shaped spicules.

Papillae. The second pair of papillae may be placed anteriorly to the middle of the body, or as little as one-fourth body length from the posterior end. This variation is present even among specimens from the same station. No correlation was found between the arrangement of the papillae and the size of the specimens. In all specimens a rudimentary third pair of papillae is present immediately behind the second pair.

Deposits (Fig. 83) examined in all the specimens.

The West African specimens (St. 32) have small and slender rods; the four rods shown in Fig. 83: 1–4 represent their variation both in size and shape.

The Kermadec specimens have rods of two, rather distinct types. In the specimens from the deepest stations (Sts. 654, 653, 650, and 658; depth 5850–6770 m) the rods are strongly spinous (Fig. 83: 5–8), whereas the specimens from the two shallow stations (Sts. 665 and 668; depth 2470–2640 m) have smooth or feebly spinous rods (13–16). The deposits (9–12) of the specimens from St. 663 (depth 4410 m) are most similar to those from the shallow stations, although they are slightly more spinous and thus to some degree form a transition to the hadal type.

No correlation is present between the shape and size of the rods and the size of the specimens.

The C-shaped deposits vary somewhat in size and sturdiness, but there is no correlation between the locality of the specimens and the type of the C-es.

Calcareous ring (Fig. 95: 4) examined both in West African and Kermadec specimens. As also described by Théel, the segments are reduced and possess four pairs of arms, thus belonging to the usual type in *Amperima, Ellipinion,* and *Scotoplanes.*

Remarks: Agatep (1967b) reported the species from 23 Antarctic stations of the *Eltanin* (depth 598–5289 m). The specimens were 1.7–10 cm long, had 6–8 pairs of tubefeet, and deposits consisting of C-es and spinous rods. In the specimens from two stations many of the rods had two pairs of obliquely placed arms, thus having a peculiar similarity to those of *Elpidia* (p. 184).

Deep-sea photographs provided by the PROA Expedition (Lemche *et al.* in press) reveal the occurrence of *Scotoplanes* (probably *S. globosa)* in the New Britain Trench (depth 6780–7710 m) and the New Hebrides Trench (depth 6740–6760 m).

Herds of *Scotoplanes (S. globosa* or *S. clarki)* were observed and photographed in the San Diego Trough (depth 1060–1243 m) from the U.S. Navy bathyscaphe *Trieste I* (Barham *et al.* 1967). The observations revealed an affinity of *Scotoplanes* to accumulated sediments (pp. 196). Based on the same photographs Hansen (1972) suggested a peculiar mechanism for walking, apparently common to three families of the Elasipoda (pp. 205–206).

Synonymy: *S. theeli* Ohshima was previously (Hansen 1956) proposed as a synonym of *S. globosa.*

S. murrayi Théel, known from a single specimen taken at 2303 m in the Antarctic Ocean, is likewise here considered a synonym of *S. globosa.* Théel did not specify the differences between the two species, but it appears that the presence of only five pairs of tubefeet, compared to seven pairs in *S. globosa,* and the brittle and glassy skin were regarded as the distinguishing features of *S. murrayi.* However, the number of tubefeet falls within the variation of the *Galathea* specimens of *S. globosa.* The different consistency of the skin was seen on re-examination of the type specimen to be caused by the densely crowded deposits.

On the other hand, the four specimens from the eastern Pacific which Clark (1920) referred to *S. murrayi* are not identical with *S. globosa.* These specimens are here referred to *S. clarki* n. sp.

Baranova (1957) and Savel'eva (1966) mentioned *S. murrayi* from abyssal depths in the Bering Sea. The specimen illustrated by Savel'eva has a smooth skin, indicating that the species is *S. globosa.*

Variation: The parallel variation found in the shape of the deposits and the number of tubefeet suggests a taxonomic difference between the specimens from the abyssal (2470–4410 m) and hadal (5850–6770 m) stations in the Kermadec Trench. Contact between populations is apparently more pronounced in a horizontal than in a vertical direction. It is not possible to decide from the material whether there is an abrupt or a gradual transition in taxonomic characters between the hadal and abyssal populations. However, the fact that specimens from the deepest abyssal station have deposits somewhat reminiscent of those from the hadal stations suggests that the transition is gradual.

The deposits of the hadal specimens are rather similar to those of the abyssal specimens described by Théel from the Antarctic Ocean and off Valparaiso.

Distribution: *S. globosa* has an almost cosmopolitan distribution. However, it is remarkable that it has never been recorded from the North Atlantic. The closely related species, *S. clarki,* seems to replace *S. globosa* in a region along the Pacific coast of Central America and northern South America (p. 246).

Although a dominant species in some of the Pacific trenches, it has on several occasions been recorded from remarkably shallow water. Ohshima (1915) recorded it (as *S. theeli)* from 545 and 970 m northeast of Hokkaido (temp. 2.2° and 1.6°C, respectively). The penetration to shallow depths may here as well as in the Antartic Ocean (598 m) be conditioned by low temperature. The specimens recorded from a depth of 1060–1243 m in the San Diego Trough also lived at a rather low temperature (c. 3°C). The fact, however, that the species is here associated with an abundant supply of sediments indicates that the ascent of the species to shallow water does not depend on the temperature alone.

Scotoplanes clarki n. sp.

Figs. 84–85

Scotoplanes murrayi Théel, Clark 1920, pp. 133–134, pl. III: 6.
Scotoplanes sp., Hansen 1967, p. 490, fig. 6.

Diagnosis: Skin covered with vesicular warts. Dorsal papillae in the extended state slender and pointed.

Material:
St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – About 100 specimens (including type specimen).

Description: The specimens are 2.5–7.0 cm long. Type specimen (Fig. 84) 6 cm long.

Skin greyish and covered with vesicular warts, which are especially well developed on the dorsal surface. The warts resemble those in *Ellipinion molle.*

Tentacles 10; discs with few and large papillae on the surface and conspicuous, retractile knobs on the margin. A pair of large, marginal lobes is seen on some of the discs. The shape of the discs is probably identical in the two species of *Scotoplanes.*

Tubefeet 5–6 pairs. The sixth pair, when present, is always reduced, whereas the fifth pair may vary in size from being the same length as the anterior tubefeet to half as long. The ends of the tubefeet are rounded and have no sucking-discs. Usually, the tubefeet are slightly smaller than in *S. globosa.*

Papillae similar in number, size distribution, and arrangement to those of *S. globosa,* including the presence of a rudimentary third pair. The large papillae are apparently very contractile, as indicated by a number of transverse lines on many of them. In the fully extended state the papillae are slender and pointed. In most specimens they measure about one-third of the body length; a few of the smaller specimens possess papillae which are the same length as the body.

Deposits (Fig. 85) examined in 15 specimens. They all have rather smooth and spindle-shaped rods, resembling those in specimens of *S. globosa* from Sts. 665 and 668. In the preparations from

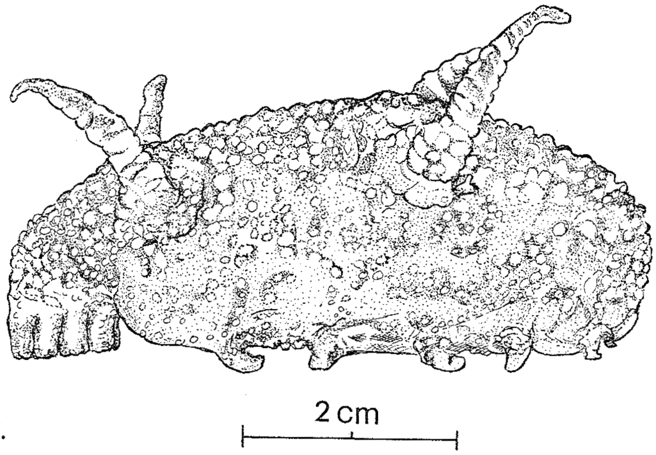


Fig. 84. *Scotoplanes clarki.* St. 716. Type specimen. LJ.

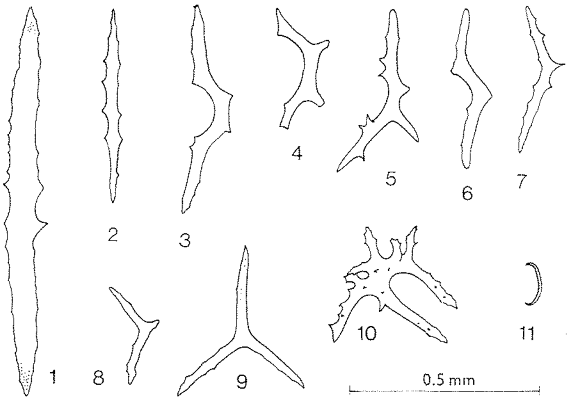


Fig. 85. *Scotoplanes clarki.* Deposits. St. 716. 1–8, rods from dorsum and ventrum; 9, tripartite spicule; 10, irregular spicule from papilla; 11, C-shaped spicule.

two of the specimens a number of irregularly shaped rods are present, some of which seem to derive from primary crosses (Fig. 85: 3–4) – a similarity to two of the rods illustrated by Théel (1882, pl. XXXIV: 2) for *S. globosa.* In some preparations a few tripartite deposits are present.

Numerous rods present in tentacles, tubefeet, and papillae. End plates absent from tubefeet. C-shaped spicules numerous in the skin, mesenteries, and gonads.

Calcareous ring (examined in one specimen), rudimentary, each piece with four pairs of arms.

Remarks: To *S. clarki* are referred four specimens taken by the *Albatross* at two stations off Peru (4809 and 5107 m), and by Clark referred to *S. murrayi* Théel. While the type specimen of *S. murrayi* appeared on re-examination to be identical with *S. globosa,* Clark's specimens showed the warty skin and the strongly contractile papillae distinguishing the present species. The re-examination comprised a specimen from either station (St. 4651, in MCZ; St. 4672, in USNM).

Distribution: Gulf of Panama and off the coast of Peru, 3570– 5107 m.

Genus **Kolga** Danielssen & Koren, 1879
Fig. 123

Danielssen & Koren 1879, p. 99; Danielssen & Koren 1882, p. 17. – Type species: *Kolga hyalina* Danielssen & Koren, 1879, by monotypy.

Diagnosis: Dorsal papillae anteriorly placed, forming a velum. Tentacle discs with 5–7 marginal lobes, each divided into about 3 lobules. Deposits spinous rods and irregularly shaped C-es. Calcareous ring consisting of five delicate pieces, which are isolated or adjoin each other loosely; each piece with five pairs of arms, a number of which may be secondarily subdivided.

Kolga hyalina Danielssen & Koren, 1879
Figs. 86, 95: 2–3, pls. IX: 8, XII: 11

Kolga hyalina Danielssen & Koren, 1879, pp. 83–106, pls. I–II; Danielssen & Koren 1882, pp. 3–20, pls. I–III; Mikhajlovskij 1902, p. 463; Mortensen 1932, pp. 43–44, fig. 5; Heding 1942, p. 19, fig. 18; Gorbunov 1946, p. 47; Koltun 1964, pp. 13–78; Baranova 1964, p. 368; Agatep 1967c, p. 140.

Elpidia nana Théel, 1879, pp. 15–16, figs. 20–22.

Kolga nana (Théel), Théel 1882, pp. 39–42, pls. II: 3–4, XXXIII: 1–2, XXXIV: 5, XXXVI: 25, XLII: 5, 8.

Diagnosis: Body ovoid. Tubefeet 7–9 pairs, bordering the entire ventral sole, decreasing in size and placed with decreasing intervals posteriorly. Velum very contractile, consisting of one large median pair and one or two smaller lateral pairs. Deposits spinous rods, often bent at an angle, and small, irregularly C-shaped spicules with an enlargement in the middle; irregular perforated plates occasionally present in oral disc.

Re-examination: The numerous specimens from the *Godthaab* and the *Ingolf* were found to agree with the thorough description given by Danielssen & Koren, although a greater variation was observed in the shape of the tentacles and the calcareous ring.

The *tentacles* (Pl. IX: 8) show a marked variation in shape, although they typically possess five marginal lobes, each divided into three lobules. This type of tentacle is otherwise found only in the genus *Irpa.*

The *deposits* (Fig. 86) consist of numerous minute, irregularly C-shaped spicules with an enlargement in the middle, and large, robust and spinous rods which are often bent at an angle. The rods are numerous in the ambulacral appendages, but very scattered in the rest of the skin.

The small reticulated plates, which according to Danielssen & Koren and Théel occur in the oral disc, were not found in the examined specimens.

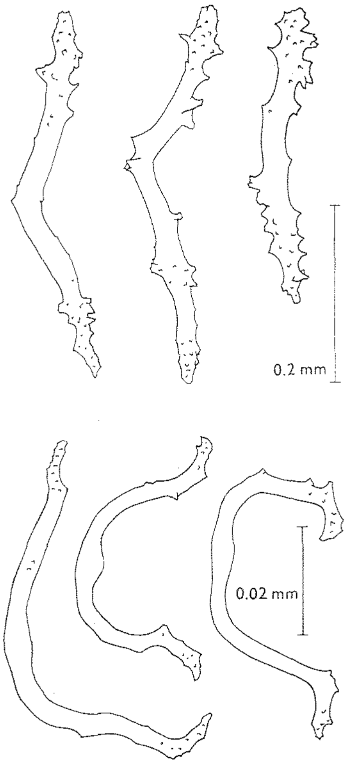


Fig. 86. *Kolga hyalina.* Deposits from ventrum. *Ingolf* St. 113.

The *calcareous ring* (Fig. 95: 2–3) was examined in four specimens from *Ingolf* St. 113 and in one from *Godthaab* St. 54 (pp. 187–188).

Remarks: Agatep (1967c) reported 57 specimens of *K. hyalina* from the Canadian Basin of the Arctic Ocean (depth 2850 m). The tentacles were said to possess four knobs, each divided into two smaller processes. The tubefeet number was stated to be 14 pairs (probably a lapse for 7 pairs).

Agatep in the same paper mentioned that *K. hyalina* was found at two Antarctic stations of the *Eltanin* (depths 4473 and 4850 m).

Synonymy: *Kolga nana* (Théel) was taken by the *Challenger* in several specimens off Nova Scotia at 2282 m and in one specimen in the Antarctic Ocean at 2305 m. Although Théel suspected that the specimens belonged to *K. hyalina,* he preferred to describe them as a new species for lack of specimens for comparison.

Re-examination of the *Challenger* specimens (in BM) showed that the Nova Scotia specimens are within the variation shown by *K. hyalina.* The Antarctic specimen was too damaged to allow a determination.

Distribution: Arctic Basin, North-West Atlantic, and Antarctic. Depth 1510–4850 m.

Genus ***Irpa*** Danielssen & Koren, 1878

Fig. 123

Danielssen & Koren 1878, p. 264; Danielssen & Koren 1882, p. 28. – Type species: *Irpa abyssicola* Danielssen & Koren, 1878, by monotypy.

Diagnosis: Dorsal papillae 3–5 pairs, anteriorly placed, not forming a velum. Tentacle discs with 5–7 marginal lobes, each divided into about 3 lobules. Deposits spinous rods and irregularly shaped C-es. Calcareous ring strong and continuous, each piece with four pairs of arms.

Remarks: In addition to the type species, *I. abyssicola,* the species *Kolga ludwigi* is here regarded as belonging to *Irpa* because of the structure of the calcareous ring (p. 130).

Key to the species of *Irpa*

1. Body elongate. Tubefeet 12 pairs, bordering the entire ventral sole. Dorsal papillae 5 pairs . . . . *abyssicola* (p. 171)
1. Body ovoid. Tubefeet 6 pairs, bordering the posterior half of the ventral sole. Dorsal papillae 3 pairs . . . . *ludwigi* (p. 172)

Irpa abyssicola Danielssen & Koren, 1878

Danielssen & Koren 1878, pp. 257–266, pl. IV; Danielssen & Koren 1882, pp. 21–28, pl. IV.

Diagnosis: Body elongate. Tubefeet 12 pairs, bordering the entire ventral sole. Dorsal papillae 5 pairs. Deposits, spinous rods in the tubefeet, and irregularly C-shaped spicules, usually with an enlargement in the middle, in the body wall.

Record: Norwegian Sea, 1977 m. One specimen.

Relationships: See *I. ludwigi.*

Irpa ludwigi (von Marenzeller, 1893)

Kolga ludwigi von Marenzeller, 1893b, pp. 20–23, pls. III: 7, IV: 8.
Periamma ludwigi (von Marenzeller), Hérouard 1923, p. 83.

Diagnosis: Body ovoid. Tubefeet 6 pairs, bordering the posterior half of the ventral sole. Dorsal papillae 3 pairs. Deposits, simple or slightly branched rods in ambulacral appendages, and scattered wheels in the body wall.

Records: Mediterranean south of Sicily, 755–1292 m.

Relationships: *I. ludwigi* and *I. abyssicola* differ in shape of body, number and distribution of tubefeet, and absence in *I. ludwigi* of irregular C-shaped spicules. The absence of the latter is probably not important, in view of the extremely reduced state of the deposits in this species. The presence of wheel-shaped deposits in the body wall of *I. ludwigi* is shared with a number of species of Elpidiidae (pp. 185–186).

Genus *Elpidia* Théel, 1876

Figs. 124–125

Elpidia Théel, 1876, pp. 1–7; Théel 1877, pp. 1–30, pls. I–V. – Type species: *Elpidia glacialis* Théel, 1876, by monotypy.
Tutela R. Perrier, 1896, p. 901.

Diagnosis: Tentacle discs with long and slender, retractile processes. Tubefeet 4(–5) pairs, large, well spaced, and equal in size. Papillae separate, present throughout the length of the dorsal radii, or distributed into an anterior and posterior group. Deposits rod-shaped with two pairs of obliquely placed, horizontal arms and two vertical, pointed apophyses. Calcareous ring strong and continuous, each piece with four pairs of arms.

Taxonomy: The genus *Elpidia* occupies an isolated position within the Elpidiidae (p. 130). The relationship is closest with the genus *Irpa*, as indicated by the identical structure of the calcareous ring (p. 189).

Hansen (1956), in a previous report on the *Galathea* specimens, regarded the genus as monotypic with the species *E. glacialis*, divided into five geographic subspecies.

Belyaev (1971) revised the genus on the basis of the rich and varied collections of Russian expeditions. He divided the genus into 16 named species and an additional five, provisionally termed "species 1–5". The five subspecies erected by Hansen (1956) were all raised to the rank of species.

In Belyaev's revision, the species *E. hanseni* is divided into two geographic subspecies, but otherwise the subspecies concept is not applied.

In the present survey, forms which overlap in taxonomic characters are regarded as geographic subspecies and not as distinct species.

The segregation of *Elpidia glacialis* and *E. hanseni* into endemic trench subspecies, and the existence in the Kurile-Kamchatka Trench of four closely related species of the genus, provide information on the evolutionary processes in the hadal fauna (p. 242).

As pointed out by Belyaev (1971), the species fall into two groups, which differ in the robustness of the deposits.

(1) *E. theeli, E. minutissima, E. chilensis,* and *E. adenensis* have slender deposits (diameter of axis less than 0.04 mm, and usually less than 0.03 mm). All the species are abyssal.

(2) *E. glacialis, E. longicirrata, E. birsteini, E. hanseni,* and *E. atakama* have robust deposits (diameter of axis 0.04–0.25 mm). Deposits of extreme robustness are characteristic of the two deepest living species, *E. birsteini* and *E. hanseni* (p. 241). All the hadal forms belong to this group, which is represented at smaller depths in polar seas only.

The mutual relationship of the two species groups, as well as the geographic and bathymetric place of origin of the genus, can only be conjectured. Belyaev (1971) regarded the species group with slender deposits as the most primitive and suggested that the genus originated at abyssal depths in the southern parts of the Pacific and Indian Oceans.

Most species descriptions given below are very short. Detailed descriptions are found in Belyaev's recent thorough and well-illustrated revision.

Ecology: The genus *Elpidia*, and *E. glacialis* in particular, differs strikingly from all other holothurians in geographic as well as bathymetric distribution. It penetrates to the bottom of the deepest trenches, while in the Arctic it occurs at shallower depths than any other member of the Elasipoda. The background for the peculiar distribution of *Elpidia* is to be sought for among ecological features which are common to the different localities of the genus.

A preference for, or a tolerance to, extremely low temperatures may partly explain its occurrence in the Arctic Basin. However, it does not explain the occurrence of the genus at hadal depths in the trenches, where the temperature is not lower than in the abyssal zone.

The nutritive conditions seem to be much more important than the temperature in determining the distribution of *Elpidia*. Belyaev (1971) emphasized that, with the exception of the Arctic, the species of *Elpidia* are restricted to highly productive regions, in particular those close to the coast. Belyaev explained the special preference for the hadal depths of the trenches by the abundant sedimentation due to which the nutritive conditions are better than in the surrounding abyssal regions. The highest density of population was found in the Kurile-Kamchatka Trench which is situated in one of the most productive regions of the ocean. The Mariana and Tonga Trenches, which are more oceanic and have a poorer supply of nutrient matter, do not seem to be inhabited by *Elpidia*.

The species of *Elpidia* most often exhibit a high density of population. This is especially pronounced in the trenches, but also the Arctic and Antarctic localities are usually rich in number of individuals. A rather abundant occurrence of *Elpidia* off the coast of North-West Africa is indicated by the fact that it was taken by all three research vessels *(Travailleur, Talisman, Valdivia)* which investigated the region.

The different *Elpidia* localities may have in common that the food supply, although abundant, is irregular or limited to a short period of the year.

The bottom deposits of the trenches, to a considerable degree, consist of material brought down by turbidity currents and mud slides. These processes, which may lead to sudden large supplies of organic matter, seem to have a great influence on the composition of the hadal animal communities (p. 240).

The region off the coast of North-West Africa is remarkable in having the richest upwelling in the North Atlantic. LaFond (1966) suggested that large amounts of organic matter may accumulate on the continental slope in such regions, swept off the shelf through turbulence and turbidity currents. The accumulation and mass burial of organic matter, according to LaFond, creates conditions resembling those prevailing in trenches and isolated basins.

The Antarctic Ocean has a high organic production due to a persistent upwelling at the highest latitudes. The high concentrations of nitrate and phosphate combined with the short duration of the illuminated period result in a "phytoplankton outburst of incredible richness" for a period of three or four months (Raymont 1963). This may lead to periodic accumulations of organic matter on the bottom, and thus to ecological conditions resembling those found in the trenches and on the lower continental slope off North-West Africa.

The distribution of *Elpidia glacialis* in the Arctic region may similarly depend on a periodicity in the supply of food to the bottom, correlated with the short duration of the illuminated period.

The ascent of *Elpidia glacialis* to a depth of only 70 m in the western Kara Sea may be due to ecological conditions which are favourable not only to this species, as many other deep-sea species ascend to shallow depths in this sea. The western Kara Sea is remarkable for the great dominance of echinoderms, which account for four-fifths of the biomass. Zenkevich (1963) suggested that the ascent of deep-sea species is made possible partly by the temperature which, below a depth of 50 m, is negative throughout the year, and partly by the darkness due to the low transparency of the water and the ice cover which lasts almost all the year round.

However, the long-lasting ice cover also limits the phytoplankton production and the supply of food to the bottom to a short period of the year – a similarity to other localities of *Elpidia*.

Despite the fact that the species of *Elpidia* seem to be adapted to the exploitation of large supplies of sediment or organic matter, they are apparently not indiscriminate mud swallowers. A selectivity in food uptake is suggested by the long, digitiform processes on the tentacle discs and by the relatively small volume of the intestine (p. 196).

Key to the species of *Elpidia*

1. Deposits slender (diam. of axis less than 0.04 mm) 2
1. Deposits robust (diam. of axis at least 0.04 mm) 5
2. Deposits up to 0.80 mm long. Apophyses 20–50 % the length of the deposits . . . 3
2. Deposits up to 1.25 mm long. Apophyses 7–15 % the length of the deposits . . . 4
3. Dorsal papillae 3 pairs . . . . *minutissima* (p. 175)
3. Dorsal papillae 5–7 pairs . . . . *theeli* (p. 174)
4. Deposits slightly serrate. Dorsal papillae 2 pairs . . . . *chilensis* (p. 175)
4. Deposits smooth. Dorsal papillae 4 pairs . . . . *adenensis* (p. 175)
5. Deposits ventrally extremely robust, including ellipsoid bodies without arms . . . . *hanseni* (p. 181)
5. Deposits less robust, never ellipsoid in shape 6
6. Dorsal papillae 3 pairs, at least the first pair long and filiform 7
6. Dorsal papillae 3–8 pairs, rudimentary or well developed, but never filiform . . 8
7. Dorsal papillae, all long and filiform . . . . *longicirrata* (p. 181)
7. Dorsal papillae of first pair long and filiform, the others rudimentary *birsteini* (p. 181)
8. Apophyses 20–50 % the length of the deposits . . . . *atakama* (p. 181)
8. Apophyses 0–10 % the length of the deposits . . . . *glacialis* (p. 175)

Elpidia theeli Hansen, 1956

Figs. 87, 88, 93: 3

Elpidia glacialis theeli Hansen, 1956, pp. 34–38, fig. 6; Hansen 1967, p. 491, figs. 7, 8: 3.
Elpidia theeli Hansen, Belyaev 1971, pp. 350–351, fig. 14B.
Elpidia antarctica Belyaev, 1971, pp. 352–353, fig. 16.

Diagnosis: Body length up to 33 mm. Dorsal papillae 5–7 pairs, up to 12 mm long (rudimentary in small specimens). Deposits up to 0.60 mm long; diam. of axis c. 0.02 mm. Apophyses 20–50 % the length of the deposits.

Records: Tasman Sea, 4510 m. 14 specimens. – Antarctic, 650–700 m. Two specimens.

Remarks: The 14 specimens from *Galathea* St. 602 in the Tasman Sea were originally (Hansen 1956) described as a subspecies of *E. glacialis.* However, as the deposits are (with no overlapping) much smaller than those of the other subspecies of *E. glacialis,* I agree with Belyaev (1971) that it should be raised to the rank of a species. In fact, the deposits are the smallest in the genus.

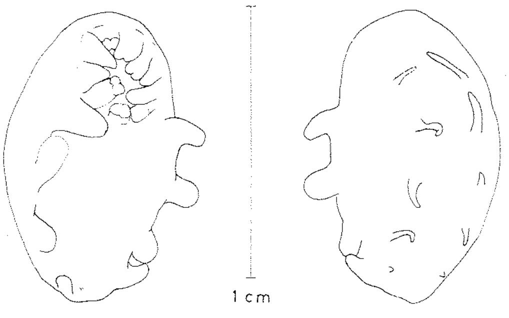


Fig. 87. *Elpidia theeli.* St. 602.

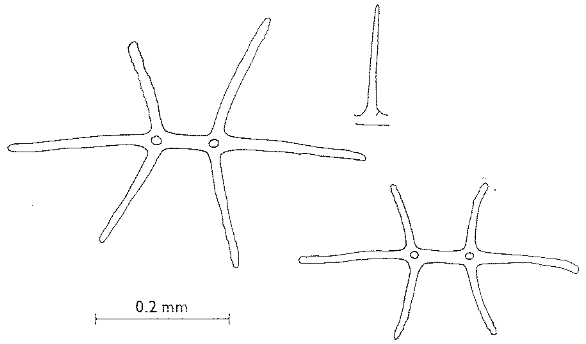


Fig. 88. *Elpidia theeli.* Deposits. St. 602.

The *Galathea* specimens are 7–12 mm long. The dorsal papillae in the largest specimen (Fig. 87) are 0.3–1.6 mm long. In the smaller specimens, all the papillae are rudimentary. In the preliminary report (Hansen 1956) it was incorrectly stated that the subspecies has rudimentary papillae.

The fact that the papillae increase in length (also proportionately) with the body size points to *E. antarctica* as a synonym of *E. theeli. E. antarctica* is known from two specimens, 22 and 33 mm long. The small specimen had 4 left and 6 right papillae, 1.3–3.7 mm long. The large specimen had 5 pairs of 9–12 mm long papillae. The deposits agreed in size and slenderness, as well as in height of apophyses, with those of *E. theeli*.

Elpidia minutissima Belyaev, 1971

Belyaev 1971, pp. 342–344, figs. 8–9.

Diagnosis: Body length up to 13 mm. Dorsal papillae 3 pairs, 0.5–1.0 mm long. Deposits up to 0.80 mm long; diam. of axis c. 0.02 mm. Apophyses 25–35 $^0/_0$ the length of the deposits.

Records: Aleutian Trench, 5740 m. 359 specimens. – Bering Sea, 4382 m. One specimen.

Elpidia chilensis Belyaev, 1971

Belyaev 1971, pp. 344–345, fig. 10.

Diagnosis: Dorsal papillae 2 pairs, on the anterior half of the body, 8–9 mm long (in specimens 18–22 mm long). Deposits up to 1.25 mm long, slightly serrate; diam. of axis 0.02–0.03 mm. Apophyses 10–14 $^0/_0$ the length of the deposits.

Records: Peru-Chile Trench, 2710–4600 m. Three specimens.

Elpidia adenensis Belyaev, 1971

Belyaev 1971, pp. 351–352, fig. 15.

Diagnosis: Dorsal papillae 4 pairs, decreasing in length posteriorly from 2.0 to 0.4 mm (in a specimen 11 mm long). Deposits up to 1.25 mm long, smooth (but otherwise resembling those of *E. chilensis*); diam. of axis c. 0.02 mm. Apophyses 7–15 $^0/_0$ the length of the deposits.

Record: Gulf of Aden, 3070 m. One specimen.

***Elpidia* sp. 2** Belyaev, 1971

Belyaev 1971, p. 357.

The name refers to the specimens reported from off Morocco (2210–2480 m) by Perrier (1896, 1902) and Heding (1940). Perrier, in his first paper, described the specimens as *Tutela echinata* n. g., n. sp., and stated that they had three pairs of papillae, some of which were almost invisible. This information was overlooked by Hansen (1956, 1967), who referred the specimens to the subspecies *E. g. glacialis,* because of Heding's information that the arrangement of the papillae of the *Valdivia* specimen agreed with that of Arctic specimens. (The specimen is now so damaged that the arrangement of the papillae cannot be made out).

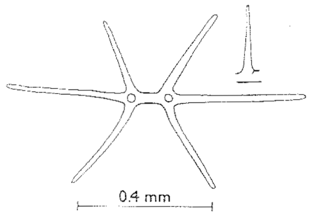


Fig. 89. *Elpidia* sp. 2 Belyaev, 1971. *Valdivia* St. 33.

The deposits of the *Valdivia* specimen (Fig. 89) are slender (diam. of axis c. 0.02 mm), up to 1.0 mm long dorsally, and 0.6 mm long ventrally. Apophyses 10–25 $^0/_0$ the length of the deposits.

Elpidia glacialis Théel, 1876

Figs. 90, 91, 92, 95: 5, pls. X: 11–13, XII: 10

Théel 1876, pp. 1–7; Théel 1877, pp. 1–30, pls. I–V.

Diagnosis: Body length up to 62 mm. Dorsal papillae 3–8 pairs, rudimentary or well developed, but never long and filiform. Deposits varying from 1.20–1.75 mm in maximum length; diam. of axis 0.04–0.20 mm. Apophyses 0–10 $^0/_0$ the length of the deposits.

Remarks: *E. glacialis* is found at abyssal and bathyal depths in Arctic and Antarctic seas, and at hadal depths in a number of trenches. The species is divided into six geographic subspecies, all of which were regarded as distinct species by Belyaev (1971).

Lemche *et al.* (in press) provided photographic evidence of the occurrence of *Elpidia* in the Palau Trench (8026–8046 m). The specimens had rudimentary papillae (actually invisible in the photographs) and may represent yet another Pacific trench subspecies of *E. glacialis.*

Key to the subspecies of Elpidia glacialis

1. Dorsal papillae well developed, arranged in an anterior and posterior group .... *glacialis* (p. 176)
1. Dorsal papillae well developed or rudimentary, following each other in a regular sequence 2
2. Dorsal papillae 3(–4) pairs, well developed 3
2. Dorsal papillae 4–8 pairs, rudimentary 4
3. Dorsal papillae up to 12 mm long (specimens up to 42 mm long). Deposits up to 1.55 mm long; diam. of axis c. 0.04–0.05 mm .... *sundensis* (p. 178)
3. Dorsal papillae up to 3 mm long (specimens up to 33 mm long). Deposits up to 1.75 mm long; diam. of axis c. 0.08–0.09 mm .... *uschakovi* (p. 180)
4. Dorsal papillae 6–8 pairs .... *solomonensis* (p. 180)
4. Dorsal papillae 4–6 pairs 5
5. Deposits up to 1.75 mm long; diam. of axis 0.09–0.20 mm .... *kurilensis* (p. 180)
5. Deposits up to 1.30 mm long; diam. of axis c. 0.05–0.06 mm .... *kermadecensis* (p. 180)

Elpidia glacialis glacialis Théel, 1876
Figs. 90: 1–3, 91

Elpidia glacialis Théel, 1876, pp. 1–7; Théel 1877, pp. 1–30, pls. I–V; Mortensen 1932, pp. 41–43, pl. I: 4–5; Heding 1942, pp. 16–19, figs. 16–17; Belyaev 1971, 332–333, fig. 1 (complete list of references).

Elpidia glacialis glacialis Théel, Hansen 1956, pp. 34–38; Hansen 1967, p. 491, figs. 7, 8: 1.

Elpidia sp. 1 Belyaev, 1971, pp. 356–357.

Diagnosis: Body length up to 62 mm. Dorsal papillae well developed, arranged in an anterior and posterior group, usually with 2–3 and 1 pair, respectively. Deposits up to 1.20 mm long; diam. of axis c. 0.04–0.05 mm.

Distribution: *E. g. glacialis* is found at bathyal and abyssal depths in the Arctic Ocean and the Baffin Bay. In two localities it has been found at depths less than 300 m: The Kara Sea (east coast of Novaja Zemlja): 70–230 m (Théel 1877,

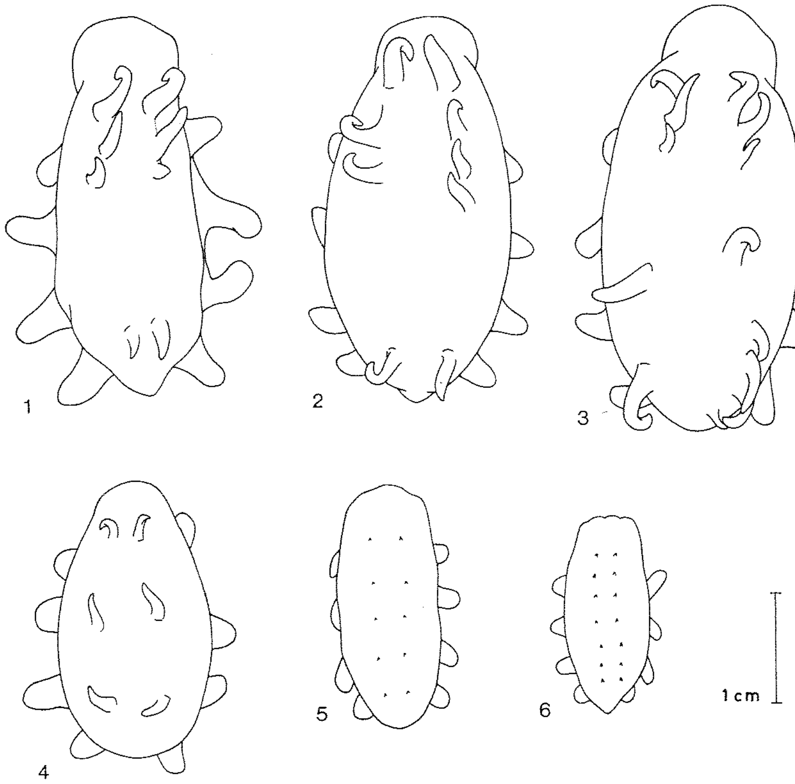


Fig. 90. *Elpidia glacialis*. 1–3, *E. g. glacialis* (*Godthaab* St. 54); 4, *E. g. sundensis* (*Galathea* St. 466); 5, *E. g. kermadecensis* (*Galathea* St. 649); 6, *E. g. solomonensis* (*Galathea* St. 521).

Zenkevich 1963), and Jørgen Brønlund Fjord (Peary Land): 190–200 m (Andersen 1971).

The absence of shallow records from other regions is not only due to lack of investigation. In three regions investigated also at sublittoral depths the upper records of the species are remarkably deep: Baffin Bay (Mortensen 1932), 610 m. Off the Novosiberian Islands (Gorbunov 1946), 520 m. Off Spitsbergen (Mikhajlovskij 1902), 2203 m. Similarly, investigations in the sublittoral zone of the Chukotsk Sea (D'yakonov 1952b), off Point Barrow, Alaska (MacGinitie 1955), and in the Bering Sea (Ivanov 1964) failed to reveal its presence. Probably, the extensive areas with depths less than 200 m on both sides of the Bering Strait are uninhabited by *Elpidia*. The Arctic populations of *E. glacialis* thus appear to be separated from the Pacific populations by a distance of at least 1500 kilometres.

Variation:

(1) Papillae and tubefeet. Information in literature suggests that there is some geographic or local variation in the number of papillae within the Arctic region. Specimens with 3 anterior and 1 posterior pair predominated at 1412–2386 m northeast of Iceland (Heding 1942); at 311–362 m between Franz Joseph Land and Novaja Zemlja (Mikhajlovskij 1904); at 70–230 m in the Kara Sea; and at the deepest *Godthaab* station, 1880 m, in the Baffin Bay. Specimens with 2 anterior and 1 posterior pair predominated at 2203–2992 m west of Spitsbergen (Mikhajlovskij 1902) and at 3175 m in the Canadian Basin (Agatep 1967c).

The 150 specimens from the five shallowest *Godthaab* stations in the Baffin Bay (610–850 m) had the highest number of papillae known from the Arctic region: 85 % of the specimens had 4 or more pairs of anterior papillae, and 40 % had 2 or more pairs of posterior papillae.

The papillae in the specimens from the shallow Baffin Bay stations were often placed in irregular sequence along the radii, sometimes with papillae between the anterior and posterior group. A similar irregularity was found in many of the Kara Sea specimens.

The shallow Baffin Bay specimens were also remarkable by the fact that 95 % had 5 pairs of tubefeet.

The 86 specimens from the deep *Godthaab* station (1880 m) agreed in number of papillae (3 and 1 pairs) with those of most other Arctic populations, and only two of the specimens had 5 pairs of tubefeet. A number of 5 pairs has not otherwise been recorded within the genus.

The difference in number of papillae and tubefeet between the shallow and deep Baffin Bay populations was observed by Heding (1942) who, however, counted the papillae for only three of the five shallow stations. A high number of papillae and tubefeet is, however, also found in the specimens from the two remaining shallow sta-

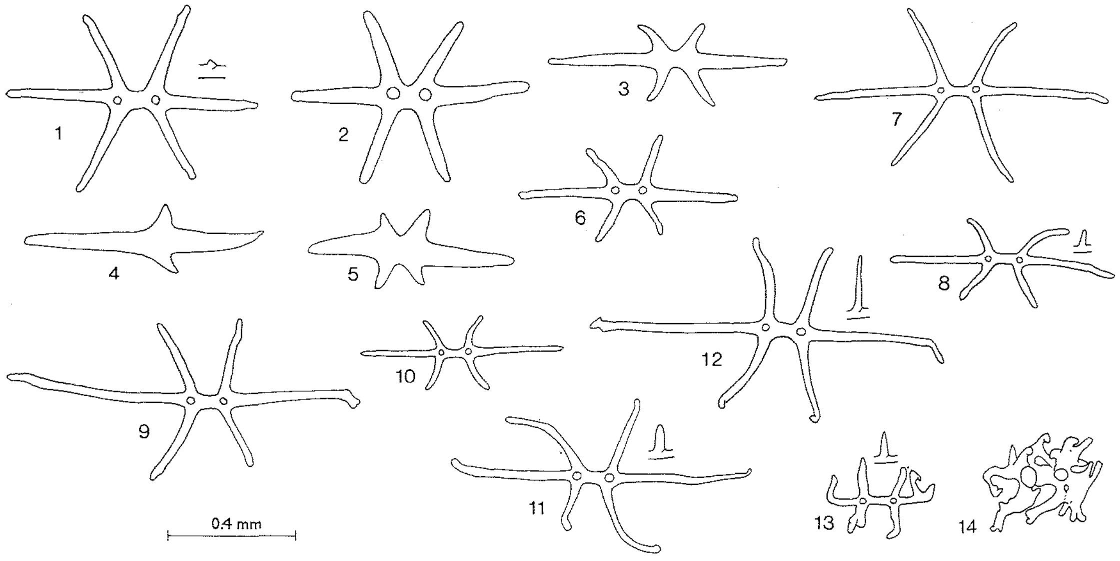


Fig. 91. *Elpidia glacialis glacialis*. Deposits. 1–5, *Ingolf* St. 113, ventrum; 6–8, *Ingolf* St. 120, ventrum; 9–10, *Godthaab* St. 144, ventrum; 11, *Godthaab* St. 119, ventrum; 12–14 *Godthaab* St. 54, dorsum.

tions. The five stations are situated on both sides of the Baffin Bay.

(2) Deposits. The deposits were compared in 60 specimens (ten from each station) from three *Ingolf* stations between Iceland and Jan Mayen (St. 113, 2465 m; St. 117, 1889 m; St. 120, 1666 m) and three *Godthaab* stations from the Baffin Bay (St. 54, 1880 m; St. 119, 610 m; St. 144, 733 m).

The specimens from *Ingolf* St. 113 differed from those of the other five stations by their robust deposits (Fig. 91: 1–5) which usually lack the apophyses. Some of the specimens showed reduction of the arms. Length of deposits up to 0.8 mm (occasionally 0.9 mm). Diam. of axis up to 0.07 mm. The dorsal deposits were less robust than the ventral ones (all deposits illustrated are ventral), but nevertheless they were distinctly more robust than those of the specimens from the other stations.

The deposits were more slender (diam. of axis 0.04 mm) in the specimens from the two other *Ingolf* stations (6–8) and the three *Godthaab* stations (9–12). They were up to 1.0 mm long in the *Ingolf* specimens and 1.2 mm in the *Godthaab* specimens. There was no difference in appearance and size between the deposits of the deep and the shallow *Godthaab* specimens. In one *Godthaab* specimen all the deposits were completely deformed (Fig. 91: 13–14).

Relationship of the Baffin Bay population: Heding (1942), comparing the *Godthaab* and *Ingolf* specimens, concluded that "the specimens from Baffin Bay may be regarded as survivors now developing into an endemic species". This apparently induced Belyaev (1971) to refer the Baffin Bay specimens to a separate species (*Elpidia* sp. 1).

However, the view is contradicted by the fact that the differences between the deposits of the Baffin Bay specimens and those of the specimens from *Ingolf* Sts. 117 and 120 are very small compared to the differences between the deposits from the two latter stations and the closely situated *Ingolf* St. 113. Further, the specimens from the deep Baffin Bay station agree in number and arrangement of the papillae with the usual Arctic form. The differences found in the latter feature are between the specimens from the shallow and deep Baffin Bay stations, and not between those from the Baffin Bay as a whole and the Arctic Ocean.

Moreover, it seems doubtful whether the deep-sea fauna of the Baffin Bay is effectively isolated from the main Arctic deep-sea fauna. Bailey (1956) presented evidence that the deep water (1250–2100 m) of the Baffin Bay originates in the Arctic Ocean. At depths greater than 250 m the Arctic Ocean water is heavier than any waters found in the Baffin Bay. As the sill depth in the Smith Sound Channel (connecting the Baffin Bay with the Arctic Ocean) is about 200 m, "it may be expected that a flow of heavy Arctic water may take place at relatively frequent intervals".

The straits connecting the Baffin Bay with the Arctic Ocean were investigated at a depth down to 90 m by the *Fram* (Grieg 1907). *Elpidia glacialis* was, however, not among the 26 species of echinoderms taken.

Elpidia glacialis sundensis Hansen, 1956

Figs. 90: 4, 92: 1–5

Elpidia glacialis sundensis Hansen, 1956, pp. 34–38, figs. 1, 5; Hansen 1967, p. 491, figs. 7, 8: 2.
Elpidia glacialis Théel, Théel 1882, pp. 18–19; Agatep 1967b, p. 61, pl. 7: 1–5.
Elpidia sundensis Hansen, Belyaev 1971, pp. 355–356, fig. 18.
Elpidia javanica Belyaev, 1971, pp. 354–355, fig. 17.
Elpidia sp. 5 Belyaev, 1971, pp. 358–359.

Diagnosis: Body length up to 42 mm. Dorsal papillae 3 pairs, up to 12 mm long. Deposits up to 1.55 mm long, slightly serrate; diam. of axis c. 0.04–0.05 mm.

Records: Sunda Trench, 6433–7160 m. C. 3000 specimens. – Antarctic, 1153–4840 m. 115 specimens.

Remarks: Hansen (1956) referred to the subspecies *E. g. sundensis* not only the specimens from the Sunda Trench but also the single Antarctic specimen taken by the *Challenger*. The Antarctic specimens of the *Eltanin* (Agatep 1967b) are here referred to the same subspecies because all the intact specimens had three pairs of well-developed papillae. Agatep erroneously stated that the specimens "belong to *Elpidia glacialis glacialis*, based on Hansen's (1956) 5 geographical subspecies".

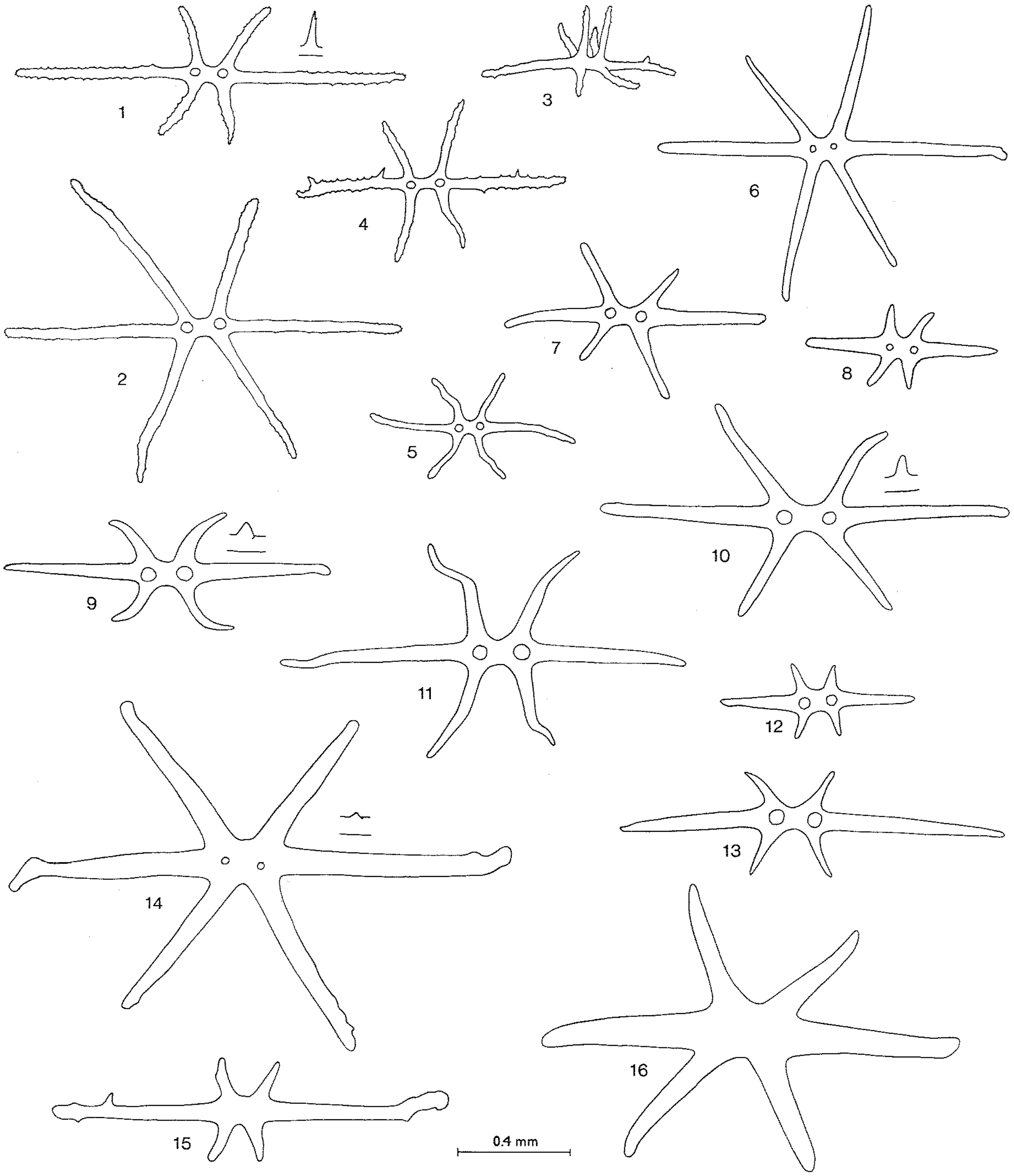


Fig. 92. *Elpidia glacialis*. The hadal subspecies. Deposits. 1–5, *E. g. sundensis* (1–3, St. 466, ventrum; 4, St. 465, ventrum; 5, St. 465, dorsum); 6–8, *E. g. kermadecensis* (6, St. 650, ventrum; 7–8, St. 649, ventrum); 9–13, *E. g. solomonensis* (9–10, St. 521, ventrum; 11 and 13, St. 517, dorsum; 12, St. 517, ventrum); 14–16, *E. g. kurilensis*, *Ryofu Maru* St. E 2, Japan Trench (14, dorsum; 15–16, ventrum).

Belyaev (1971) regarded the species *E. sundensis* as endemic to the Sunda Trench. The abovementioned Antarctic specimens, as well as two Antarctic specimens taken by the *Ob*, were provisionally referred to as *Elpidia* sp. 5, a name which was even suspected to cover more than one species.

The relationships of the Antarctic specimens are uncertain due to insufficient knowledge of the variation of the deposits. The present referring of the specimens to *E. g. sundensis* is based on the similarity in external features only.

The *Galathea* specimens from the Sunda Trench (Fig. 90: 4) are up to 42 mm long. Breadth of body 55–71 % of length.

Dorsal papillae 3 pairs, varying in length from 2 mm (in a 23 mm long specimen) to 7 mm (in a 28 mm long specimen). Belyaev found a variation in length of 6–12 mm.

Deposits in the Sunda Trench specimens rather slender and almost all serrate (Fig. 92: 1–5). They were up to 1.55 mm long in Belyaev's specimens. In the *Galathea* specimens they reach only 1.25 mm. Apophyses usually less than 10 % the length of the deposits.

Elpidia javanica Belyaev, 1971, is known from five specimens in the Sunda Trench (6820–6850 m). The species was held to differ from all other species of *Elpidia* by the absence of dorsal papillae. The deposits show a very specific similarity to those of *E. sundensis*. This suggests that *E. javanica* was erected on specimens of *E. sundensis* which had lost the papillae (the papillae may be so small that they leave little trace when torn off) or that the ventral side was mistaken for the dorsal side (cf. Belyaev 1971, fig. 17: 9).

Elpidia glacialis uschakovi Belyaev, 1971

Elpidia uschakovi Belyaev, 1971, pp. 346–348, fig. 12.

Elpidia glacialis uschakovi Belyaev, Lemche *et al.* (in press), photographic evidence.

Diagnosis: Body length up to 33 mm. Dorsal papillae 3(–4) pairs, up to 3 mm long. Deposits up to 1.75 mm long, slightly serrate; diam. of axis c. 0.08–0.09 mm.

Records: New Hebrides Trench, 6680–6830 m. Nine specimens.

Remarks: *E. g. uschakovi*, according to Belyaev, differs from *E. g. sundensis* by the more slender body form (breadth about 40 % of length), the smaller size of the papillae, and by the greater thickness of the calcareous rods of the tentacles (0.08–0.10 mm, against 0.05 mm in *E. g. sundensis*). The latter feature is connected with the greater robustness of all the deposits.

E. g. uschakovi, in the size (and partly in the number) of the papillae, is intermediate between *E. g. sundensis* on one hand, and *E. g. kermadecensis, E. g. solomonensis,* and *E. g. kurilensis* on the other. In the elongate body form it resembles the three latter. In the length (and partly in the robustness) of the deposits it agress with *E. g. kurilensis.*

Elpidia glacialis kermadecensis Hansen, 1956

Figs. 90: 5, 92: 6–8

Elpidia glacialis kermadecensis Hansen, 1956, pp. 34–38, figs. 2–3; Hansen 1967, p. 491, figs. 7, 8: 4.

Elpidia kermadecensis Hansen, Belyaev 1971, pp. 349–350, fig. 14A.

Diagnosis: Body length up to 30 mm. Dorsal papillae 4–6 pairs, rudimentary (rarely approaching 1.0 mm in length). Deposits up to 1.30 mm long; diam. of axis c. 0.05–0.06 mm.

Records: Kermadec Trench, 6620–8300 m. C. 1800 specimens.

Elpidia glacialis solomonensis Hansen, 1956

Figs. 90: 6, 92: 9–13

Elpidia glacialis solomonensis Hansen, 1956, pp. 34–38, figs. 2, 4; Hansen 1967, p. 491, figs. 7, 8: 5; Lemche *et al.* (in press), photographic evidence.

Elpidia solomonensis Hansen, Belyaev 1971, pp. 348–349, fig. 13.

Diagnosis: Body length up to 27 mm. Dorsal papillae 6–8 pairs, rudimentary. Deposits up to 1.50 mm long; diam. of axis c. 0.06–0.07 mm. Axis tapered; arms outwardly curved and tapered.

Records: New Britain Trench, 6780–9043 m. 115 specimens.

Elpidia glacialis kurilensis Baranova et Belyaev, 1971

Fig. 92: 14–16

Elpidia kurilensis Baranova et Belyaev, 1971, in Belyaev 1971, pp. 333–336, figs. 2–3.

Diagnosis: Body length up to 53 mm. Dorsal papillae 4–5 pairs, rudimentary. Deposits up to 1.75 mm long; diam. of axis 0.09–0.15 mm in dorsal, 0.09–0.20 mm in ventral deposits. Apophyses rudimentary or absent.

Records: Aleutian, Kurile-Kamchatka, and Japan Trenches, 6156–8100 m. 214 specimens.

Material:
Fourth cruise of the Japanese Expedition of Deep Seas (JEDS-4) St. E 2, eastern slope of the Japan Trench (38°00'N, 144°05'E – 37°57'N, 143°57'E), 6700–7340 m. – 2 specimens.

Description: The specimens are 25 and 35 mm long. They have four pairs of tubefeet and ten tentacles with completely retracted disc processes. The large specimen, and probably also the small one, has four equidistant pairs of rudimentary and completely retracted dorsal papillae. The skin is hard, due to the crowded deposits (Fig. 92: 14–16). Most of the deposits are about 1.0 mm long, some up to 1.5 mm. Diameter of axis 0.09–0.15 mm in dorsal, 0.09–0.20 mm in ventral deposits. (Belyaev (1971) stated the maximum length of the deposits to be 1.75 mm, and the diameter of the axis to be 0.09–0.15 mm). The apophyses are reduced – in most of the ventral deposits absent.

The deposits of *E. g. kurilensis* are the largest and most robust in the species. In robustness, the deposits of the here described specimens approach those of *E. birsteini*.

Remarks: The specimens, taken by the *Ryofu Maru*, were kindly placed at my disposal by Dr. Masuoki Horikoshi. A brief account of the expedition was given by Suyehiro *et al.* (1962), but without description of the animals.

Elpidia longicirrata Belyaev, 1971

Belyaev 1971, pp. 338–339, fig 5.

Diagnosis: Body length up to 55 mm. Dorsal papillae 3 pairs, all long and filiform. Deposits up to 1.75 mm long; diam. of axis 0.07–0.09 mm. Apophyses absent.

Records: Kurile-Kamchatka Trench, 8035–8345 m. Five specimens.

Elpidia birsteini Belyaev, 1971

Belyaev 1971, pp. 336–338, fig. 4.

Diagnosis: Body length up to 47 mm. Dorsal papillae 3 pairs, the first pair long and filiform, the others rudimentary. Deposits up to 1.55 mm long; diam. of axis 0.07–0.10 mm in dorsal, 0.10–0.20 mm in ventral deposits. Apophyses absent.

Records: Kurile-Kamchatka Trench, 8060–9345 m. 1423 specimens. – Idzu-Bonin Trench, 8530–8540 m. One specimen.

Elpidia hanseni Belyaev, 1971

Belyaev 1971, pp. 339–342, figs. 6–7.

Diagnosis: Dorsal papillae 2(–3) pairs. Ventral deposits extremely robust, the largest ones ellipsoid and without arms; diam. of axis 0.10–0.25 mm. Apophyses of ventral deposits reduced or absent.

Elpidia hanseni hanseni Belyaev, 1971

Elpidia hanseni Belyaev, 1971, pp. 339–342, fig. 6.

Diagnosis: Body length up to 31 mm. Dorsal papillae 2 pairs, from less than 1.0 to 4.5 mm long, and occasionally a third pair, less than 1.5 mm long. Deposits up to 1.10 mm long, the dorsal ones with axis 0.07–0.18 mm in diam. Axis and arms tapered, arms often outwardly curved (the slenderer deposits resembling those of *E. glacialis solomonensis)*.

Records: Kurile-Kamchatka Trench, 8610–9530 m. C. 34000 specimens.

Elpidia hanseni idzubonensis Belyaev, 1971

Elpidia hanseni idzubonensis Belyaev, 1971, pp. 339–342, fig. 7.

Diagnosis: Body length up to 23 mm. Dorsal papillae 3 pairs, 1.0–1.5 mm long. Deposits up to 1.35 mm long, the dorsal ones with axis 0.05–0.09 mm in diam. Axis and arms less tapered and arms less curved than in *E. h. hanseni*.

Records: Idzu-Bonin Trench, 8800–9735 m. 153 specimens.

Elpidia atakama Belyaev, 1971

Belyaev 1971, pp. 345–346, fig. 11.

Diagnosis: Dorsal papillae 5–6 pairs, 2–4 mm long (in specimens 33–46 mm long). Deposits up to 1.50 mm long; diam. of axis 0.05–0.09 mm in dorsal, 0.10–0.15 mm in ventral deposits. Apophyses 20–50 % the length of the deposits.

Records: Peru-Chile Trench, 7720 m. Two specimens.

Elpidia sp. 3 Belyaev, 1971

Belyaev 1971, pp. 357–358, fig. 19.

A few skin fragments taken in the Romanche Trench at 7340 m. Deposits up to 0.85 mm long; diam. of axis c. 0.04 mm.

Elpidia sp. 4 Belyaev, 1971

Belyaev 1971, p. 358, fig. 20.

A skin fragment taken in the Peru-Chile Trench at 2140 m. Deposits up to 0.71 mm long, as robust as the ventral deposits of *E. atakama.*

III. GENERAL PART

A. THE TAXONOMIC CHARACTERS AND THEIR VARIATION

In order to estimate the importance of the different taxonomic characters the range of variation within each species should be known. An examination of a large number of specimens of many species showed that there was a pronounced variation in most taxonomic characters.

An *individual variation* is unambiguously revealed by differences between specimens from one and the same station. If two stations are involved, the differences might be due to local variation.

The range of individual variation in a taxonomic character may differ from one locality to another. This is clearly shown by the variation in number of dorsal papillae in *Oneirophanta mutabilis.* In the 14 specimens from St. 654 in the Kermadec Trench the papillae were surprisingly constant both in number and arrangement, while in the 30 specimens from St. 716 in the eastern Pacific the papillae varied greatly in number and showed no regular features in the arrangement and type of reduction.

A *local variation* seems to be of common occurrence among the Elasipoda. Striking examples are shown by four species of the Kermadec Trench, in particular *Oneirophanta mutabilis* (p. 243).

A *geographic variation,* i. e. a variation of a larger scale, was found in practically all the widely distributed species known from many specimens.

An *age variation* has been found in a few species only. This may to some degree be ascribed to the almost complete absence of small specimens in the material (p. 10). Specimens smaller than 20 mm were caught in five species only: *Ellipinion galatheae* (17 mm), *Elpidia glacialis* (11–35 mm), *E. theeli* (7–12 mm), *Laetmogone fimbriata* (9–60 mm), and an unidentified species of *Peniagone* from St. 626 (9–10 mm).

The papillae and tubefeet increase in number with advancing age in the species *Laetmogone maculata, L. fimbriata,* and *Orphnurgus glaber.* In *Laetmogone violacea* the papillae increase in number, while the tubefeet number does not increase to any appreciable degree. As a rule, the number of ambulacral appendages increases with the size of the specimens in those species of the Deimatidae and Laetmogonidae in which they are present in a large number.

Juvenile giant crosses are found in *Psychropotes longicauda,* but otherwise an age variation in the calcareous deposits is unknown in the Elasipoda. In many molpadonians the deposits become irregular in shape and decrease in number with the age of the specimens. Similar changes were found in some aspidochirotes (e. g. Mitsukuri 1897a). In the Antarctic dendrochirote, *Staurocucumis liouvillei,* several generations of deposit types were found in specimens ranging from 0.7 to 13 mm in length (Ekman 1927).

The calcareous deposits

The endoskeleton in holothurians consists of isolated calcareous bodies, the *deposits.* Synonymous terms are ossicles, sclerites, and spicules, the latter term usually designating small and pointed bodies, as found in the Elpidiidae and Psychropotidae.

Düben & Koren (1844a, b) were the first to use the deposits consistently in the description of the species. Working on Scandinavian species they found that these could be most clearly distinguished by their deposits. This high evaluation of the deposits as specific characters has been adopted by subsequent authors, sometimes to such a degree that the deposits were the only feature illustrated.

The importance of the deposits in characterizing genera and higher categories of holothurians has been differently estimated. Théel (1882), when creating his system for the Elasipoda, attached little generic importance to the deposits, while considerable attention was paid to them in the systems of R. Perrier (1902) and Hérouard (1923). The interrelationship of the different types of deposit and its bearing on the taxonomy of the Elasipoda was discussed by Hérouard (1923) and Ekman (1926).

1. Intraspecific variation.

The range of intraspecific variation in the deposits, contrary to that in other taxonomic features, can be estimated from selected body samples only, and not from the examination of whole specimens. It is, therefore, important that the samples are representative of the variation within the specimen. In most species there is a consistent difference between the dorsal and ventral deposits – the ventral ones being more robust. This difference may to some degree be phenotypic.

Differences between deposits from different parts of the dorsum or ventrum are usually of doubtful taxonomic value. The difference is generally smaller than between dorsal and ventral deposits and is seldom refound from one specimen to another. Even when conspicuous differences occur, as in the dorsum of one of the specimens of *Psycheotrephes magna* from St. 234, they are generally incidental. An exception is constituted by *Orphnurgus glaber,* in which the deformed deposits are increasingly robust towards the posterior end of the ventrum.

The deposits of the ambulacral appendages are usually elongated or rod-shaped bodies which are less characteristic specifically than are the fully developed deposits of the dorsum and ventrum. They were as a rule examined in only a few specimens of each species.

Sometimes species, even belonging to different genera, are indistinguishable by their deposits *(Oneirophanta setigera* and *Orphnurgus protectus; Benthogone rosea, B. fragilis,* and *Laetmogone interjacens; Laetmogone wyvillethomsoni* and *L. theeli;* and some species of *Peniagone).* Nevertheless, the deposits proved to be the most reliable of the species characters.

The deposits are important also to the study of geographic and local variation.

2. Interrelationship of the different types of deposit.

(1) *The primary cross.* Most holothurian deposits begin as a rod with a bifurcation at either end – a primary cross. It has been commonly assumed that the types of deposit which cannot be traced back directly to a primary cross are secondarily transformed. Only the wheels of the Apoda have been regarded as a possible exception (Ludwig 1889–1892).

The bifurcation of the primary cross generally continues into successive dichotomous ramifications, leading to the various types of reticulated plates which occur in all five orders of the Holothurioidea. The large and feebly differentiated plates of many Dendrochirota and of the genera *Deima* and *Oneirophanta* within the Deimatidae represent the least specialized type.

Hérouard (1923) considered the reticulated plate such a fundamental type of deposit that he derived even the various spicule types of Elpidiidae from reticulated plates. The arms of the elpidiid spicules, according to Hérouard, represent zigzag-lines of internodia, emerging through alternating reduction of one of the two branches in each ramification. Hérouard divided the spicules in this family into 1) a quaternary type, with the central growing point lying in the middle of an internodium, and 2) a trinary type, with the central growing point at a nodal point. The dual origin of the spicules, according to Hérouard, indicated that, at an early stage, the family separated into two distinct evolutionary trends.

This complicated derivation of simple spicules was based wholly on speculation. No intermediary stages have been observed between reticulated plates and the spicules of the Elpidiidae, and nothing in the morphology of the spicules suggests that their arms are constructed from a line of internodia. Hérouard's ideas of spicule derivations may, therefore, be left out of consideration.

Ekman (1926) rejected the view of the primary cross as the prototype of all holothurian deposits. He maintained that, at least in the Elasipoda and Aspidochirota, some types of deposit were derivatives of a "Spitzstäbchen" – a rod which is primarily undivided. This view led Ekman to remarkable conclusions regarding the taxonomy of the Elasipoda.

As the relationship of the different spicule types is of fundamental importance for an understanding of the phylogeny and taxonomy of the Elasipoda, it seems relevant to discuss Ekman's views.

Deimatidae. According to Ekman, both spicule types are represented. While the reticulated plates and the crosses with spatulated, perforated arm ends were derived from primary crosses, some of the rod-shaped spicules in the ambulacral appendages in species of *Orphnurgus, Oneirophanta,* and *Deima* were derived from "Spitzstäbchen".

As an example of a "Spitzstäbchen" in *Deima,* Ekman reproduced one of the four tentacular spicules illustrated by Ludwig (1894, pl. IX: 1–4) for *D. pacificum,* disregarding the fact that the three other illustrated spicules are intermediates between rods and reticulated plates.

The pointed, spindle-shaped rods in the ambulacral appendages in species of the other deimatid genera may seem to offer a more convincing example of "Spitzstäbchen". However, the present study showed that they were connected by intermediary stages to rods with terminal ramifications.

Even the amorphous, ellipsoid, and rounded bodies of *Orphnurgus glaber* (Fig. 13) can be traced back to deposits with terminal, dichotomous ramifications.

Laetmogonidae. Ekman stated that "Spitzstäbchen" occur in all the genera, while "Gabelstäbe" (i. e. elongated primary crosses) seem to occur only in *Laetmogone.* Nevertheless, one of the two "Gabelstäbe" illustrated in his paper was from *Laetmophasma fecundum (= Pannychia moseleyi).* According to Ekman, it is difficult to make a clear distinction between the two types of spicule as it is often doubtful whether or not the terminal spines of a rod represent bifurcations. In actual fact, all intermediates between pointed rods and rods with bifurcated ends are found in the family.

Elpidiidae. Ekman divided the family into two subfamilies, based solely on the types of spicule. In Elpidiinae, all the spicules were derived from "Spitzstäbchen", while in Peniagoninae both spicule types were represented. The tripartite spicules of *Amperima* and *Achlyonice* (both referred to Elpidiinae) were derived from rods through development of one oblique spine. This derivation was based on the presence of intermediary forms of spicule in *Amperima naresi.*

The presence in *Amperima naresi* (Fig. 76) of regular tripartite spicules together with irregularly shaped spicules, however, does not necessitate a derivation of the former from the latter. In my opinion, the irregular "intermediary" spicules are more likely reduced stages of regular tripartite spicules, which again may derive from a primary cross through reduction of two of its arms.

The rod-shaped spicules of *Scotoplanes* and *Ellipinion* may be derived through reduction of tripartite spicules or directly from primary crosses. Intermediary stages were found in *Scotoplanes clarki* (Fig. 85) and *S. globosa* (Théel 1882, pl. XXXIV: 2).

The spicules of *Elpidia* remain as the only type which cannot be traced back directly to a primary cross. The uniqueness of these spicules is further underlined by their unusual optical features. Schmidt (1925), determining the position of the optical axis in representatives of the five holothurian orders, found that in all deposits which from their morphology could be seen to derive from a primary cross the optical axis was vertical to the plane of the deposit. Only two deposit types had the axis horizontal to the plane: The *Elpidia* spicules and the "Schnallen" (buttons) in some species of the aspidochirote genus *Holothuria.*

The two pairs of obliquely placed arms of the *Elpidia* spicule apparently are not homologous with the arms of a primary cross, but rather represent two pairs of secondary processes on a rod-shaped spicule, vertical to the plane of the original primary cross. Transitional stages between rods and *Elpidia*-like spicules occur in Antarctic specimens of *Scotoplanes globosa,* as evidenced by the spicules illustrated by Agatep (1967b, pl. IV). The spicules included simple rods, as well as rods with two pairs of smooth or spinous arms. The presence of such transitional spicules in a genus related to *Elpidia* is remarkable.

Psychropotidae. Ekman derived the cross-shaped spicules of this family from "Spitzstäbchen", in contrast to the quite similar crosses occurring in a number of species of *Peniagone.* The different derivation was concluded from the fact that primary crosses do not occur in the family, and that the ventral spicules in many of its species include intermediary stages between crosses and rods. However, as in *Amperima naresi,* the intermediary stages are, in my opinion, more naturally regarded as reduced spicules.

The optical axis is vertical to the plane of the cross, which agrees with a derivation of the latter from a primary cross (see above).

Ekman's derivation of the psychropotid crosses obscures a remarkable similarity between the spicules of Psychropotidae and those of Elpidiidae. In both families all spicules (except the rare wheels of the Elpidiidae) completely lack dichotomous ramifications other than those of the primary cross proper. Only two other examples are known of spicules which apparently lack the tendency of the primary cross to undergo ramification at the ends of the arms, viz. the spinous crosses of *Laetmogone violacea* and the crosses of the synallactid genus *Galatheathuria* Hansen & Madsen, 1956. However, in a specimen of *Galatheathuria* from *Galathea* St. 450, most of the crosses have terminal arm spines, possibly representing reduced ramifications. The type specimen of *G. (Paelopatides) aspera* also had the arm ends "slightly enlarged and spinous" (Théel 1886a, p. 158, pl. X: 13). In the specimens described by Hansen & Madsen (1956), terminal arm spines may have been lost through corrosion.

The peculiar similarity between the spicules of the Psychropotidae and Elpidiidae is one of the arguments for uniting these two families (together with the spicule-free, pelagic family, Pelagothuriidae) to form the new suborder, Psychropotina (pp. 206–207).

The absence of dichotomous ramifications in the spicules of the Psychropotina is probably a secondary feature. Spicules which are close to the hypothetical prototype of the Psychropotina spicules have been described as the fossil family Palelpidiidae Mostler, 1968a (p. 208).

(2) *Wheels* are the prevailing type of deposit in the Laetmogonidae. Only rod-shaped and (in *Laetmogone violacea*) cross-shaped spicules occur in addition. The centre of the wheels consists of a primary cross, or a five- or six-rayed structure deriving from a primary cross.

Ekman (1926) distinguished between two wheel types in the family – the flat wheel with a flat primary cross in the centre, and the concave wheel with a concave primary cross or a concave five- or six-rayed structure in the centre. While the flat wheels were simply regarded as small perforated plates, the concave wheels were supposed to derive from cross-shaped spicules of the type found in *L. violacea.*

However, apart from its concavity, the central structure of the concave wheel type has no similarity to the spinous crosses of *L. violacea*. Besides, so many intermediates are found between the concave, six-rayed structure and the flat primary cross that a dual origin of the laetmogonid wheels is unlikely.

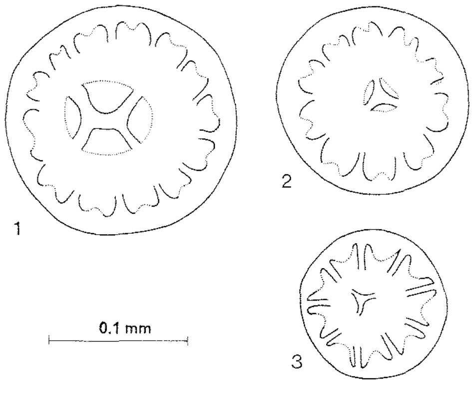


Fig. 93. Wheels of Elpidiidae. 1, *Achlyonice ecalcarea (Galathea* St. 663); 2, *Amperima rosea* (Monaco St. 2994); 3, *Elpidia theeli (Galathea* St. 602).

In the Elpidiidae, small wheels (Fig. 93) have previously been found as rare, accessory deposits in *Peniagone theeli, Achlyonice ecalcarea, Amperima rosea, A. velacula, Irpa ludwigi,* and *Elpidia glacialis.*

Examination was made of specimens of three of these species *(Achlyonice ecalcarea, Amperima rosea,* and *Elpidia glacialis),* and wheels were found in all of them. The specimens of *Amperima rosea* included those described by R. Perrier (1902); wheels were previously known only from the specimens described by Hérouard (1923). In *Elpidia glacialis,* wheels were found in the subspecies *glacialis,* but not in the other subspecies.

Only two additional species with wheels, *Amperima naresi* and *Elpidia theeli,* were found during the present study, which confirms the rare occurrence of this type of deposit in the Elpidiidae. On the other hand, wheels seem to be a rather constant feature in the species possessing them.

The wheels of the Elpidiidae differ from those of the Laetmogonidae by the presence of a calcareous membrane which connects the nave with the rim, and completely or partly fills in the interspaces between the spokes.

The central part of the elpidiid wheel consists either of a primary cross *(Peniagone theeli* and

Achlyonice ecalcarea) or a three-rayed structure *(Amperima rosea, A. naresi, A. velacula, Irpa ludwigi, Elpidia glacialis,* and *E. theeli).* It is notable that the type with a central primary cross is found in the genera which have a primitive calcareous ring, whereas the type with a central three-rayed structure is found in genera with a specialized calcareous ring.

The wheels which Théel (1882) recorded for *Elpidia ambigua (= Peniagone purpurea* were probably foreign bodies. They were similar to the wheels in *Benthogone* and *Apodogaster* of the family Laetmogonidae.

Hérouard (1923) supposed that the wheels of the Elpidiidae were rudiments from a larval stage. This view is supported by the fact that the wheels occur scatteredly throughout the family – in primitive as well as in specialized genera. The occurrence of wheels in two only distantly related families of Elasipoda even suggests that the wheels are persisting spicules from a larval stage common to all Elasipoda. However, a direct proof of a larval origin of the wheels is still lacking because the larval development of the Elasipoda is completely unknown.

In contrast to the wheels of the Elasipoda, the wheels of the Apoda can be traced back directly to a larval stage. However, a homology between the wheels in the two orders is doubtful, because the wheels of the Apoda in no case possess a central primary cross, or a structure derived from a primary cross.

(3) *C-shaped spicules* occur in all species of *Scotoplanes, Ellipinion,* and *Amperima* (presence not established in *A. furcata).* The curved rods of *Kolga* and *Irpa* are probably homologous with the C-es of the three other genera, although it is uncertain whether they represent degenerate or primitive stages.

The aspidochirote genera *Stichopus* and *Bathyplotes* have C-shaped spicules which are similar in shape to those of the Elpidiidae (the similarity includes the presence of a middle enlargement). However, the aspidochirote C-es are not likely to be homologous with those of the Elasipoda. The fact that C-shaped spicules of similar shape are found also in echinoids and sponges shows that they need not be monophyletic in the Holothurioidea.

The calcareous ring

Two types of calcareous ring are found in the Elasipoda:

1. – Deimatidae. Laetmogonidae, and Psychropotidae. The ring is similar in structure to that of the other holothurian orders, apart from its low degree of calcification. The few detailed descriptions and illustrations which are found in literature indicate conspicuous differences in ring structure. In order to examine the taxonomic value of these differences, the ring was examined in a number of representatives of the three families.

The structure of the ring may be illustrated by the example of *Oneirophanta setigera* (Fig. 94: 1). The five radial pieces each possesses a median slit for the passage of the radial nerve and water-vascular canal, and two lateral depressions for the bottoms of the tentacular cavities. The five interradial pieces each possesses a median septum which separates two tentacular cavities.

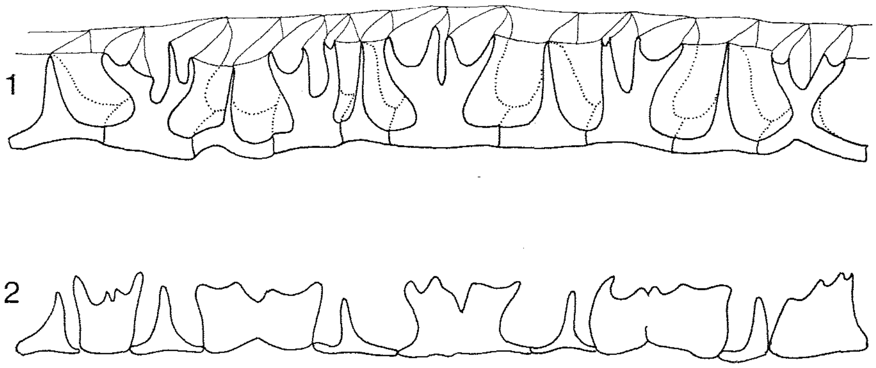


Fig. 94. Calcareous rings. 1, *Oneirophanta setigera (Galathea* St. 726); 2, *Oneirophanta mutabilis (Galathea* St. 716). Both figures show the complete ring, with five radial and five interradial pieces. The lower figure shows the ring in external outline only.

The tentacular cavities form the basal part of the wide water-vascular canals of the tentacles. Each cavity communicates through a slender canal with one of the five broad radial canals issuing from the water-vascular ring. The calcareous ring is formed by calcifications in the connective tissue surrounding the bottoms of the tentacular cavities. The calcification is most pronounced at the base of the cavities and in the septa between them, while the internal and external membranes of the ring are less calcified.

Due to the low degree of calcification, the shape of the ten pieces varies according to the state of contraction of the specimen, and especially to that of the tentacles. Evidently, recorded specific differences in the shape of the calcareous ring should be regarded with reservations. Even if the ring is more strongly calcified, as in a specimen of *Oneirophanta mutabilis* (Fig. 94: 2), the pieces are still irregular in shape.

The degree of calcification may vary rather irregularly in the ring, and the transition from the stronger to the more feebly calcified parts is often so gradual that the ring has no exact delimitation. If the calcification of the external membrane is weak, the ring will show a number of indentations corresponding to the number of tentacles. If, however, the calcifications of the external membrane are so pronounced that the septa between the tentacular cavities are invisible from the outside, the ring will appear as an unsculptured ribbon. Thus, there is no essential difference between the two ring "types".

Treatment with sodium hypoclorite (cf. Théel 1882, pl. XXXVII: 4) may cause the ring to fall into fragments which do not reflect its structure.

The ring in the Laetmogonidae and Psychropotidae seems in general to be even less calcified than in the Deimatidae. Calcifications may even be absent in some species, the ring consisting only of a firm connective tissue (e. g. *Benthogone rosea, Benthodytes typica,* and *Psychropotes longicauda).* A specimen of *Psychropotes depressa* showed a loose calcareous meshwork at the base of the tentacular cavities. These calcifications have no similarity to the five star-shaped ring pieces in the Elpidiidae. Apparently, the feebly developed ring in these families represents a reduction and not, as in the Elpidiidae, an embryonic stage.

2. – Elpidiidae. The ring (Fig. 95), unlike that of all other holothurians, consists of five radial pieces only, each with two clusters of arms radiating from a common centre.

Hansen (1967) pointed out that a peculiar evolution of the ring had taken place within the Elpidiidae, suggesting a paedomorphic origin of the whole family.

Three types of calcareous ring may be distinguished, derived from each other in the following order:

(1) In *Peniagone, Achlyonice, Kolga,* and probably *Psychrelpidia,* the ring pieces are small, delicate, and usually isolated from each other. The number of arms on each piece shows an individual variation (as far as can be judged from the few species of which sufficient material has been examined). The arms may also be irregularly subdivided. This type of ring is reminiscent of the embryonic ring of other holothurians and represents the beginning of the ring's unique evolution within the family.

The ring structure is known in the following species of *Peniagone* (the figures in parentheses indicate the number of arm pairs on each piece): *P. convexa* (c. 7; Fig. 95: 1), *P. azorica* (10–12), *P. affinis* (c. 12), *P. willemoesi* (10–15), *P. papillata* (7–9), *P. japonica* ("numerous"), *P. elongata* (10–14), *P. vitrea* (4–8), *P. purpurea* (c. 8), and *P. diaphana* (c. 7).

The ring may dissolve with advancing age. Thus, the ring was absent in some *P. azorica* from the Kermadec Trench and in one *P. diaphana* from St. 574. Hérouard (1902) similarly stated that the ring was absent in his specimens of *Scotoanassa translucida (= P. diaphana).*

The ring of *Achlyonice ecalcarea* has about 12 pairs of arms on each piece (Théel 1882), whereas *A. monactinica* has 6 pairs (Ohshima 1915). The ring of *A. tui,* according to Pawson (1965a), consists of a "fragile network"; the structure of the five pieces was not specifically described.

The ring of *Psychrelpidia,* according to Sluiter with 8 pairs of arms on each piece, probably belongs to the type found in *Peniagone* and *Achlyonice.*

The pieces of the ring in *Kolga* (Fig. 95: 2–3) are of a delicate structure. Six specimens examined of *K. hyalina* (four from *Ingolf* St. 113 and two from *Godthaab* St. 54) all possessed basically five pairs of arms on each piece, arranged as two anterior and three posterior pairs. Some pieces had some of the arms wholly or partially split. Danielssen & Koren (1882, pl. III: 27–28) illus-

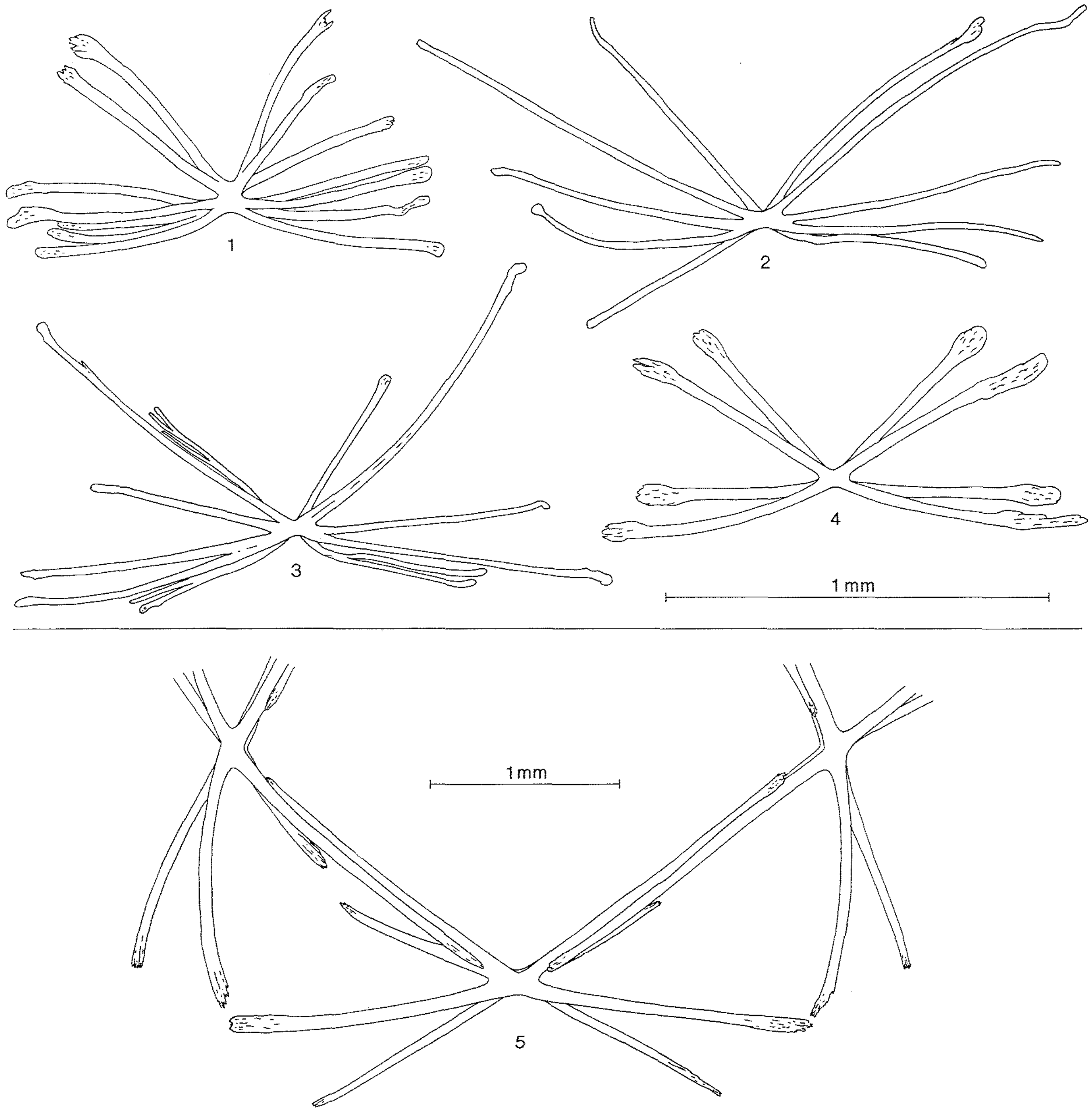


Fig. 95. Calcareous ring pieces of Elpidiidae (all viewed from posterior end of body). 1, *Peniagone convexa (Galathea* St. 234); 2–3, *Kolga hyalina,* two pieces belonging to the same specimen *(Ingolf* St. 113); 4, *Scotoplanes globosa (Galathea* St. 32); 5, *Elpidia glacialis glacialis,* three adjoining pieces *(Godthaab* St. 143).

trated a ring in which the arms on each piece consisted of three anterior pairs (two of which were partially split) and four posterior pairs. A derivation from five basic pairs is not obvious from the illustration. Théel (1882), however, found that *K. nana* (here considered a synonym of *K. hyalina),* had five pairs of arms on each piece.

The ring of *Kolga* resembles the *Peniagone-Achlyonice* type in having a varying number of arms on each piece. On the other hand, the fact that the basic arm number seems to be constant recalls the conditions in the related genera *Irpa, Elpidia, Amperima, Ellipinion,* and *Scotoplanes,* although in all these genera the arm number is four pairs only.

The five ring pieces in *Kolga* are isolated from each other, although some of the arms are so long that they almost touch those of the neighbouring pieces. The reduction and partial fixation of the arm number may, as in *Amperima, Ellipinion,* and *Scotoplanes,* have taken place during a former continuous state of the ring.

The supposition that the ring of *Peniagone* and

Achlyonice represents an embryonic stage cannot be proved directly, as no larval stages of Elasipoda are known. However, in some species of Apoda the first rudiment of the ring consists of five radial pieces, each representing a primary cross with successive divisions of the arms. Thus, the ring of *Synaptula hydriformis* (Lesueur) passes through a stage resembling the ring of *Peniagone* and *Achlyonice* (Clark 1907, pl. VI: 9). The ring of *Leptosynapta inhaerens* (O. F. Müller) begins with the formation of five similarly shaped radial pieces, followed by the formation of five interradial pieces. From the beginning, the interradial pieces seem to consist of an irregular meshwork (Runnström 1928).

Almost nothing is known about the formation of the ring in the other holothurian orders. In *Psolus phantapus* Strussenfelt the ring begins as five radial rod-shaped pieces with some irregular branches, but with no obvious derivation from a primary cross (Runnström & Runnström 1921). In *Cucumaria echinata* v. Marenzeller the ring begins its formation as a diffuse, continuous meshwork (Ohshima 1921). The ring of the molpadonian *Caudina chilensis* (J. Müller) seems to start in the same way (Kitao 1933).

Although the derivation of the radial pieces of the calcareous ring from primary crosses through a "*Peniagone*-stage" has been observed only within the Apoda, it is probably the original derivation also in the groups in which the ring was found to begin its formation as a continuous meshwork.

(2) In *Elpidia* and *Irpa* the ring is continuous and of a firm structure. Each piece has four pairs of arms, forming a large posterior and a somewhat smaller anterior cross (Fig. 95: 5). The inner arms of the posterior cross are throughout their length joined firmly to the corresponding arms of the neighbouring pieces. The outer arms of the posterior cross meet the corresponding arms at the tip (or are connected with them by means of connective tissue fibers). Muscle fibers connect the ring with the pharynx. The ring represents a specialized type, derived from the *Peniagone-Achlyonice* type through an increase in size of the pieces, concomitant to a reduction in the number of those arms which do not take part in the firm construction of the ring.

The ring of *Irpa ludwigi* differs from that of *I. abyssicola* and *Elpidia glacialis* in having a flattened, irregularly shaped process on two pairs of the arms. Although the presence of these processes was apparently verified for several specimens (von Marenzeller 1893b), they may not represent a constant feature in the species. They belong to the two pairs of arms that take no part in the firm construction of the ring.

The identical, and very specialized, ring structure is a remarkable similarity between the two genera. The simplification and regular formation of the ring pieces apparently evolved as a means of strengthening the construction of the ring, when the latter had regained its continuous state.

(3) In *Amperima, Ellipinion,* and *Scotoplanes* (Fig. 95: 4) each piece of the ring possesses four pairs of arms as in *Irpa* and *Elpidia,* but the ring is discontinuous and of a delicate structure. Although a derivation of the ring directly from the *Peniagone* type cannot be excluded, a derivation from the *Elpidia-Irpa* type seems more likely. A reduced and constant arm number was probably attained in a ring in which each piece performs a definite mechanical function.

The structure of the ring is known in *Amperima robusta, Ellipinion papillosum, E. kumai* (in this species an additional unpaired arm was present on each piece), *Scotoplanes globosa,* and *S. clarki.* Agatep (1967b) described the ring of *S. globosa* as consisting of "a very fine network of spicules", which apparently refers to incidental spicules, and not to the five distinct segments which are known to be present in this species. Similar descriptions were given of the rings in *Scotoplanes facetus (= Ellipinion facetum)* and *S. angelicus (= E. papillosum).*

The tubefeet and papillae

Conspicuous ambulacral appendages are characteristic of most Elasipoda. The *tubefeet* are locomotory and sometimes provided with a sucking-disc, while the *papillae* are sensory or respiratory. The abundant development of the papillae, which has produced many bizarre animal forms within this order, is connected with the absence of respiratory trees (p. 208).

(1) Tubefeet. The well-defined ventral sole of the Elasipoda is bordered by ventrolateral tubefeet which are usually conspicuous. The midventral tubefeet, on the other hand, are reduced or absent.

In Elpidiidae the ventrolateral tubefeet are large and few in number; in some species of *Peniagone* they border only the posterior part of the ventral sole. As suggested by Hérouard (1923), the presence of few and large-sized tubefeet in this family may be a larval feature.

Large-sized, but more numerous, tubefeet characterize the Deimatidae and Laetmogonidae. As in Elpidiidae, the tubefeet are never fused into a brim.

The communication of the tubefeet, and in some species the papillae, with large water-vascular, dermal cavities is a feature peculiar to the Deimatidae, Laetmogonidae, and Elpidiidae. The cavities are branched in Deimatidae and Laetmogonidae, as well as in the elpidiid genus *Achlyonice.* The remaining Elpidiidae have unbranched cavities. The Psychropotidae may possess similar cavities at the base of the unpaired appendage.

The function of the cavities is considered elsewhere (pp. 205–206).

In most species of Psychropotidae the tubefeet are numerous, pointed, and fused into a brim which surrounds the body. Separate and rather large tubefeet are found along the side of the body in *Psychropotes longicauda.*

(2) Papillae belonging to the two dorsal radii are present in practically all species of Elasipoda. Papillae are present along the ventrolateral radii in the Deimatidae and in the laetmogonid genus *Apodogaster;* in the latter genus the papillae are small and fused into a brim which surrounds the body above the ventrolateral tubefeet.

The papillae and tubefeet not only provide valuable characters in the separation of species, genera, and families. The fact that they present numerical differences makes them especially adequate for the study of intraspecific variation. The geographic subspecies erected for the species *Deima validum, Oneirophanta mutabilis,* and *Elpidia glacialis* are based mainly on differences in number of dorsal papillae. Similarly, the geographic variation found in *Orphnurgus glaber* consists to a high degree of differences in number of papillae and tubefeet.

In view of the importance attached to the tubefeet and papillae as revealing geographic variation it is essential that descriptions of holothurians show the variation in number of these features for each locality.

(3) Velum. The Elpidiidae possess a velum formed by partial fusion of two pairs of large and usually one pair of reduced papillae. The taxonomic value of the velum has been differently estimated. Théel (1882) used its relative size as a generic character, whereas Hérouard (1923) did not even regard presence or absence of a velum as of generic importance. The latter view was confirmed by the present investigation.

It is remarkable that a velum, or papillae homologous with this structure, is present in all the genera of the family, with the exception of *Elpidia.* Thus, in *Rhipidothuria* the two most anterior pairs of papillae are placed closely together on an elevation of the skin corresponding in position to a velum. Similarly, the two pairs of minute papillae present in *Parelpidia* (here synonymized with *Peniagone)* are, like a velum, placed on the anterior part of the dorsum. *Scotoplanes* has two pairs of large and one pair of reduced papillae. As pointed out by Hérouard (1923), the papillae differ from those of a velum only by the large interspace between the first two pairs. The papillae of *Scotoplanes* may thus be derived from those of a velum through a process of allometric growth.

The velum may be a rudiment of a swimming-brim of the type present in the Pelagothuriidae. This view is supported by the presence of a similar brim (composed of dorsal and lateral papillae) in *Psychrelpidia,* a genus which both in the structure of the calcareous ring and the presence of 10 tentacles agrees with the Elpidiidae.

Thus, the absence in *Elpidia* of every trace of a velum is as remarkable as the presence of a unique type of spicule in the same genus. Nevertheless, the fact that *Elpidia* has a specialized calcareous ring similar to that of the velum-bearing genus *Irpa* indicates that the absence of a velum is also in *Elpidia* a secondary feature.

(4) Circum-oral papillae. A ring of often inconspicuous papillae surrounds the tentacle crown in *Deima, Benthogone,* and *Benthodytes.* Its (at least partial) presence has been established for all the species, except *Benthodytes superba.*

Circum-oral papillae have not been found outside these three genera. *Ilyodaemon abstrusus,* which also has circum-oral papillae, is here transferred to *Benthogone,* with which it agrees also in the simply shaped wheels and the high tentacle number.

Only one species of *Benthodytes (B. lingua)* was previously known to possess circum-oral papillae. Post-oral papillae were, however, known from a number of species. The present study confirmed that *B. sanguinolenta* has only post-oral papillae. In all other species the observed post-oral papillae probably form part of a complete ring.

A contractile oral membrane is known to accompany the ring of circum-oral papillae in *Deima validum, Benthogone rosea, Benthodytes incerta, B. lingua,* and *B. typica.* The membrane is inserted on the internal side of the ring of papillae and may be narrowed to a small opening through contraction of a sphincter muscle, thus covering the whole of the tentacle crown. As the membrane is visible only when somewhat contracted, it may be present in all species with circum-oral papillae.

The presence of circum-oral papillae together with a sphincter muscle is a remarkable similarity between these genera which belong to three different families.

The tentacles

The tentacles show a variation of taxonomic significance both in number and shape.

(1) Number. The Deimatidae, Laetmogonidae, and Psychropotidae all show a variation of 15–20 tentacles. The whole variation in number may be found within one and the same species *(Orphnurgus glaber, Benthogone rosea, Benthodytes typica),* but usually the number is species constant. Similarity in number may reflect taxonomic relationship.

All laetmogonids with 15 tentacles belong to *Laetmogone,* in which there are only two exceptions to this number: *L. theeli* (20) and *L. interjacens* (15–17). The latter resembles *Benthogone* (with 15–20 tentacles) also in body form and in the shape of the deposits.

A constant number of 15 tentacles is in *Benthodytes* combined with the presence of cross-shaped deposits with a bipartite apophysis. Higher tentacle numbers are found in the two species with reduced rod-shaped deposits, *B. typica* (15–20) and *B. sanguinolenta* (18).

The species of *Psychropotes* have 16 tentacles, except *P. depressa* and *P. longicauda,* both with 18 tentacles. The closely related genus, *Psycheotrephes,* has similar tentacle numbers: *P. magna* (16–18) and *P. recta* (16).

Juvenile tentacle numbers are found in two species of Psychropotidae: *Psychropotes loveni* (10–12) and *Psycheotrephes exigua* (10). Both species were erected on small-sized specimens, which may not have attained the full tentacle number of the species. Specimens of *Psychropotes depressa* (1.7–12.0 cm long) showed an increase in tentacle number from 10 to 18 (Fig. 44). A similar increase was found in *P. longicauda.*

A juvenile tentacle number characterizes the whole family Elpidiidae. The only exceptions to the number of 10 tentacles are provided by the genus *Achlyonice* (10–12) and the species *Peniagone islandica* (8).

(2) Shape. Differences in the shape of the tentacle discs are probably correlated with different modes of food uptake (p. 196). Besides, they may reflect taxonomic relationship. But unfortunately the tentacle discs are often so contracted that their shape cannot be made out.

Deimatidae. In the present work, a generic importance has been attached to the two distinct types of tentacle in this family (p. 16). *Deima* and *Oneirophanta* have rounded tentacle discs with a smooth surface and with the margin smooth or provided with subglobular or digitiform processes (Pl. VIII: 1–3). *Orphnurgus* has tentacle discs with conspicuous papillae on the surface and branched (but contractile) processes on the margin (Pl. VIII: 5–7). The tentacles of the young of the brood-protecting subspecies *Oneirophanta mutabilis affinis* (Pl. VIII: 4) resemble those of the genus *Orphnurgus.*

Laetmogonidae. Although the tentacles show less conspicuous differences than in the Deimatidae, there seems to be some correlation between tentacle type and taxonomic affinity.

In *Benthogone rosea* and *B. fragilis* (Pl. VIII: 11) the discs are covered with conspicuous papillae arranged in radial fields which may proceed into marginal processes. Such processes are present in the Indian Ocean specimen of *B. rosea* from *Galathea* St. 241 and in *B. fragilis* from *Galathea* St. 324. In the examined Atlantic specimens of *B. rosea* the surface of the tentacle discs is likewise covered with conspicuous papillae, but the margin is more smooth, probably due to retraction of the processes.

In *Laetmogone violacea* (Pl. VIII: 8), *L. wyvillethomsoni,* and *L. theeli* the discs have a smooth surface and a smooth margin.

In *L. maculata* (Pl. VIII: 9–10), *L. fimbriata,* and *L. biserialis* the discs have a smooth surface (although often wrinkled due to contraction). The edge of the disc is smooth or irregularly lobated. The tentacles of *L. ijimai* probably show the same variation.

Pannychia and *Apodogaster* (the unidentified species from the Kermadec Trench) have tentacle discs with retractile papillae on the surface and well-developed marginal processes.

Psychropotidae. *Psychropotes* (Pl. VII: 6) and *Psycheotrephes* have rounded, vaulted discs with subglobular marginal knobs. The discs are of a fixed shape, and two species only (*Psychropotes depressa* and *P. semperiana*) show retractility of the discs into the tentacle stalk.

Benthodytes (Pl. IX: 1–7, Fig. 36) has large and flat discs which in all the species are retractile into the tentacle stalk. Species differences are present but difficult to make out because the tentacles are soft and changeable in shape. In addition to the retractility of the single tentacles, the whole crown can be concealed under a contractile oral membrane, present inside the circumoral ring of papillae (p. 191).

Young specimens of *Benthodytes* have more regularly shaped discs, reminiscent of those of *Psychropotes* and *Psycheotrephes*.

Elpidiidae. *Elpidia* (Pl. X: 11–13) has not only a unique type of deposit but also of tentacle. The discs bear a number of marginal processes of which 1–3 aboral pairs are often extended to a great length.

Kolga (Pl. IX: 8) and *Irpa* have in common another characteristic type of tentacle with 5–7 marginal lobes, each divided into 3 lobuli.

A third type of tentacle, with a pair of lobes on the aboral margin of the discs, is found in a number of species of *Peniagone* (Pl. X: 1–5, 7–8), *Achlyonice* (Pl. X: 9), *Amperima, Ellipinion,* and *Scotoplanes* (Pl. IX: 9). The lobes are particularly long and slender in *Peniagone diaphana* (Pl. X: 7–8), whereas in other species (e. g. *Amperima naresi,* Pl. X: 6) they are barely distinguishable. The fact that the lobes are usually contractile (cf. the tentacles illustrated for *Peniagone azorica* and *P. convexa*) suggests that bilobed tentacle discs occur in even more species than known at present. However, some species (e. g. *Ellipinion galatheae,* Pl. X: 10) do not possess tentacles of this type.

The alimentary canal

The Elasipoda, as usual in the holothurians, has a looped intestine consisting of three parts. A remarkable variation in the gross morphology is the highly distensible rectum, usually provided with a large caecum, in most of the elpidiid genera (*Amperima, Ellipinion, Scotoplanes, Kolga, Elpidia,* and *Achlyonice*).

The caecum is absent in the primitive genera *Psychrelpidia* and *Peniagone.* Of the specialized genera, only *Irpa* seems to have a small rectum devoid of a caecum. The state of the rectum is unknown in *Rhipidothuria.*

Ludwig (1889–1892) suggested that the caecum of the Elpidiidae is a rudiment of a respiratory tree. This view was opposed by Ekman (1926) who pointed out that the origin of the caecum from the ventral side of the rectum, as well as the fact that it is almost without exception stuffed with mud, contradicts such a derivation.

The absence of the caecum in the primitive genera of the family is a further indication that it is not a rudiment but an organ developed within this particular family. The species of the Elpidiidae are notable for their high buoyancy. Possibly, they are unable to keep to the sea floor without a considerable amount of bottom material stored in their intestinal canal. The function of the caecum may be that of increasing the volume of the intestinal canal and thereby the specific gravity of the animals.

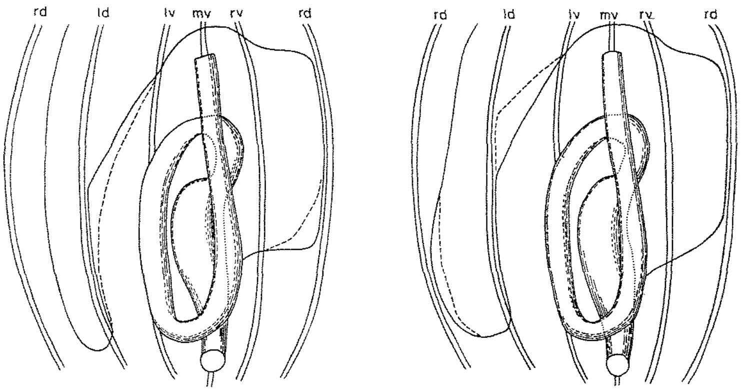
The mesentery

As already noted by Théel (1882), the mesentery of the Elasipoda differs from that of other holothurians in having a dorsal attachment throughout its length. Ekman (1926) proved that this course of the mesentery was common to all five families of Elasipoda – the three parts of the mesentery being attached to the mid-dorsal, left-dorsal, and right-dorsal interradius, respectively. (Only posteriorly, the third part may have a ventral attachment).

In all other holothurians the three parts of the mesentery are attached to the mid-dorsal, left-dorsal, and right-ventral interradius, respectively. This even applies to the Apoda in which the intestine has almost completely lost its looping.

Ekman (1926) suggested that the dorsal attachment of the mesentery throughout its length serves to increase the oxygen supply to the intestine, which in the absence of respiratory trees is supplied with oxygen mainly from the dorsal body surface.

Fig. 96. *Oneirophanta mutabilis*. Variation in the line of attachment of the mesentery (difference between full-drawn and dotted line) in four specimens from St. 654 (left) and four specimens from St. 716 (right). rd, right dorsal, ld, left dorsal, lv, left ventrolateral, mv, midventral, and rv, right ventrolateral longitudinal muscle.



However, the discovery of the peculiar walking-mechanism in the Elasipoda (p. 205) suggests another explanation of the dorsal attachment of the mesentery: An intestine resting upon the ventral body wall might interfere with the function of the intradermal pockets responsible for the protraction of the tubefeet.

Differences in the course of attachment of the mesentery on the body wall might, according to Ekman, distinguish genera and even species. Ekman illustrated the course in a number of species, but without stating number of specimens examined. The differences illustrated might, therefore, represent individual rather than specific differences.

In order to estimate the range of intraspecific variation in the course of the mesentery, four specimens of *Oneirophanta mutabilis* from St. 654 (Kermadec Trench) and four specimens from St. 716 (eastern Pacific) were examined (Fig. 96). At each station a remarkable variation was found. There was also a small, but possibly consistent difference between the specimens from the two stations.

The first part of the mesentery in all specimens from St. 654 ran in the dorsal midline throughout its length. In the specimens from St. 716 the first part of the mesentery started in the dorsal midline, then approached or even touched the right dorsal longitudinal muscle.

The second part of the mesentery in the St. 654 specimens, after having crossed the left dorsal muscle, either proceeded obliquely forwards towards the left ventral muscle, or followed the left dorsal muscle up to about half its length. In the St. 716 specimens the second part followed the left dorsal muscle from a little more than half, to about $^3/_4$ its length.

The mesentery, after having crossed the left ventral muscle, passed uninterruptedly across the ventral side of the body wall until it reached the right dorsal muscle. Ekman failed to find this part of the mesentery in *Oneirophanta mutabilis* and suggested that the absence distinguished the family Deimatidae from the Laetmogonidae. Actually, already Hérouard (1902, pp. 34–35) found that the genus *Deima* has an uninterrupted mesentery.

The third part of the mesentery was attached close to the right dorsal muscle for about half its length; then the attachment ran to the right ventral interradius close to the midventral muscle. The course of the third part showed only little variation in the examined *Galathea* specimens.

The mesentery formed a continuous membrane, except for the rectal part, which was disintegrated into single threads. The membrane was perforated throughout its length in the St. 654 specimens. In the St. 716 specimens the mesentery was unperforated, at least in its first part.

The variation in the course of the mesentery in *O. mutabilis* is almost the largest possible for a three-looped intestine with dorsal attachment of all three parts of the mesentery. In view of this large variation it is not advisable to introduce possible average specific or subspecific differences in the course of the mesentery into the taxonomy of the holothurians. Similarly, the great intraspecific variation in the degree of perforation of the mesentery shows that also this feature is of limited taxonomic value.

The disintegration of the mesentery of the Elpidiidae into single threads throughout its length, in contrast to the membranaceous mesentery in the four other families, remains as the only difference of taxonomic significance shown by the mesentery of the Elasipoda.

Heding (1935, pl. IX) illustrated the course of the mesentery in eleven species of Molpadonia, accepting Ekman's view on the significance of this feature in characterizing species. Ten species were illustrated by one drawing each, with no comments on the possible range of intraspecific variation. The variability in the course of the mesentery in the Elasipoda makes it unlikely that the differences illustrated by Heding are taxonomically valid.

The external morphology of the gonads

The present chapter deals with the taxonomic significance of the external morphology of the gonads. The reproductive biology of the species is considered elsewhere (pp. 196–204).

Deimatidae (Pl. XI: 1–4). Each of the two gonads consists of a single cluster of unbranched, elongated sac-shaped tubules. By this feature the gonads differ from those of the other elasipod families.

The gonads are similar in the two sexes, except that the tubules are more numerous and slender in the males.

Deima validum has ovaries with 3–7 tubules and testes with 5–15 tubules on each side. Théel (1882) illustrated (for *D. fastosum*) testes with slender tubules possessing a number of globular distensions. Such tubules were not present in any of the *Galathea* specimens.

Oneirophanta mutabilis. The ovaries showed the following variation in number of tubules on each side: Western Indian Ocean (3 specimens), 3–5; Kermadec Trench, Sts. 663 and 664 (4 specimens), 3–5; Kermadec Trench, St. 654 (5 specimens), 5–13; eastern Pacific, St. 716 (11 specimens), 2–4.

Théel (1882) found the variation in number of ovarian tubules to be 3–9 on each side (numbers not specified for each locality).

The testes were examined in one specimen from St. 192, six from St. 654, and 12 from St. 716. At Sts. 192 and 716 the testes consisted of two clusters of numerous slender tubules, usually somewhat dilated at the end. This type was also reported from the *Challenger* specimens.

In the specimens from St. 654 the testes were similar to the ovaries in external morphology. The tubules were thick and few in number (7–10 on each side in specimens 6.0–9.5 cm long, and 4 in a 5.0 cm long specimen). There were no males among the specimens from the two other Kermadec Trench stations.

The gonads in *Oneirophanta setigera* and *Orphnurgus glaber* agreed in morphology with those of *Deima validum* and *Oneirophanta mutabilis.*

Laetmogonidae (Pl. XI: 9–12). The gonads consist on each side of one or more clusters of branched tubules and thus differ distinctly from the gonads of the Deimatidae. There is also some intra-family variation in the morphology. However, too few species were examined to permit a demonstration of generic or specific differences.

Psychropotidae (Pl. XII: 1–9). The cross-bearing species of *Benthodytes* have ovaries with a few groups of large and feebly subdivided lobes placed along an undivided duct on each side. *B. sanguinolenta* and *B. typica,* which also in other respects stand apart in the genus, have branched ovaries with follicles opening directly into the ducts. *Psycheotrephes magna* and *Psychropotes longicauda* have ovaries with a few large, rounded or somewhat elongated sacs opening into an undivided duct on each side. In *Psychropotes depressa* the sacs are smaller, more numerous, and closely set – the ovary attaining the shape of a corncob. In *P. verrucosa, P. belyaevi,* and *P. semperiana* the corncob-shaped fertile part of the ovary is very thick and covered with small, closely set lobules. The ovaries of the Psychropotidae contain the largest eggs known in holothurians (pp. 202–203).

The testes consist of groups of tubules opening into a common duct on each side. The length of the testes may vary within a species. However, the extreme length in *B. sanguinolenta* is probably a specific character.

Elpidiidae (Pl. XII: 10–11). The paired gonads in *Psychrelpidia* and *Peniagone,* in contrast to the unpaired gonads in the other genera (unknown only in *Rhipidothuria),* is one of the features pointing to an original position of these two genera within the family.

The unpaired gonad is probably always the left one. (Due to a strong reduction of the dorsal mesentery its position cannot always be established).

The gonads usually consist of clusters of tubules opening into a duct of varying length. A deviating type is found in the two closely related genera *Kolga* and *Irpa,* in which the gonads consist of a ramified duct ending in long and slender fertile tubules.

In agreement with the small size attained by the eggs, the ovaries resemble the testes in external morphology.

Conclusion

The present investigation confirmed the view that the calcareous deposits generally provide the best taxonomic characters. Higher categories such as the suborder Psychropotina and the family Laetmogonidae within the suborder Deimatina are characterized, in particular, by their deposit type. Differences between species are often most clearly shown by their deposits, although different species may have identical deposits. The intraspecific variation is often great, and in many species a geographic and local variation can be distinguished.

Differences in number, shape, and arrangement of tubefeet and papillae may similarly distinguish families, genera, species, and intraspecific categories. For the analysis of intraspecific variation numerical differences are especially important, as this type of variation is generally quantitative rather than qualitative in character. Numerical characters in holothurians are practically only provided by the number of ambulacral appendages and by the spoke number in the wheel-shaped deposits.

The number and shape of the tentacles may distinguish genera and species groups within genera, but are generally of little value in characterizing species. A juvenile tentacle number (10–12) distinguishes the Elpidiidae.

Differences in body shape, including breadth of lateral brim and shape and size of velum, depend on the degree of contraction and state of preservation and should, therefore, be used with reservation in species distinctions.

A highly distensible rectum with a caecum is found in most genera of Elpidiidae. The absence of the caecum in the primitive genera *Psychrelpidia* and *Peniagone* suggests that the caecum is a specialized feature developed in this family. The caecum may serve to increase the specific gravity of these extremely buoyant animals, thus preventing them from being swept from the bottom.

The dorsal attachment of the whole mesentery characterizes the order Elasipoda. Differences in the course of the mesentery within the Elasipoda are without taxonomic significance.

The external morphology of the gonads may be characteristic of groups of species, and even of a family (Deimatidae). However, their different appearance according to the degree of ripeness makes the demonstration of species differences doubtful.

B. BIOLOGY

Feeding

The increasing dominance of the holothurians with depth is accounted for by deposit-feeding forms. The filter-feeding order, Dendrochirota, is almost entirely absent in the deep sea. The faculty of the holothurians of ingesting large amounts of sediment, combined with their low food requirements due to their low content of organic matter, makes this group well fitted for subsisting on the nutrient-poor deep-sea sediments.

The majority of the deep-sea holothurians seem to spend their life upon the surface of the bottom, and not buried within it. This is suggested by their ventrally turned tentacle crown and their flattened ventrum, and it has in recent time been confirmed by deep-sea photography. The surface-dwelling holothurians include probably the whole order Elasipoda, most of the Synallactidae, and *Hadalothuria,* the only hadal representative of the order Molpadonia. *Hadalothuria,* which differs from other Molpadonia in having a ventrally turned tentacle crown, has been photographed crawling on the bottom (Lemche *et al.* in press).

A surface-dwelling habit seems to offer a particular advantage in the deep sea where the nutrients are present as a thin surface layer of the sediments and where it may be necessary to cover a large area in search of food. Life upon the surface is favoured by the scarcity of carnivores, in particular of fishes. The latter are likely to represent the chief potential enemies of holothurians.

The highest degree of adaptation for feeding on large amounts of sediment is reached by the Elpidiidae. Many of these have the lowest content of organic matter in all echinoderms and their alimentary canal is often excessively developed. Their enormous dominance in the trenches is in agreement with the large supply of sediments to this environment. It is interesting that one of the dominating hadal species, *Scotoplanes globosa* (or its close relative, *S. clarki)* is also abundant in the much shallower San Diego Trough (depth 930–1420 m) where similar sedimentary conditions prevail. This trough receives large amounts of sediment through the canyons transecting the southern California continental borderland. Bathyscaphe observations (Barham *et al.* 1967) showed that *Scotoplanes* was particularly abundant (up to 15/m^2) at the base of the canyons where sediments accumulated.

There is also evidence that the dominance of *Elpidia* at hadal depths is conditioned by a rich supply of sediments (p. 173).

Sokolova (1958) pointed out that differences in the shape of the tentacle discs are likely to be correlated with a different degree of selectivity in food uptake – tentacles with well-developed marginal processes on the discs (e. g. *Elpidia)* being able to pick up single food particles from the bottom, while tentacles with more undifferentiated discs (e. g. *Psychropotes)* convey the surface layer of the sediment indiscriminately to the mouth. Differences in type of intestinal content correlated with the different types of tentacle were, however, not demonstrated.

Samples of the content of the anteriormost part of the gut in 16 species of Elasipoda from the *Galathea* (belonging to all four benthic families and representing the different types of tentacle found in the order) likewise failed to reveal any correlation between tentacle type and type of intestinal content. The intestinal content was mostly fine-grained and undeterminable, except for scattered foraminiferan shells. There was no indication that the Elasipoda are able to select smaller animals, e. g. small crustaceans or molluscs.

A selectivity in food uptake is suggested not only by the different shape of the tentacles, but also by the different degree of filling of the intestine in species living on the same type of sediment. Thus, in *Amperima naresi, Scotoplanes globosa,* and *S. clarki* the intestine was so stuffed with bottom material that it occupied the entire coelomic cavity, while in *Elpidia glacialis* (taken simultaneously with the two former species) the intestine was much less filled. This suggests a higher nutritive value of the material ingested by *E. glacialis,* which is in agreement with the fact that its tentacles are more specialized than those of the other species mentioned. The tentacles of *Elpidia,* with their long digitiform processes, may be capable of selective feeding, for instance by avoiding the ingestion of larger particles devoid of nutritive value. On the other hand, the supposed differences in the nutritive value of the ingested sediment may also be due to the *Elpidia* specimens grazing on patches on the sea floor with an especially rich flora of bacteria (Lemche *et al.* in press).

Reproduction

1. Introductory remarks.

The taxonomic significance of the variation in external morphology of the gonads is considered elsewhere (pp. 194–195). The present chapter deals with the reproductive biology of the species, with special regard to the following aspects:

(1) Developmental types, as indicated by the egg size. Very little direct information is available on the type of larval development in deep-sea animals. Mortensen (1921) reared pelagic larvae from specimens of the echinoid *Laganum diplopora* taken at a depth of 800 m off Japan. He maintained (without stating the egg diameter) that "judging from the character of the eggs, many other deep-sea forms must have pelagic larvae" (l. c., p. 249).

As hardly any direct observations exist, conclusions regarding developmental types have to be made from the egg diameter attained. Thorson (1952) found that in littoral-sublittoral echinoderms eggs measuring 0.04–0.15 mm yield planktotrophic larvae, whereas eggs measuring 0.18–1.00 mm yield lecitotrophic larvae. Eggs of intermediate size lead to either of the two types, or to a combination of both.

Schoener (1972) compared the number and size of the eggs in five species of deep-sea ophiuroids with those of shallow water species with known type of development. One *Ophiura ljungmani* (depth 2178 m) contained 93000 eggs, with a maximum diameter of 0.08 mm. According to Schoener, both number and size indicate that the species has pelagic larvae. The reproductive habits of the other four species were less certain.

A lecitotrophic development does not exclude the possibility of a planktonic stage. Thus, the larva of *Psolus phantapus,* emerging from 0.59 mm large eggs, has been taken in the plankton (Thorson 1946).

Ockelmann (1965) similarly demonstrated the presence of three types of larval development in marine bivalves, each type corresponding to a definite interval in egg size: 1) planktotrophic development (egg size 0.040–0.085 mm); 2) lecitotrophic development with a short pelagic stage which is independent of food uptake from the plankton (egg size 0.09–0.14 mm); 3) direct development, often combined with brood protection (egg size 0.15–0.20 mm).

The second type of development predominates among the bivalves of the deep sea (Ockelmann 1965, Knudsen 1970). A direct development seems to be rare, and brood protection even more so.

(2) Histology of the gonads in relation to sexual phase. Histological changes in the gonads in connection with the sexual cycle have been described in detail for various sublittoral species of echinoids and asteroids.

Giard (1877) observed, in the gonads of sea urchins, a peculiar type of large nutritive cells proliferating into the lumen of the gonads after spawning. Each cell contained a large vacuole (erroneously interpreted as a hypertrophied nucleus) and a number of small cytoplasmic globules of reserve which were later utilized by the growing gametocytes.

Caullery & Siedlecki (1903) and Caullery (1925) found that not only did these vacuolated cells perform a nutritive function, but they were also phagocytic, ingesting the eggs and sperm which remain in the gonads after each spawning.

The nutritive-phagocytic cells have subsequently been demonstrated in many species of echinoids and may be universally present in this class. Holland & Giese (1965), by means of an autoradiographic technique, examined the histological changes in the gonads of *Strongylocentrotus purpuratus,* including the functional relations of the nutritive phagocytes.

The nutritive phagocytes, after proliferation into the lumen of the empty gonads, increase in size due to the development of a large vacuole and the accumulation of cytoplasmic globules of reserve. Concurrently with the transfer of nutrients from the cytoplasmic globules to the sexual cells, the nutritive phagocytes shrink, although their vacuoles are usually retained. The tissue in the deglobulated phase has a net-like appearance although it probably still consists of individual, vacuolated cells.

Nutritive phagocytes are also commonly present in the gonads of asteroids (Cognetti & Delavault 1962). However, in some species they appear to be absent, their nutritive function being taken over by nutrients stored in the pyloric caeca (Pearse 1965, Mauzey 1966).

Seasonal changes in the gonads of the holothurian *Stichopus japonicus* were described by Tanaka (1958). Although no mention was made of a nutritive-phagocytic tissue, its presence is indicated in a photograph of the ovary in the "recovery stage" (l. c., pl. I: 2).

(3) Reproductive periodicity. This cannot be conclusively demonstrated without samples from one locality throughout the year. The materials collected by the various deep-sea expeditions are, therefore, not well suited for such an examination, and it is not surprising that little information on this subject can be gathered from the literature.

In a population of the sea urchin *Allocentrotus fragilis,* from c. 150 m depth, Boolootian *et al.* (1959) demonstrated a distinct breeding-cycle, probably correlated with planktonic larvae utilizing a phytoplankton bloom. This species occurs down to 840 m, but it is not known whether the reproductive periodicity applies to the whole depth range of the species.

Madsen (1961b) stated that, although variations in the annual food supply to the bottom might induce a rhythmic spawning in deep-sea animals, there was still nothing to indicate that this really takes place. An examination of the gonads of the Porcellanasteridae suggested that they produce eggs throughout the year.

Wolff (1962), on the other hand, in a material of North Atlantic bathyal and abyssal isopods, found that the large majority of the females had feebly developed brood sacs. The fact that the specimens were taken mainly during the summer season indicated that most of the species develop their young during the winter months. Wolff suggested that this periodicity of spawning was due to the origin of the North Atlantic deep-sea isopods from Arctic shallow water forms.

George & Menzies (1967) suspected a rhythmic spawning at bathyal and abyssal depths in three Antarctic species of the isopod genus *Storthyngura.* However, too few specimens were examined to permit reliable conclusions.

Schoener (1968) produced evidence for a winter spawning in two North Atlantic species of abyssal ophiurans. Samples taken during the winter contained adult specimens with well-developed gonads, while summer samples from the same locality contained adult specimens with feebly developed gonads together with juvenile specimens.

Sanders & Hessler (1969), on the other hand, found indications of a continuous reproduction throughout the year in the bivalve *Nucula cancellata* and in a species of the isopod genus *Ilyarachna,* both from bathyal depths in the North Atlantic.

2. The material examined.

The histology of the gonads was examined by means of sections of 23 specimens, belonging to 10 species of Deimatidae, Psychropotidae, and Elpidiidae. The purpose was a comparison with the conditions known from various shallow-water echinoderms (the gonadal histology of deep-sea echinoderms has not previously been examined). A large-scale examination of the histological changes in the gonads accompanying the different sexual phases has not been attempted. The results of such an examination would be of doubtful value in the absence of samples taken from the same population at different seasons. For the same reason, no measurements were made of the size distribution of the eggs in each ovary.

The maximum egg size was established in representatives of all the four benthic families of Elasipoda.

The results permit only few conclusions regarding the presence or absence of a reproductive periodicity. An aperiodic egg production is suggested where the maximum egg size varies conspicuously from one specimen to another. On the other hand, the presence of a reproductive periodicity cannot without further proof be concluded from the presence of eggs of maximum size in all the females of a population.

Deimatidae. The eggs reach a diameter of 0.8–0.9 mm in both *Deima validum* and *Oneirophanta mutabilis.* In *O. setigera* and *Orphnurgus glaber* the eggs measured up to 0.3 mm; but these eggs may not represent the maximum size in the species – the material comprising only two and one adult females, respectively.

Deima validum. Of the total of 19 specimens from the western Indian Ocean, 12 had empty gonads with thin and transparent walls. These specimens, 2.3–12.0 cm long, probably comprised juveniles, as well as adult males and females in an inactive sexual phase. In the remaining seven specimens eggs could be seen on external inspection of the ovaries. The eggs varied in maximum size from one specimen to another (Table 18).

Table 18. *Deima validum.* Maximum egg size in the egg-bearing females from the Indian Ocean.

Station	Length of specimens cm	Maximum egg size mm
190	5.0	0.1
193	8.0	0.8
217	5.0	0.4
234	6.0	0.1
–	11.0	0.6
235	9.0	0.4
279	5.0	0.1

In all these females the eggs were few and very spaced in position. While ovaries with eggs not exceeding 0.1 mm in diameter might be at the onset of a new sexual phase, ovaries with scattered eggs of larger size were probably at a post-spawning stage, with a few unspawned eggs remaining.

None of the gonads with sexual products were testes. Apparently, all the adult males were in an inactive sexual phase.

The fact that all the specimens from the western Indian Ocean were emptied of sexual products (with the exception of some relict ova in a few specimens) or were at the very beginning of egg development suggests a periodicity of spawning. The specimens were all taken during a relatively short period (3.II–10.IV).

Histological examination was made of the ovaries of four specimens with different maximum egg size: 0.1 mm (St. 234), 0.4 mm (St. 235), 0.6 mm (St. 234), and 0.8 mm (St. 193).

In the ovary with eggs up to 0.1 mm all the eggs were attached to the ovarian wall, being covered with the inner epithelium of the gonad. The lumen of the gonad was empty, except for the presence of inconspicuous patches of a reticular tissue, probably representing remnants of a nutritive-phagocytic tissue similar to that found in echinoid and asteroid gonads.

In the ovaries with eggs up to 0.4 and 0.6 mm (Pl. XIII: 1–2) some of the larger eggs were loose in the lumen of the gonad. Most of them were necrotic, with the yolk more or less vacuolated and containing fine, basophilic grains, and with disintegrated nuclei. Many of these eggs were invaded by phagocytes either at their periphery, or throughout. The phagocytes had conspicuous, basophilic nuclei and a vacuolated cytoplasm. Patches of a reticular tissue were present in these gonads also.

In the ovary with eggs up to 0.8 mm there was practically no phagocytosis of eggs. Patches of a reticular tissue were present, especially at the distal end of the gonadal tube.

Deima validum thus agrees with the echinoids and most of the asteroids in the role played by the nutritive phagocytes. These cells first ingest the relict ova and afterwards change into a reticular tissue occupying part of the lumen of the gonad.

The lively phagocytosis of the eggs in two of the three ovaries with scattered large eggs confirms that these ovaries were in a post-spawning phase.

Oneirophanta mutabilis mutabilis. The 21 specimens examined comprised 12 females (4.0–10.0 cm long), all of which contained eggs (Table 19), 8 males (5.0–10.0 cm long), and one specimen (5.0 cm long) with feebly developed gonads, indeterminable to sex on external inspection.

Table 19. *Oneirophanta mutabilis mutabilis.* Maximum egg size in the *Galathea* specimens.

Station	Length of specimens cm	Maximum egg size mm
192	8.0	0.8
–	9.0	0.9
217	10.0	0.5
654	4.0	0.07
–	6.5	0.3
–	7.5	0.8
–	7.5	0.9
–	7.5	0.9
663	5.5	0.05
664	5.5	0.2
–	6.0	0.15
–	7.0	0.5

Both in the western Indian Ocean and the Kermadec Trench the eggs reach a diameter of 0.9 mm. Sexual ripeness seems to be attained at a body size of 7.5 cm. While five of the six specimens measuring 7.5–10.0 cm had eggs up to 0.9 mm in diameter, the six specimens measuring 4.0–7.0 cm had eggs of smaller maximum size. The latter specimens show an increase in egg size with the size of the specimens, which confirms that they are developing their first batch of eggs.

In the ovaries with maximum egg size up to 0.2 mm the eggs were spaced in position on the ovarian wall. Ovaries with maximum egg size of 0.3 mm and more were usually completely filled with eggs.

The specimens of *Oneirophanta mutabilis* thus formed a marked contrast to those of *Deima validum,* in which only one out of eight females had eggs reaching the maximum size in the species and in which none of the ovaries were filled with eggs.

Histological examination was made of the ovary of the specimen from St. 192 in which the eggs measured up to 0.8 mm in diameter (Pl. XIII: 3). Eggs up to 0.4 mm in diameter were present on the ovarian wall. The basophilic egg membrane was strongly developed towards the ovarian wall, and very thin towards the lumen, where it was covered with the inner epithelium of the ovary. Some of the eggs were crowded with phagocytes. Assemblages of phagocytes, apparently from eggs with a disintegrated egg membrane, were seen, in some places, to pass gradually into the fine reticular tissue which filled a large part of the ovarian lumen.

Eggs of a larger size, and some of smaller size, were found loose in the lumen of the ovary. These eggs showed no sign of phagocytosis or disintegration.

Oneirophanta mutabilis affinis. A total of 27 specimens from St. 716, measuring 4.0–9.5 cm, were examined. Specimens larger than 5 cm could be determined to sex on external inspection of the gonads. There were 11 females and 12 males – both sexes ranging in size from 5.0 to 9.5 cm.

As stated previously (Hansen 1968) the specimens from this station are remarkable in having intra-ovarian brood protection.

The young ranged in size from 7 to 30 mm (Table 20). The largest young thus approached the size of the smallest free-living specimens (40 mm).

Table 20. *Oneirophanta mutabilis affinis.* Number and size of young in the females from St. 716.

Mother	Young	
Length mm	Number	Length mm
50	0	–
55	0	–
60	0	–
70	6	7–8
75	0	–
75	2	30
80	2	13–24
85	4	16–19
90	0	–
90	8	15–19
95	1	10

The ovaries with no young were small in size (even in the 75 mm long specimen the tubules were only up to 2 mm long). An exception was the 90 mm long empty specimen, in which the ovarian tubules were up to 20 mm long. This specimen was, probably, in a post-spawning phase, while the other empty specimens were juveniles which had not yet developed their first batch of young. It also differed from the other specimens by its large genital opening – a further indication that it had recently borne its young.

Very scattered eggs were present on the ovarian wall in all the specimens which did not contain any young. In the 90 mm long specimen the eggs were up to 0.2 mm in diameter, while in the other empty specimens they did not exceed 0.1 mm.

The fact that all the adult females had either large young in their ovaries, or had recently borne, suggests a reproductive periodicity at this locality. This was further supported by the histological examination of the gonads (see below). *Galathea* St. 716 was situated beneath the Costa Rica Dome where an intense upwelling takes place from December to May (Smith 1968). The specimens were taken at the end of the upwelling season (on May 6), which indicates that the development of the young is correlated with a period of a rich production in the surface plankton.

The young in their first stages possibly eat up the undeveloping eggs. But since no eggs were found in the examined young-containing ovaries the young before they are 7 mm long apparently change to nutrients secreted into the ovary. The young are not in any way attached to the ovarian wall.

Usually, only one young is present in each sac. However, in the female with eight young, five were contained in the same sac. In all the ovaries some sacs are empty. The young in each ovary are usually rather equal in size, which indicates that they all derive from one fertilization.

Histological examination was made of five ovaries and one testis.

In the 9.0 cm long female with empty ovaries the ovarian wall showed conspicuous proliferations of large, highly vacuolated cells with clearly defined nuclei and distinct cell boundaries (Pl. XIII: 4–5). The vacuolated tissue in some places passed gradually into the connective tissue of the ovarian wall; in other places it was separated from the connective tissue by a distinct boundary. Apparently, the vacuolated cells proliferate from limited places and spread from there over the remaining part of the ovarian wall. The proliferations are covered with the uninterrupted inner epithelium of the ovary.

The extremely scattered eggs were situated between the vacuolated tissue and the inner epithelium. They measured up to 0.2 mm in diameter. The basophilic egg membrane was strongly developed towards the underlying vacuolated tissue. Most of the larger eggs were invaded by phagocytes with a vacuolated cytoplasm; these cells are probably identical with the vacuolated cells of the ovarian wall. There was almost no trace of the fine reticular tissue which was well developed in the specimen of *Oneirophanta m. mutabilis* from St. 192.

The lively phagocytosis of the eggs indicates that the eggs did not belong to a new batch.

In the specimen with young measuring 7–8 mm the ovarian wall likewise showed proliferations of vacuolated tissue (Pl. XIII: 6). However, the cells had to some degree disintegrated, their vacuoli being ruptured. Some of the proliferations had almost completely collapsed; their epithelium, however, was uninterrupted. Most of the few eggs remaining were invaded by phagocytes (the two eggs seen in the photograph are not). The reticular tissue had completely disappeared from the lumen of the ovary.

In the 8.5 cm long specimen with young 16–19 mm long the proliferations had almost completely collapsed and contained practically no vacuolated tissue (Pl. XIII: 7). Phagocytes were present in the very few eggs remaining.

The 6.0 cm long specimen with empty ovaries showed well-developed proliferations. As in the specimen with the smallest young the vacuolated cells of the proliferations had somewhat disintegrated, but none of the proliferations had collapsed.

In the 5.5 cm long female the ovarian wall showed no proliferations of vacuolated tissue.

The vacuolated tissue probably acts as a store which provides nutrients for the growing embryos. It develops shortly after spawning and collapses with the growth of the young. The fact that the proliferations had completely collapsed already in the sections of the ovary with 16–19 mm long embryos does not exclude the possibility that they are still present in other parts of the ovary.

The presence of proliferations with somewhat disintegrated vacuolated cells in the 6.0 cm long female suggests that this specimen was prepared for the development of a batch of young, but had failed to carry it through because of its small size.

Histological sections of a 9.0 cm long male showed testicular tissue in the process of phagocytosis (Pl. XIII: 8–9). Ingested heads of spermatozoa were present in the cytoplasm of many of the vacuolated phagocytes, but no free spermatozoa were present. Thus, also the testes appeared to be in a post-spawning phase.

The developmental stages of the young. The presence of a gradual series of young ranging from 7 to 30 mm in length makes it possible to follow the development of the different features. Already the smallest young possess all types of ambulacral appendages.

Tentacles. Of the six smallest young (7–8 mm long) three possessed 5 tentacles, while the other three possessed 2, 3, and 4 tentacles, with small rudiments of additional ones. The 16–19 mm long young had 5–8 tentacles, whereas the young measuring 24 and 30 mm had 10. Since even the smallest free-living specimens had 20 tentacles, the increase in number from 10 to 20 takes place at a body size of 30–40 mm.

The discs of the tentacles (Pl. VIII: 4) are different in structure from those of adult specimens, having papillae on the surface and incisions on the margin. The tentacles probably function as soon as they are formed, taking up nutrient matter secreted from the ovarian wall. This may explain their different structure.

Tubefeet. All the young possessed tubefeet throughout the length of the three ventral radii. Even in the smallest young at least some were provided with sucking-discs. The smallest young had about 5 midventral and 5 pairs of ventrolateral tubefeet. The largest young had about 8 midventral and 14 pairs of ventrolateral tubefeet.

Papillae. Both lateral and dorsal papillae increased in number from about 5 pairs of each in the smallest to 7 pairs in the largest young. While the smallest young had low conical papillae, the two 30 mm long ones had papillae as long as in adult specimens.

Deposits. The two 30 mm long young possessed irregularly branched, delicate rods in the skin. They represent the deeper-lying ramified spicules of adult specimens; the outer, reticulated plates which form a strong armour of the skin in adult specimens had not yet started their formation. (The plates are fully formed in 40 mm long free-living specimens). Strong rods with somewhat irregular terminal ramifications were present in the tubefeet and papillae.

The young smaller than 30 mm lacked deposits altogether.

Intestine forming a straight tube in the 7–8 mm long young, but already at a size of 16 mm the intestinal loop begins its formation.

Although young have not been found in any specimen of *Oneirophanta m. mutabilis,* there are two features suggesting that brood protection occurs also in this subspecies. Firstly, the minimum size was 3.5 cm both in the *Challenger, Galathea,* and *Eltanin* specimens, and smaller specimens have not been recorded from any expedition. Secondly, the subspecies has apparently unusually limited means of dispersal, as evidenced by the pronounced local variation at St. 654 in the Kermadec Trench.

Laetmogonidae. Conspicuous differences in egg size are found in this family, which indicates that different types of larval development are represented.

Laetmogone violacea. The material from *Michael Sars* St. 76 consisted of 18 females (3.5–12.0 cm long), 16 males (4.0–13.5 cm long), and five juveniles (2.2–3.5 cm long) which could not be determined to sex on external inspection of the gonads. The maximum egg size in relation to body size was examined in the 18 females (Fig.

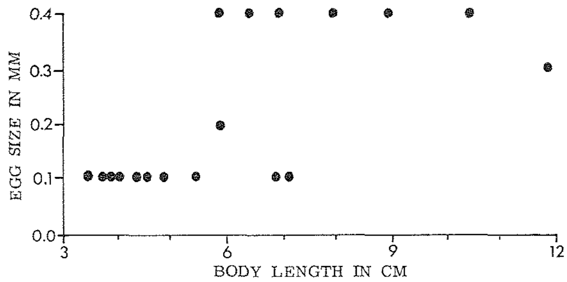


Fig. 97. *Laetmogone violacea.* Maximum egg diameter in relation to body length in 18 specimens from *Michael Sars* St. 76.

97). The growth of the oocytes appears to start at a body length of 5 cm, and already at a body length of 6 cm some of the eggs may have attained the full size of 0.4 mm. Examination of 17 females from other North Atlantic localities confirmed that the maximum egg size in the species is 0.4 mm. The material did not permit conclusions regarding the presence or absence of a reproductive periodicity.

Laetmogone maculata. The specimens from *Valdivia* St. 202 comprised five females and three males; both sexes ranged in size from 6 to 9 cm. A maximum egg size of 0.15 mm was found both in these specimens and in a specimen from off Tasmania.

Laetmogone fimbriata. A 1.8 cm long female taken off Durban had eggs up to 0.19 mm. Two other examined females had eggs of smaller maximum size.

Benthogone rosea. Of nine examined North Atlantic females (8–16 cm long) two had eggs up to 0.9 mm in diameter, and five had eggs up to 0.7–0.8 mm. The size of 0.9 mm probably represents the full size. This size was attained already in an 8 cm long female.

Pannychia moseleyi. Two examined females (fragmentary) had eggs up to 0.4 and 0.8 mm.

The results indicate a correlation between egg size and depth occurrence:

Laetmogone maculata, 0.15 mm in females from 141–293 m (total depth range 141–732 m).

L. fimbriata, 0.19 mm in a female from 412 m (total depth range 164–1300 m).

L. violacea, 0.4 mm in females from 256–1300 m (total depth range 256–1804 m).

Pannychia moseleyi, 0.8 mm in a female from 915–975 m (total depth range 212–2598 m).

Benthogone rosea, 0.9 mm in females from 2480 m (total depth range 1103–2480 m).

The material does not permit conclusions regarding a possible intraspecific correlation between egg size and depth occurrence. In *L. violacea* the eggs reached the same size in specimens from 256 m and 1300 m; the maximum egg size is not known in specimens from the deeper part of the depth range (1300–1804 m).

Psychropotidae. A very large egg size is characteristic of this family.

Benthodytes typica. The maximum egg size was ascertained for 35 females taken by the *Galathea* (Table 21).

Table 21. *Benthodytes typica.* Maximum egg size in 35 *Galathea* specimens.

Station	Length of specimens cm	Maximum egg size mm
186	7	1.6
–	8	0.6
192	7	2.1
217	6	0.4
–	6	0.4
–	6	1.1
–	7	1.6
–	7	0.6
–	7	1.7
–	8	0.3
–	8	1.5
–	8	2.1
–	8	1.6
–	9	0.6
–	9	0.6
–	9	0.2
–	9	1.8
–	10	1.9
281	9	0.5
299	5	0.2
–	6	0.4
–	6	0.6
–	7	0.1
–	7	0.3
–	7	1.7
–	8	0.1
–	8	0.4
–	8	0.2
575	7	1.5
–	7	1.6
–	7	2.2
–	8	2.6
–	9	3.0
–	9	1.9
–	9	2.0

It is remarkable that all the specimens from St. 575 (Tasman Sea) have eggs of large size, while the specimens from St. 299 (Bay of Bengal) have small eggs, with the exception of one specimen with eggs up to 1.7 mm in diameter. This conspicuous difference in egg size may be due to a periodicity of spawning at these two localities. On the other hand, the great variation in maximum egg size at St. 217 (western Indian Ocean) is more consistent with an aperiodic egg production.

The maximum egg size found in the other species of *Benthodytes* is: *B. incerta,* 1.7 mm (seven females examined); *B. lingua,* 2.0 mm (seven females examined); *B. sibogae,* 1.9 mm (four females examined); *B. sanguinolenta,* 2.2 mm (in Ludwig's specimens).

Psycheotrephes exigua. Maximum egg size in three females from the *Galathea:* St. 234 (10 cm long), 0.4 mm; St. 234 (28 cm long), 3.6 mm; St. 663 (30 cm long), 3.7 mm.

Psychropotes longicauda. The distribution of the maximum egg size in the 24 females from the *Galathea* indicates that sexual ripeness is attained at a body length (exclusive of the tail) of about 18 cm (Table 22).

Table 22. *Psychropotes longicauda.* Maximum egg size in the *Galathea* specimens.

Station	Length of specimens cm	Maximum egg size mm
234	12	0.6
–	13	0.4
235	15	0.5
–	18	2.5
601	14	1.0
–	18	3.0
663	6	0.3
–	10	0.5
–	11	0.3
–	14	0.5
–	16	0.9
–	19	4.0
–	20	4.4
–	23	3.9
664	9	1.8
–	13	0.8
–	15	1.0
–	16	2.5
–	17	0.2
–	17	1.1
–	18	0.4
–	18	4.1
–	19	4.0
716	21	0.7

The maximum egg size found in the species of *Psychropotes* with corncob-shaped ovaries is: *P. belyaevi,* 3.6 mm (five females examined); *P. verrucosa,* 3.0 mm (three females examined); *P. depressa,* 1.9 mm (six females examined); *P. semperiana,* 0.5 mm (four females examined).

The eggs of the Psychropotidae are much larger than those of other echinoderms. In bulk, the eggs of *Psychropotes longicauda* (diam. 4.4 mm) surpass those of the hitherto largest known eggs of echinoderms (diam. 1.0 mm) by 85 times.

The fact that a 3.2 cm long specimen of *P. longicauda* was taken in a pelagic net (pp. 124–125) suggests that the enormous egg size in the Psychropotidae is an adaptation which ensures a long pelagic development independent of food uptake from the plankton – thus an adaptation to life in the nutrient-poor deep sea.

A correlation between egg size and depth occurrence is indicated in this family also. Eggs measuring 3–4 mm in diameter were found in the most pronouncedly abyssal species, while eggs of 1.7–2.2 mm were found in the bathyal and bathyal-abyssal species.

Histological examination was made of the ovaries of four specimens, belonging to *Psychropotes depressa, P. semperiana, P. belyaevi,* and *Benthodytes typica.*

The wall of the ovary in the three species of *Psychropotes* consists of a thick layer of highly vacuolated cells. Scattered in this vacuolated tissue are cells with a strongly basophilic nucleus and a cytoplasm stuffed with eosinophilic globules. In the sections of the ovary of *P. depressa* (Pl. XIV: 1–2) the globulated cells were represented by different stages. In most of them the cytoplasm formed a thin layer around the nucleus, but in others the cytoplasm had increased in bulk, and the nucleus had become eccentric in position. The latter cells were especially abundant near and within eggs under disintegration. At a later stage, vacuoli arise in the cytoplasm, while the globules disappear. The cells in this vacuolated and deglobulated state are probably identical with the vacuolated cells of the ovarian wall, the two cell types representing two phases of the nutritive-phagocytic tissue.

The sections from *P. semperiana* and *P. belyaevi* (Pl. XIV: 3–5) showed a vacuolated tissue interspersed with cells with eosinophilic globules; most of the latter cells had a well-developed cytoplasm. There were no transitional stages between the globulated cells and the vacuolated cells of the ovarian wall, and there were no eggs under disintegration.

In *P. belyaevi* the greater part of the vacuolated tissue had undergone some disintegration, resembling that of the vacuolated tissue accompanying the development of the young in *Oneirophanta mutabilis affinis.*

The abundant development of the vacuolated, nutritive tissue probably forms the basis of the enormous size reached by the eggs in these species.

The sectioned ovary of *Benthodytes typica* showed only a feebly developed nutritive-phagocytic tissue.

Elpidiidae. A maximum egg size of about 0.2 mm was found in *Elpidia glacialis* (both in the Kermadec Trench and in the Baffin Bay), *Scotoplanes globosa, S. clarki, Amperima naresi,* and *Peniagone azorica.* The small diameter of the ovarian tubules indicates that this egg size is not appreciably surpassed in other elpidiids.

Although the eggs are much smaller than those of the other families of benthic Elasipoda, they are still so large that a lecitotrophic development is to be expected.

3. Conclusion.

The egg size varies greatly within the Elasipoda, but even the smallest eggs probably produce lecitotrophic larvae. Conspicuous differences in egg size are present between the families: Deimatidae, (0.3–)0.9 mm; Laetmogonidae, 0.15–0.9 mm; Psychropotidae, 1.7–4.4 mm; Elpidiidae, 0.2 mm. In Laetmogonidae and Psychropotidae a correlation was found between egg size and depth occurrence. The eggs of the Psychropotidae, which in bulk surpass the largest hitherto known echinoderm eggs by up to 85 times, may enable the juveniles to spend a long pelagic life independent of food uptake from the plankton.

Brood protection was found in a population of *Oneirophanta mutabilis affinis* at 3570 m off the Pacific coast of Costa Rica. The intra-ovarian development of the young apparently takes place during a period of rich phytoplankton production.

Another example of reproductive periodicity may be provided by the abyssal populations of *Deima validum validum* in the western Indian Ocean.

Histological examination of the gonads in members of the Deimatidae and Psychropotidae showed various stages of a nutritive-phagocytic tissue resembling that known from the gonads of sublittoral species of echinoids and many asteroids. The cells of this tissue ingest the ova and sperm which remain after a spawning. In the nutritive phase the cells are highly vacuolated. The nutritive tissue is abundantly developed in species of *Psychropotes* with eggs of giant size, and in the brood-protecting *Oneirophanta m. affinis.*

Hermaphroditic specimens have not been found, and neither was there any indication of a change of sex.

Swimming and floating

A power of swimming by means of undulatory movements of the body probably exists in many psychropotids and aspidochirotes. Michael Sars (1868, 1877) observed it in specimens of the synallactid *Bathyplotes natans* taken at a depth of 400 m off Lofoten. Pawson (1966) referred to a similar observation on the Caribbean stichopodid *Astichopus multifidus.* Gilchrist (1920, p. 381) mentioned that holothurians (unidentified) from deep water off the South African coasts had been seen swimming after capture.

A photograph of a holothurian (possibly *Psychropotes depressa)* swimming over the bottom at a depth of 1930 m off Baja California was published by Arrhenius (1963). The specimen is seen to eject intestinal content through the anus.

Hansen & Madsen (1956) reported the catch of the synallactid *Galatheathuria aspera* in the South China Sea at least 700 m above the bottom. The species in external appearance is reminiscent of the cuttlefish *Sepia,* having a compact, lense-shaped body surrounded by a brim. Possibly, *Galatheathuria* also swims like a *Sepia* – by undulatory movements of the brim.

Östergren (1938) pointed out that most of the species of the Psychropotidae and some species of the synallactid genus *Paelopatides* are more darkly coloured ventrally than dorsally. Thus, the dark (in some species almost blackish) colour of the ventral side may conceal the swimming animal from enemies looking from below, while the lighter colour of the dorsal side may conceal it when seen on the background of the bottom. It is noteworthy that *Galatheathuria aspera,* which swims in the free water masses, is uniformly dark all over.

Juvenile stages of deep-sea holothurians have on a few occasions been caught in pelagic nets. This applies to a 13 mm long specimen of *Benthodytes typica* (p. 93), to specimens up to 30 mm long of *Peniagone diaphana* (pp. 154–155), and to a 32 mm long specimen of *Psychropotes longicauda* (pp. 124–125). The latter was by Belyaev & Vinogradov (1969) recorded as a new genus and species, *Nectothuria translucida.*

The four juveniles (9–10 mm long) of *Peniagone* (p. 155) taken in a bottom trawl west of New Zealand (St. 626, depth 610 m) are also likely to have been pelagic. This is indicated not only by the gelatinous and transparent state of the specimens, but also by the shallow depth, which is unusual for a member of this genus.

These pelagic juvenile specimens drift with the currents, sometimes at a great distance from the bottom. Their specific gravity is close to that of the water, and they have little power of active locomotion. They seem to be important to the dispersal of various bathyal and abyssal species of Elasipoda (p. 238).

Function of the water-vascular dermal cavities

The ambulacral appendages of the Elasipoda are not, as in most other echinoderms, connected with water-vascular ampullae suspended in the coelomic fluid. In Elpidiidae, Deimatidae, and Laetmogonidae, the water-vascular canals of the tubefeet, and usually also of the papillae and the velum, communicate with large intradermal cavities (p. 190).

The intradermal ambulacral cavities were first described by Théel (1877) for *Elpidia glacialis,* and later (Théel 1882) for a considerable number of species of Elpidiidae, Deimatidae, and Laetmogonidae. Danielssen & Koren (1882) described them for *Kolga hyalina.* No descriptions are found in the subsequent literature.

The first attempt to explain the function of these peculiar ambulacral cavities was made by Östergren (1938), who suggested that they facilitate the passage of oxygen through the skin, thus compensating for the lack of respiratory trees in the Elasipoda.

Hansen (1972) pointed out that recent deep-sea photographs of *Scotoplanes* suggest another function of the cavities. Walking specimens of *Scotoplanes* show a series of transverse constrictions along the length of the body, indicating peristaltic movements of the muscles of the body wall. The peristaltic movements were supposed to press fluid from the dermal cavities into the tubefeet which are greatly extended during walking. Ampullae of the normal type do not seem to be adequate instruments for the protraction of the few and very large tubefeet characteristic of the Elasipoda. The replacement of the ampullae by dermal cavities permitted an increase in capacity, and at the same time made possible the application of the powerful muscles of the body wall in the protraction of the tubefeet.

During walking the tubefeet act as stilts which raise the body of these very buoyant animals from the substratum. Walking on stilt legs, known also from deep-sea crustaceans and pycnogonids, is apparently an adaptation to movement on the soft deep-sea bottom.

Deep-sea photography has also revealed the presence of body constrictions in walking specimens of *Peniagone* (Lemche *et al.* in press).

Only in soft-skinned forms like *Scotoplanes* and *Peniagone* the peristaltic movements of the circular musculature of the body wall are probably accompanied by externally visible constrictions of the skin. However, the cavities are equally well developed in forms with a rigid and armoured skin *(Oneirophanta, Deima, Elpidia),* which indicates that the muscles of the body wall here perform a similar strong pumping action. This is confirmed by photographs of specimens of *Elpidia* (Lemche *et al.* in press) in which the tubefeet show a considerable extension despite their strong armature of spicules.

The function of the ventral, intradermal cavities is likely to be facilitated by the entirely dorsal attachment of the alimentary canal (p. 193).

The velum is connected with similar intradermal cavities which may cause changes in its size and position. Deep-sea photographs (Lemche *et al.* in press) show that at least two species of *Peniagone* are able to bend the velar papillae over the head, reaching the bottom with their tips. One of the species *(P. purpurea)* has a flattened body with a velum consisting of two pairs of long, slender papillae; the papillae can be moved independently, searching the surrounding water, as well as the surface of the bottom. The other photographed species (probably *Peniagone azorica)* has a velum of normal shape and position. It is remarkable that also in this species the velum may reach the bottom in front of the animal, thus apparently performing a sensory function.

The long papillae of many deimatids and laetmogonids may perform a similar sensory function. However, as yet there is no photographic evidence of such a function.

In addition to the locomotory or sensory function, the ambulacral appendages may have a respiratory function, as they increase the surface area of the body. This function may be further facilitated by the rapid exchange of fluid in their water-vascular canals due to the pumping action of the ambulacral, dermal cavities.

C. SYSTEMATICS, RELATIONSHIP, AND ADAPTATION

Monophyletic origin

Elasipoda are usually easy to recognize due to their conspicuous and often strangely shaped ambulacral appendages and flat ventral sole bordered by large tubefeet, or by a brim of fused tubefeet.

Common to all Elasipoda are two anatomical features – the absence of respiratory trees and the dorsal attachment of the mesentery throughout its length. Two other features, although not common to all the five elasipod families, may be taken as a further indication of a monophyletic origin of the whole group. One feature is the occurrence in a number of elpidiid species of accessory wheel-shaped deposits of the type otherwise characteristic of laetmogonids. The other feature is the replacement in the Elpidiidae, Deimatidae, and Laetmogonidae of the tubefeet ampullae by intradermal ambulacral cavities – a unique feature in echinoderms. These similarities between Elpidiidae and Deimatidae-Laetmogonidae are remarkable, as the Elpidiidae are otherwise more closely related to Psychropotidae and Pelagothuriidae.

The presence of a ring of circum-oral papillae in one genus of each of the families Deimatidae *(Deima),* Laetmogonidae *(Benthogone),* and Psychropotidae (*Benthodytes*) also points to a common elasipod ancestor.

Evolutionary trends

The Elasipoda seem at an early stage to have branched into two evolutionary lines, here proposed as the suborders Deimatina and Psychropotina.

In the following, the relationship between the two suborders and their families is discussed. The division of the families into genera is dealt with in the Systematic Part.

Deimatina, comprising the families Deimatidae and Laetmogonidae, is characterized by the large and generally numerous papillae, and by the ventral sole being bordered by large, separate tubefeet. While the two families cannot always be distinguished from each other by external features, they differ distinctly in the deposits and in the morphology of the gonads.

Deimatidae. The deposits are reticulated plates, which may change into spatulated crosses or rods, or into rounded or amorphous bodies. Wheel-shaped deposits are absent.

The reticulated plates represent a primitive type of deposit. The type is especially characteristic of the Dendrochirota; within the Elasipoda the type is confined to the Deimatidae.

The different forms of the plates and their transformations are a poor guide to the evaluation of the affinities of the genera. The occurrence of two distinct types of tentacle, however, suggests that the family evolved along two lines, one *(Orphnurgus)* comprising bathyal, the other *(Deima, Oneirophanta)* primarily abyssal species.

The gonads consist of unbranched tubules (sac-shaped in the females).

Laetmogonidae. The deposits are wheel-shaped in all the species. In addition, simple rods or (in *Laetmogone violacea*) spinous crosses occur.

The wheels are similar in type to those occurring scatteredly in the Elpidiidae, which suggests that also in Laetmogonidae they are persisting larval deposits. However, apart from the doubtful feature of the wheel-shaped deposits, the Laetmogonidae show no indication of retained larval features.

The gonads in both sexes consist of branched, slender tubules.

Psychropotina comprises the families Psychropotidae, Elpidiidae, and Pelagothuriidae. The close relationship between the families appears from the combination of features in the genus *Psychrelpidia,* and from the presence in the

Psychropotidae and Elpidiidae of a deposit type which is unknown in other holothurians (p. 185). (Deposits are absent in the Pelagothuriidae).

Psychrelpidia has an anterior brim composed of dorsal and ventrolateral papillae – a similarity to Psychropotidae and Pelagothuriidae. As in Pelagothuriidae, the brim is clearly distinct from the free ventrolateral tubefeet and it includes approximately the same number of papillae (14 in *Psychrelpidia,* 12–16 in the Pelagothuriidae). Further similarities to Psychropotidae are the numerous ventrolateral tubefeet, which almost form a brim, retractility of the tentacles (as in *Benthodytes*), and the violet body colour. The deposits are cross-shaped as in Psychropotidae and a number of species of *Peniagone*. Similarities to Elpidiidae further include the type of calcareous ring, the absence of midventral tubefeet, and the number of 10 tentacles.

Hérouard (1923) erected *Psychrelpidia* to accommodate the species *P. discrepans,* originally referred to *Peniagone.* He regarded it as belonging to the Psychropotidae, while Ekman (1926) transferred it to the Elpidiidae. In the present paper it is likewise reckoned among the Elpidiidae, although a reference to the Psychropotidae or Pelagothuriidae would be equally justified.

The brim of *Psychrelpidia* and the Pelagothuriidae may be homologous with the anterior part of the brim in the Psychropotidae, the presence of an anterior brim being apparently an original feature in the suborder Psychropotina. It seems likely that the velum of the Elpidiidae is a reduced anterior brim. A velum (or, in *Scotoplanes,* papillae deriving from a velum) is present in all the elpidiid genera except the most specialized one, *Elpidia.*

Psychropotidae. The family is characterized by the brim of fused tubefeet which surrounds the body. The deposits are cross-shaped, or reduced to rods.

Elpidiidae. The family possesses a number of features indicating its origin by paedomorphosis: The short and ovoid body form, the presence of only ten tentacles, the low number of tubefeet, the presence, in some species, of scattered wheel-shaped deposits, and the unique morphology of the calcareous ring.

The large size of the tubefeet, and their connection with intradermal ambulacral cavities, is a similarity to the Deimatidae and Laetmogonidae (pp. 205–206).

The velum, as suggested above, probably derives from an anterior brim, the latter still being present in *Psychrelpidia.*

The interrelationship of the elpidiid genera may be inferred from several features: The morphology of the spicules and the calcareous ring, the presence or absence of a velum, and a double versus a single gonad. *Peniagone* occupies, with regard to all these features, an original position within the family. The absence in this genus of a rectal caecum is also likely to be a primitive feature.

Pelagothuriidae. This pelagic family lacks deposits and calcareous ring, the relationship to the two other families being shown by the external morphology. The anterior brim is a swimming or floating organ. The family probably originated through paedomorphosis from pelagic juveniles of some benthic Psychropotina.

Madsen (1961b) suggested a paedomorphic origin of the whole order Elasipoda and of the family Porcellanasteridae among the Asteroidea. As evidence of a paedomorphic origin of the Elasipoda he adduced that the stone canal communicates with the exterior even in adult specimens, and that the deposits (of Elpidiidae and Psychropotidae) resemble initial stages of other holothurian deposits. However, the most peculiar feature of the Psychropotina deposits is not their feeble development, but the fact that they have lost the tendency to develop bifurcations other than those of the primary cross proper. These deposits, therefore, can be cited neither in favour of paedomorphosis, nor of primitiveness.

The adaptation of the Elasipoda to the deep-sea environment

The Elasipoda have sometimes been cited as an ancient and primitive group which, in the uniform and stable environment of the deep sea, has survived up to the present time (Zenkevich & Birshtein 1960). This view is contradicted by the present study of their morphology and biology. The majority of the features of the Elasipoda appear to be adaptations to the deep-sea environment. Some features are highly specialized, while none can be pointed out with certainty as being primitive. Alleged primitive features in the family Elpidiidae appear to be paedomorphic rather than primitive.

The dominance of the Elasipoda in the deep sea is due, in particular, to their faculty of subsisting on the nutrient-poor sediments (p. 195).

The flat ventral sole and the ventrally turned tentacle crown are features connected with the surface-dwelling habit (p. 195).

The absence of respiratory trees may be correlated with the excessive development of the papillae. It seems more natural to animals which have their whole body surface exposed to water to use the body appendages for respiratory purposes than to have intestinal respiration. Respiratory trees probably arose as an adaptation to a burrowing life. It is uncertain whether their absence in the Elasipoda is a primary or a secondary feature.

The replacement of the tubefeet ampullae by water-vascular cavities in the ventral skin in the Deimatidae, Laetmogonidae, and Elpidiidae is connected with a peculiar mechanism of protraction of the tubefeet, developed as an adaptation to walking on the soft deep-sea bottom (pp. 205–206).

The entirely dorsal attachment of the mesentery may be an adaptive feature, as it prevents the intestine from interfering with the function of the water-vascular cavities of the ventral skin (p. 193).

The rectal caecum present in most of the elpidiid genera may have the function of increasing the specific gravity of these extremely buoyant animals (p. 192).

The deposits in the suborder Psychropotina are highly specialized, lacking every trace of dichotomous ramifications other than those of the primary cross proper. But the adaptiveness of this specialization is not evident. The perforated plates of the Deimatidae are unspecialized, resembling deposits found in the Dendrochirota, which is a shallow water group. The wheels of the Laetmogonidae may represent a specialized or paedomorphic feature.

The communication of the stone canal with the exterior may be primitive or paedomorphic.

The unique development of the calcareous ring in the Elpidiidae is based on paedomorphosis. The highly specialized ring in *Irpa* and *Elpidia* is derivable from a normal holothurian ring only through a renewed start from an embryonic ring, as present in *Peniagone* and *Achlyonice* (p. 189). Other paedomorphic features in the family are the short and vaulted body form, the few and large tubefeet, and the number of ten tentacles.

The enormous amount of yolk in the eggs of the Psychropotidae may permit juvenile stages to spend a long pelagic life independent of food uptake from the plankton – a particular advantage in the nutrient-poor deep sea (p. 203).

The highly evolved adaptations of the Elasipoda to the deep-sea environment suggest that the group originated in the deep sea and never occurred in shallow water.

The evidence of paleontology

The firm dermal skeleton of most echinoderms has made this group one of the best known from fossil records. Unfortunately, the holothurians are the exception to the rule. The fact that the dermal skeleton of holothurians consists of separate and usually small deposits which are scattered after the death of the animal prevents paleontologists from reconstructing fossil specimens. Moreover, the same deposit type may occur in unrelated forms. The fossil "families" of holothurian deposits distinguished by paleontologists (Frizzell & Exline 1955), therefore, can only in a few cases be ranged into the system of the recent Holothurioidea. Frizzell *et al.* (1966) reckoned the fossil families Theeliidae and Protocaudinidae among the Elasipoda. However, the deposits of the Theeliidae (wheels with a solid centre) refer the family to the Apoda, and not to the Elasipoda. The deposits of the Protocaudinidae (wheels with a primary cross or a similar structure in the centre) resemble those of the recent family Laetmogonidae. But similar wheels are found in e. g. the Antarctic dendrochirote, *Staurocucumis liouvillei* (Ekman 1927, fig. 8: k). The wheels of the Protocaudinidae are known from Devonian to Jurassic.

Mostler (1968b) erected the family Palelpidiidae for the species *Palelpidia norica* from the upper Triassic of Austria. The family was referred to the Elasipoda because of the similarity of the deposits (primary crosses with five, vertical apophyses) to those of *Elpidia rigida* (= *Peniagone rigida*). However, the arms of the crosses have broad, perforated ends. The deposits, therefore, lack the distinctive feature of those of the suborder Psychropotina and are not referable to the Elasipoda, as defined by the recent forms. Nevertheless, the deposits of *Palelpidia* are very remarkable as they do represent the type from which the Psychropotina deposits are to be derived (p. 185).

The deposits of the fossil *Praeeuphronides multiperforata* Mostler (1968a, b), likewise from the upper Triassic of Austria, have four arms with broad, perforated ends, and a central apophysis. They resemble those of *Synallactes aenigma* (order Aspidochirota) and bear only a superficial similarity to those of *Euphronides (Psychropotes)*.

The deposits of the Psychropotina are so characteristic that they permit a reliable identification to this suborder. The remarkable absence of Psychropotina deposits from the known fossil sediments (which are all from shallow seas) confirms that at least this suborder of the Elasipoda has its origin in the deep sea.

It may not be possible to determine the geological age of the Elasipoda, because holothurian deposits in deep-sea sediments tend to dissolve shortly after the death of the animal (Frizzell & Exline 1955).

Madsen (1961b) similarly noted that the absence of fossil records of the Porcellanasteridae indicates that also this group evolved exclusively within the deep sea.

Relationship to the other orders of the Holothurioidea

While several features indicate that the Elasipoda is a monophyletic group, the evidence of its relationship to the other orders of Holothurioidea is doubtful.

A relationship between the Elasipoda and Aspidochirota has been supposed from the presence of shield-shaped tentacles in both groups, and from the similarity in external appearance between the Psychropotidae and various genera of the aspidochirote family Synallactidae. However, the fact that the calcareous deposits are entirely different suggests that the similarities in external appearance are due to convergent evolution. The union of the two orders into a subclass, Aspidochirotacea, as proposed by Pawson & Fell (1965) is, therefore, not adopted in the present work.

D. BATHYMETRIC DISTRIBUTION

Degree of exploration in relation to depth

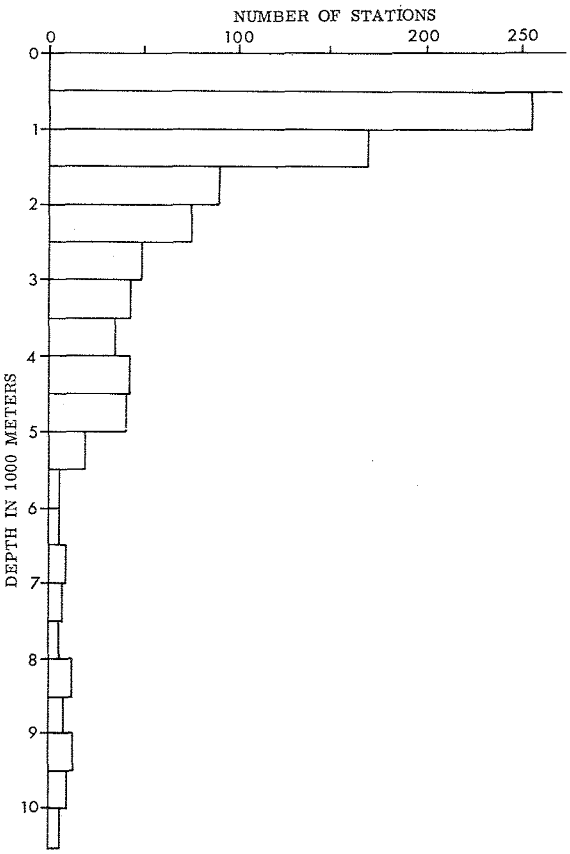


Fig. 98. Number of benthic deep-sea stations with published records of holothurians, in relation to depth.

In the discussion of the bathymetric distribution and depth preference of the species it should be noted that the different bathymetric zones have not been equally well explored. The data on the bathymetric distribution should, therefore, be compared with Fig. 98, which shows the distribution of benthic deep-sea stations in relation to depth. The figure includes all stations with published records of holothurians. Due to the omnipresence and abundance of holothurians in the deep sea, the distribution is fairly representative of the exploration of the deep sea in general.

The area of the sea bottom occupied by the different bathymetric zones should also be taken into account when the degree of exploration is illustrated by the number of stations. Thus, the

Table 23. Number of stations with published records of holothurians in relation to area in three depth intervals.

Depth interval (m)	1000	2000	6000
	2000	6000	11000
Percentage area of sea floor (Kossinna 1921)	3.4	78.4	1.3
Number of stations	254	267	58
Number of stations per unit of area	74.7	3.4	44.6

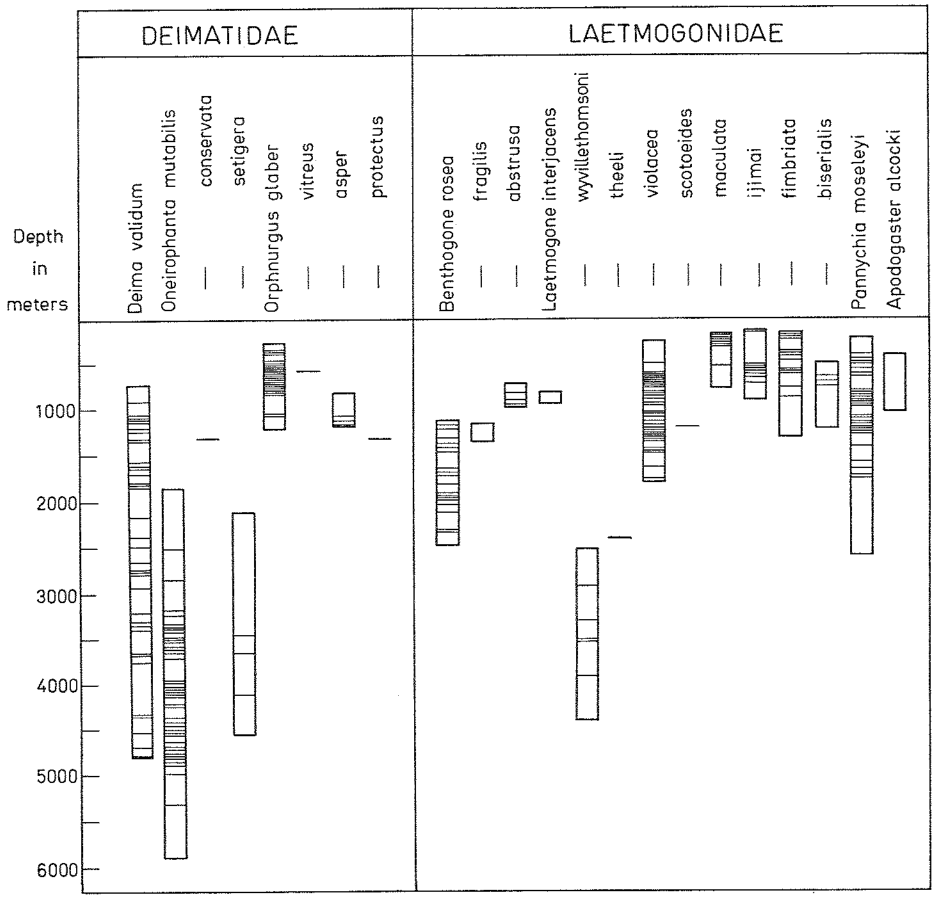


Fig. 99. Bathymetric distribution of the Deimatidae and Laetmogonidae.

number of stations per unit of area is much higher in the hadal than in the abyssal zone (Table 23). Out of the total of 58 hadal stations, 40 belong to the Russian expeditions, from which only the genera *Myriotrochus* and *Elpidia* have so far been worked up.

Bathymetric distribution of the species

Figs. 99 and 101–103 show the bathymetric distribution of the Elasipoda. All published records are included, each station being indicated by a line. This method was preferred to a pure statement of the range of bathymetric distribution because it provides some information on the depth preference of the species. It should, however, be remembered that a dense lining does not necessarily indicate a frequent occurrence of a species. It may reflect a high degree of exploration (Fig. 98).

Bathymetric zonation of the deep sea

The pronounced changes in the composition of the marine fauna with depth have led to a division of the sea into bathymetric faunal zones. There is some disagreement as to where the limits between the zones should be drawn, and there is also disagreement in terminology. The present work follows the terminology used by Bruun (1957), who divided the deep sea into a bathyal, an abyssal, and a hadal zone.

The division of the sea into bathymetric faunal zones has often been based on changes in environmental factors of supposed biological significance, rather than on actual changes in the composition of the fauna. As a matter of fact, a discussion of the environmental factors responsible for a zonation should not be made until the limits of the zones have been determined through an analysis of the distribution of the species.

The transition between two bathymetric zones will show a concentration of upper and lower limits of distribution of species (Fig. 100). On the other hand, a concentration of distributional limits is not always indicative of a faunal change. It may be due to a high degree of exploration or to a large total number of species inhabiting the depths in question.

The lower limits of distribution of the species of Elasipoda show a concentration at 900–1400 m.

The marked decrease in number of lower limits beyond a depth of 1400 m may reflect a decrease in total number of species, as well as a decrease in intensity of exploration.

The gradual increase in number of lower records towards depths of 5000–6000 m is remarkable in view of the decreasing exploration with depth. Further exploration is likely to show even more clearly that a majority of the abyssal species penetrate to depths close to 6000 m.

The scarcity of lower records at depths beyond 6000 m is not due to insufficient exploration, as these depths have more stations per unit of area than the abyssal depths. It is in part due to the fact that only some of the species of the abyssal zone get the opportunity to go deeper down. However, a change in ecological conditions is also important, as shown by the fact that only

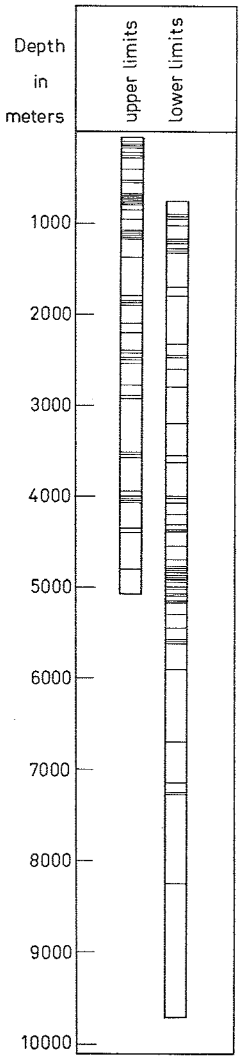


Fig. 100. Upper and lower limits of bathymetric distribution of species of Elasipoda known from at least two stations.

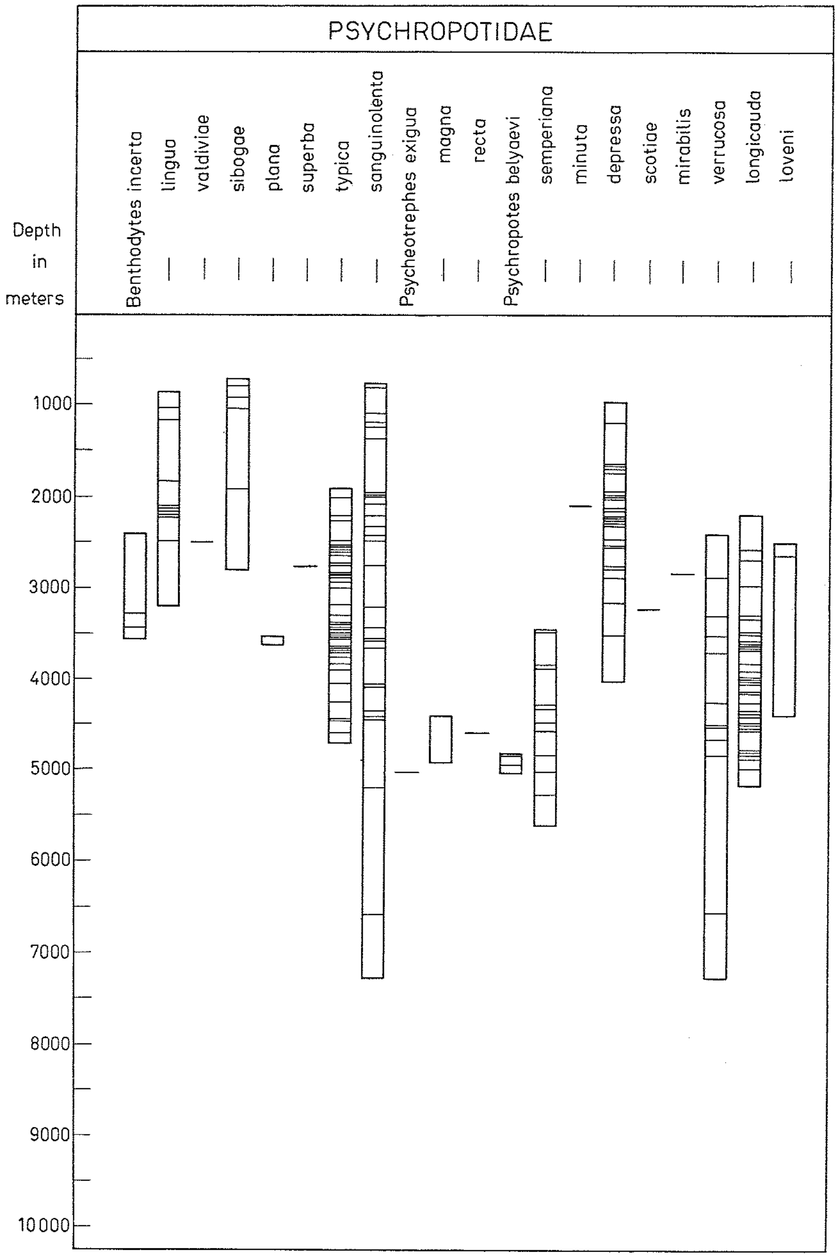


Fig. 101. Bathymetric distribution of the Psychropotidae. The bathyal occurrence of *Benthodytes typica* in the western North Atlantic (Deichmann 1954) is not depicted, in lack of reference to stations.

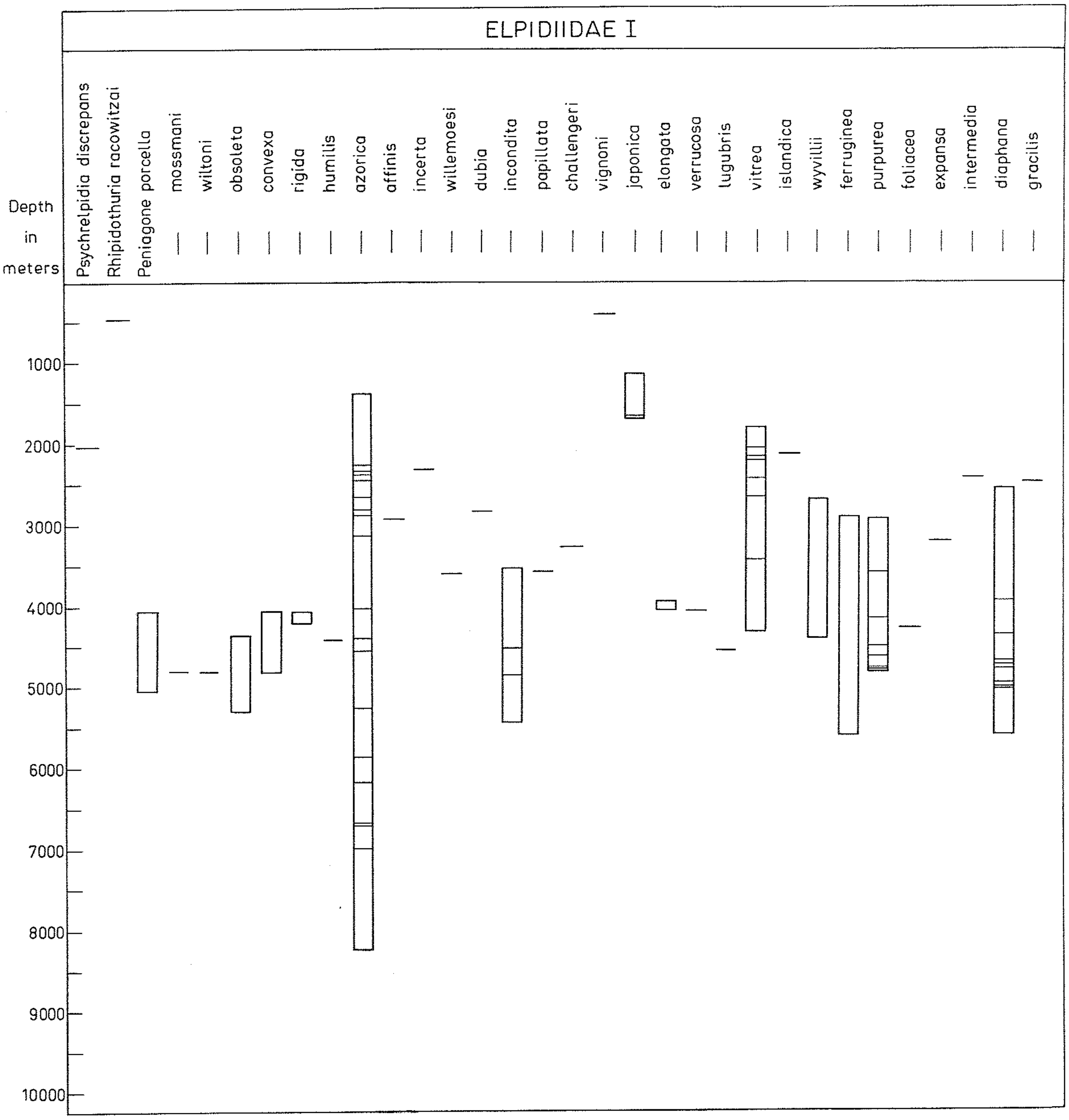


Fig. 102. Bathymetric distribution of the Elpidiidae (I).

three out of a total of 18 species of holothurians taken at the deep-abyssal *Galathea* stations in the Kermadec Trench (4410–5900 m) penetrate deeper than 6000 m.

The absent abyssal species are not to any larger degree replaced by species peculiar to the hadal zone. This may not be due to extreme conditions of life at hadal depths, but rather to a young geological age of the trenches, which has not permitted the evolution of a species diversity comparable to that of the abyssal zone (p. 219).

The upper limits of distribution of the Elasipoda show some concentration at 1800–2600 m (and especially at 2400–2600 m). Conversely, the depths of 1200–1800 m show a low number of upper limits; this is remarkable because these depths are better explored and probably also contain a higher number of species than the depths of 1800–2600 m. Apparently, the rather large number of upper records between 1800 and 2600 m indicates the upper boundary of the abyssal fauna.

The depths of 1800–2600 m show no concentration of lower limits of distribution corresponding to that of the upper limits. Apparently, the species of the bathyal zone are less uniform in their vertical range than are those of the abyssal zone. This is probably due to the greater diversity of environment in the bathyal zone and the correspondingly greater diversity in the ecology of its species.

The concentration of upper limits of distribution at about 4000 m may reflect a deep-abyssal faunal element.

Madsen (1961b) found that the Porcellanasteridae showed a change in species composition at a depth of 4000–5000 m, and suggested that the change was correlated with the beginning undersaturation of the water with calcium. However, this view finds no support in the holothurians which even at the greatest depths of the trenches are able to store abundant amounts of calcium in their deposits (p. 241).

A vertical zonation of the deep-sea fauna is indicated not only by the concentration of upper and lower limits of species distributions, but also

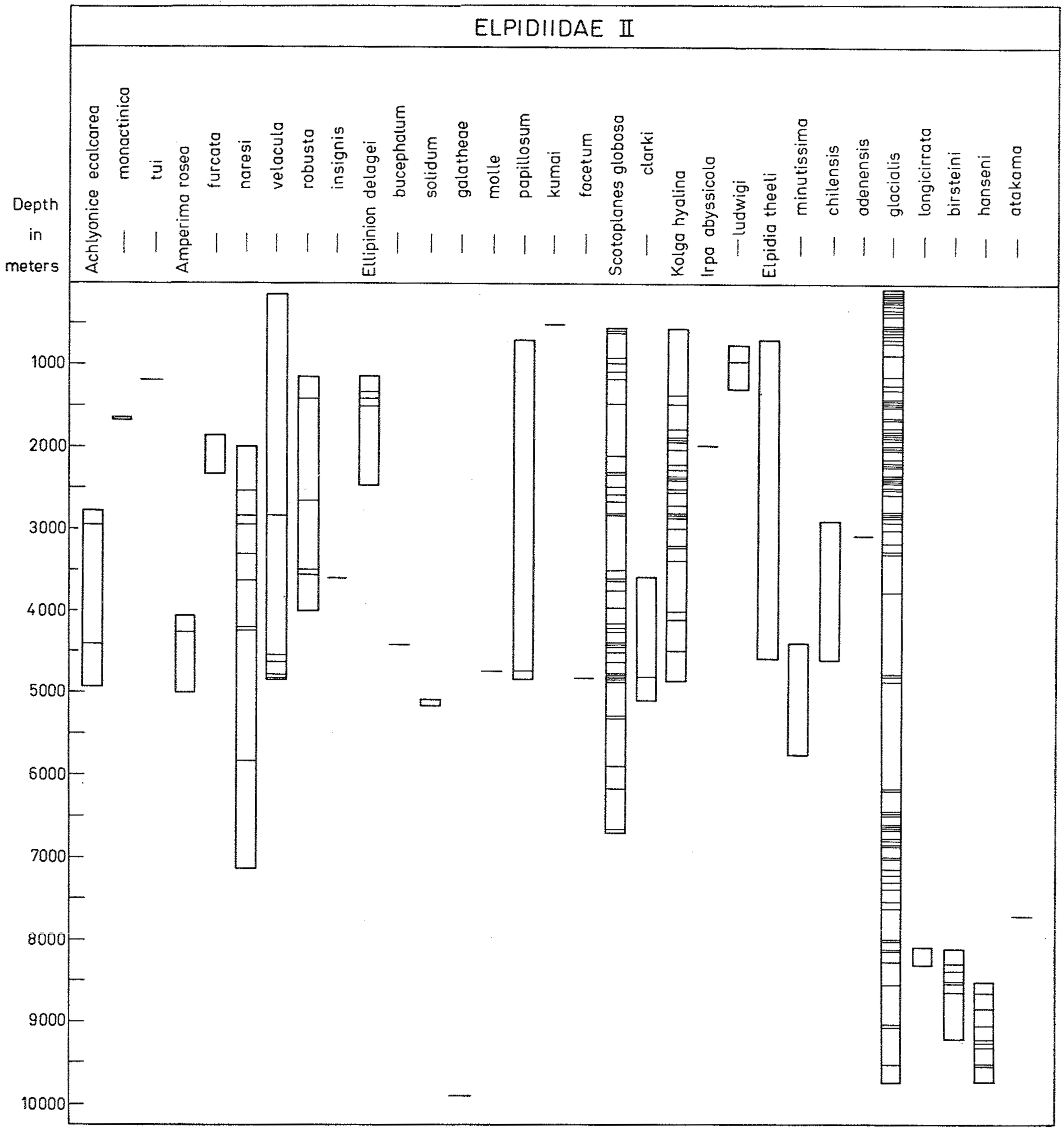


Fig. 103. Bathymetric distribution of the Elpidiidae (II).

by similarities in the range of bathymetric distribution of the different species and in the range of their preferred depths.

As seen in Figs. 99 and 101–103, most of the species occurring deeper than 2600 m have a wide bathymetric range in the abyssal zone, while few of them ascend to depths less than 1800 m. Among the exceptions are *Psychropotes depressa* and *Benthodytes lingua,* both of which mainly occur in the bathyal-abyssal transition zone. *Deima validum* varies in bathymetric range from one region to another (p. 17).

The preponderance of records between 3200 and 6000 m in *Oneirophanta mutabilis* and *Psychropotes longicauda* confirms that the deeper part of the abyssal zone contains characteristic faunal elements.

The upper boundary of the bathyal zone is not clearly defined, owing to the pronounced differences in the vertical range of the bathyal species. It is, however, remarkable that very few bathyal species have their upper limit at depths of less than 200 m. Similarly, there are only few instances of sublittoral species descending deeper than 400 m. This agrees with the view of Sanders & Hessler (1969) that the shelf-slope transition is the most pronounced bathymetric boundary in the sea.

The vertical zonation of the deep-sea fauna, as indicated by the present study of the Elasipoda, differs on essential points from that found by Vinogradova (1962a). Based on concentrations of upper and lower limits of distribution of 1144 species of benthic invertebrates from depths exceeding 2000 m she found that in all the examined groups abrupt changes in faunal composition occurred at certain depths. In some groups (including holothurians) the changes occurred at 2500–3000 and 4000–4500 m, in others at 3000–3500 and 4500–5000 m. In contrast to the present findings the transition zones were indicated by a simultaneous concentration of upper and lower limits of distribution. In holothurians, isopods, and sponges the transition zones showed, in addition, maxima in number of species, but in most other groups the number of species showed a continuous decrease with advancing depth.

The present investigation of the Holothurioidea, like an earlier investigation of the Isopoda Asellota (Wolff 1962), gave no evidence of a change in faunal composition at 4000–4500 m, nor of any maxima in number of species. Wolff suggested that the results obtained by Vinogradova were due to the inclusion of species known from one record only. The inclusion of such species may result in a coincidence of upper limits, lower limits, and species maxima.

Conclusion. The present data on the bathymetric distribution of the Elasipoda support a division of the deep sea into a bathyal, an abyssal, and a hadal zone.

The bathyal zone, comprising depths from 200/400 to 1800/2600 m, shows more varied ecological conditions than the remaining deep sea. In consequence, the bathyal species show little uniformity in bathymetric range; the boundaries of the zone are, therefore, not clearly indicated by upper and lower limits of distribution.

The abyssal zone, comprising depths from 1800/2600 to approximately 6000 m, shows uniform conditions, and many of its species range throughout the zone. The interval of 1800–2600 m is much more pronounced as an upper boundary of the abyssal fauna than as a lower boundary of the bathyal fauna.

The hadal zone, with depths beyond 6000 m, is characterized by the absence of the great majority of the abyssal species, rather than by elements peculiar to the hadal depths. The abrupt decrease in number of species at about 6000 m seems primarily to be correlated with the abrupt decrease in the total area of the sea floor and with the instability and young geological age of the trench environment, which may have permitted only a low faunal diversity.

The hadal zone is considered in detail elsewhere (pp. 239–243).

Bathymetric distribution and taxonomic relationship

The bathymetric faunal zones are characterized not only by having their own species, but also by the presence or dominance of higher taxonomic categories. The taxonomic revision of the Elasipoda showed that the relationship of species and genera, with few exceptions, is closest between forms living in the same bathymetric zone. This pronounced tendency of the sublittoral, bathyal, and abyssal zone to develop their own taxonomic categories is a general feature of the Holothurioidea.

Order Elasipoda. The order is confined to the deep sea and comprises almost half of the known species of deep-sea holothurians. Five species are known from depths of less than 200 m: *Laetmogone maculata* (141–732 m), *L. ijimai* (130–900 m), *L. fimbriata* (164–1300 m), *Amperima velacula* (131–4850 m), and *Elpidia glacialis* (70–9043 m).

Deimatidae. All four species of *Orphnurgus* are bathyal. *Oneirophanta* has two abyssal species, *O. mutabilis* and *O. setigera*. A third species, *O. conservata*, known from a single specimen taken at 1315 m, may actually be an *Orphnurgus* (p. 36).

Deima comprises only one species, *D. validum*. In some regions it ranges throughout the greater part of the bathyal and abyssal zones, while in other regions it is confined to either of the two (p. 17).

Laetmogonidae is pronouncedly bathyal, containing only three abyssal species: *Laetmogone wyvillethomsoni*, *L. theeli*, and *Apodogaster* sp. (p. 75).

L. wyvillethomsoni has sometimes been confused with *L. violacea*. Re-examination of a large number of specimens showed that the two species are distinct and that all bathyal records refer to *L. violacea*, while all abyssal records belong to *L. wyvillethomsoni*. Its closest relative is probably not *L. violacea*, but *L. theeli*.

Psychropotidae is abyssal, with the exception of *Benthodytes lingua* and *Psychropotes depressa*, which are lower bathyal to upper abyssal. No species are restricted to the bathyal zone.

Benthodytes sanguinolenta has an unusually wide vertical distribution (768–7250 m). The name, however, may cover more than one species.

Elpidiidae. *Peniagone*, comprising almost half of the species of the family, is pronouncedly abyssal; only three species have been recorded from the bathyal zone: *P. vignoni* (400 m, Antarctic), *P. japonica* (1135–1669 m, Japan), and *P. azorica* (1385–2252 m off the Azores, otherwise 2320–8210 m).

The other genera are likewise abyssal, although less markedly so than *Peniagone*. Three species are known from the bathyal zone only: *Ellipinion kumai* (500 m) and *Achlyonice tui* (1170 m) are known from one locality each and may, therefore, not be restricted to the bathyal zone, while *Irpa ludwigi* (755–1292 m) is known only from the Mediterranean, where a distinction between a bathyal and an abyssal zone can scarcely be made.

Scotoplanes globosa and *Elpidia glacialis* are bathyal-abyssal-hadal (p. 196), while *Ellipinion delagei* is one of the few species of Elasipoda which is common to the lower bathyal and the upper abyssal zones.

Order Aspidochirota. The order comprises three families:

Holothuriidae. No species occur deeper than 250 m. *Gastrothuria*, recorded from a depth of 564 m, is more rightly placed in the Synallactidae (Hansen 1967).

Stichopodidae has one bathyal species, *Stichopus tremulus*, with a bathymetric range of 240–1918 m (off the Scandinavian coasts it ascends to only 20 m). *Stichopus regalis* ranges from 30–470 m (in the Mediterranean: 5–834 m, and possibly deeper). Otherwise, the family is strictly littoral-sublittoral.

Synallactidae is restricted to the deep sea. It comprises approximately 140 species, which is more than one-third of the known species of deep-sea holothurians. Like the Laetmogonidae among the Elasipoda, the Synallactidae are especially characteristic of the bathyal zone.

The following genera are exclusively bathyal: *Gastrothuria, Bathyplotes, Amphigymnas, Dendrothuria, Meseres, Filithuria,* and *Kareniella*. *Pseudothuria* (1660–2600 m) touches the upper abyssal.

No genera are confined to the abyssal zone. *Synallactes, Paelopatides, Benthothuria, Mesothuria, Capheira,* and *Pseudostichopus* are bathyal-abyssal. Most of them are too little known for an evaluation of a possible correlation between taxonomic affinity and depth range of their species. But such a correlation is evident in *Synallactes*, the best known genus. It comprises 20 species, which may be separated into an upper bathyal (102–1018 m) and an abyssal (1669–4064 m) group.

Bathyal species of *Synallactes:*

nozawai Mitsukuri, 1912	*102–805 m*
multivesiculatus Ohshima, 1915	*195–844 m*
ishikawai Mitsukuri, 1912	*200–500 m*
monoculus (Sluiter, 1901a)	*310–462 m*
mollis Cherbonnier, 1952	*366 m*
heteroculus (Heding, 1940)	*371 m*
discoidalis Mitsukuri, 1912	*450–650 m*
viridilimus Cherbonnier, 1952	*530 m*
triplax Clark, 1920	*545 m*
alexandri Ludwig, 1894	*585–1018 m*
chuni Augustin, 1908	*650–1000 m*
challengeri (Théel, 1886a)	*1007 m*

Abyssal species of *Synallactes:*

gilberti Ohshima, 1915	*1669–1715 m*
anceps Koehler & Vaney, 1910	*2098 m*
crucifera R. Perrier, 1902	*2212 m*
aenigma Ludwig, 1894	*2404–4064 m*
profundus (Koehler & Vaney, 1905)	*2989 m*
horridus Koehler & Vaney, 1905	*3178 m*
rigidus Koehler & Vaney, 1905	*3498 m*
robertsoni Vaney, 1908	*4409 m*

The shallowest recorded species of the abyssal group, *S. gilberti,* was taken off Japan at a temperature of 2.4–2.7° C. It may constitute one of the few examples of deep-sea holothurians ascending to shallow depths in colder seas.

A close relationship between the abyssal species is indicated by the presence of fungiform papillae (otherwise present only in a few species of *Bathyplotes,* but absent in all bathyal species of *Synallactes),* a cartilaginous skin which, at capture, tends to separate from the muscular coat, the few and single-rowed ventrolateral tubefeet, the exclusively quadri-partite tables, and the reduced state of the rods of the papillae.

Order Molpadonia. The order comprises four families:

Gephyrothuriidae, comprising the abyssal genus *Gephyrothuria* (probably monotypic) and the hadal genus *Hadalothuria* (monotypic).

Eupyrgidae, with one genus, *Eupyrgus.* Two species are distinguished, the Korean *E. pacificus* (60–65 m) and the Arctic *E. scaber* (7–480 m).

Caudinidae. *Caudina, Paracaudina,* and *Acaudina* are littoral-sublittoral, while *Hedingia* is bathyal to upper abyssal. The five species of *Hedingia* are: *H. albicans* (491–3200 m), *H. californica* (864–2887 m), *H. ludwigi* (1131 m), *H. fusiforme* (600 m), and *H. planapertura* (349 m).

Molpadiidae, with three genera: *Ceraplectana,* with one species, *C. trachyderma* (3188–6580 m). *Heteromolpadia,* with three species: *H. marenzelleri* (25–1260 m), *H. tridens* (330–462 m), and *H. pikei* (370–504 m). *Molpadia,* with about 30 species. Two are abyssal, *M. blakei* (c. 2000–5220 m) and *M. granulata* (syn. *M. bathybia)* (2692–5820 m). The remaining are bathyal, and only two descend to the upper abyssal zone: *M. parva* (756–2695 m) and *M. musculus* (36–3580 m). The *Galathea* took the latter species on several occasions at depths exceeding 3000 m, but never deeper than 3580 m.

The two abyssal species, *M. blakei* and *M. granulata,* are closely related, as shown by the rudimentary state of the tail, the absence of phosphatic bodies in the skin, the similar type of deposit, and the absence *(blakei)* or reduced state *(granulata)* of the tentacle ampullae. The two species which replace each other geographically (p. 246), are so distinct from the other species of *Molpadia* that they might be considered as a separate genus.

Order Dendrochirota. The members of this order, being predominantly suspension feeders, are poorly represented in the deep sea. Of the three families, the Phyllophoridae are littoral-sublittoral Nine species of Psolidae are known from the bathyal zone, and three from the bathyal-abyssal transition: *Psolus pourtalesii* (2236–2327 m), *Psolidium disjunctum* (2798 m), and *P. panamense* (2309 m). No true abyssal species are found in the family.

Cucumariidae includes two deep-sea species, *Abyssocucumis abyssorum* (1645–4064 m) and *Sphaerothuria bitentaculata* (227–4058 m), both belonging to monotypic genera. *Abyssocucumis* is most closely related to *Staurocucumis* and *Ekmocucumis,* each with one sublittoral Antarctic species (p. 234). *Sphaerothuria* is of uncertain relationship.

Order Apoda. The order comprises three families:

Myriotrochidae, with three genera: *Trochoderma,* with one species, *T. elegans* (Arctic, 9–350 m). *Acanthotrochus,* with one species, *A. mirabilis* (Arctic Basin, 1090–2030 m). *Myriotrochus,* with 14 species. Six are hadal, two are abyssal *(M. bathybius* and *M. giganteus,* both known from 3645 m off Peru), and six are confined to the sublittoral and upper bathyal of Arctic and Subarctic seas (only one of these, *M. theeli,* was found as deep as 2000 m). The hadal species, reviewed by Belyaev (1970), show different types of relationship with the sublittoral forms. Thus, the genus exhibits no clear correlation between bathymetric occurrence and taxonomic relationship.

Chiridotidae, with nine genera, is littoral-sublittoral and mainly tropical and subtropical. Three species are known from the deep sea: *Chiridota abyssicola* (1891–2870 m), *Achiridota profunda* (2700 m), and *A. inermis* (466–772 m). *Chiridota,* in addition to the single upper-abyssal species, comprises twenty-odd sublittoral species. *Achiridota* comprises only the two species mentioned.

Synaptidae, with 15 genera. All deep-sea records belong to the genus *Protankyra,* and all abyssal records to the species *P. abyssicola* (syn. *P. brychia).* The species was taken at numerous *Galathea* stations at 2550–5160 m; possibly, all bathyal records of this species are due to erroneous identification. The interrelationship of the species of *Protankyra* remains to be clarified.

Conclusion. All Holothurioidea, except to some degree the Apoda, show correlation between taxonomic affinity and bathymetric distribution. This correlation exists even at the sub-generic level: In bathyal-abyssal genera, the species are often segregated into a bathyal and an abyssal group.

The true abyssal species of Apoda belong to two genera which are mainly sublittoral: *Protankyra* which, in addition to numerous sublittoral warm-water species, has eight bathyal and one abyssal representative; and *Myriotrochus* whose sublittoral species are Arctic or Subarctic.

The evolutionary implications of the patterns of bathymetric distribution are dealt with in a later chapter (pp. 243–244).

Number of species and individuals in relation to depth

The faunal change with increasing depth is not only qualitative in type. There is also a change in the number of species and individuals, and in the quantitative representation of the holothurians in relation to other groups.

Fig. 104 shows the number of species of holothurians known to inhabit the different depths, illustrated by intervals of 500 m. While the Elasipoda have the maximum number of species in the abyssal zone, holothurians as a whole show a continuous decrease in number from the sublittoral to the hadal zone.

Fig. 105 shows the number of species taken at each of the *Galathea* deep-sea trawling stations, with different signatures for each type of gear. As appears from the station list (Bruun 1958), the duration of haul was, on an average, the same in the three bathymetric zones. The number of spe-

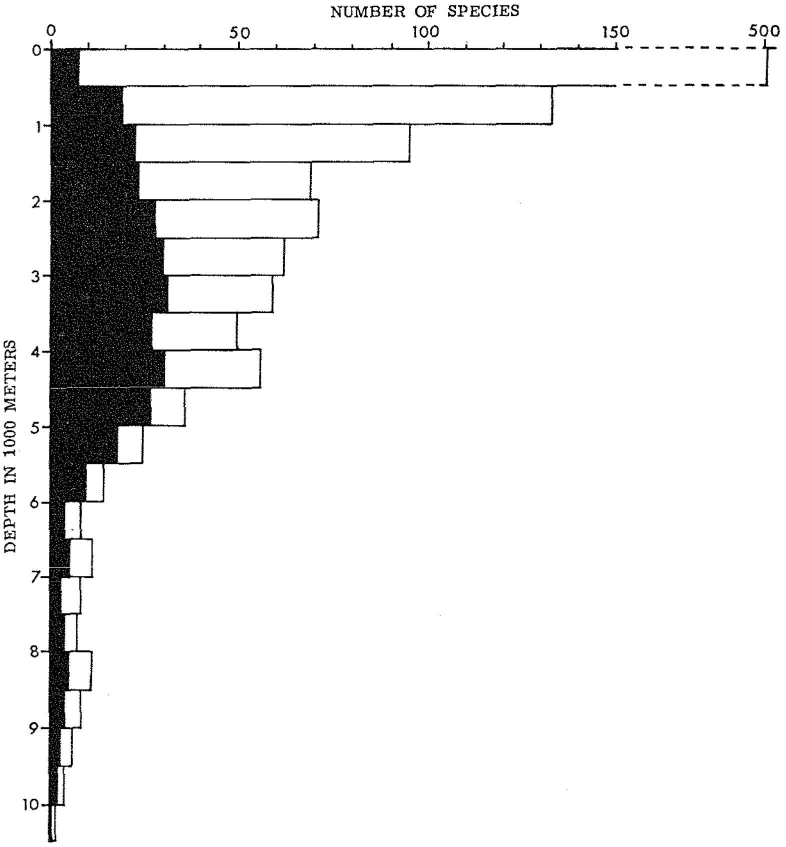


Fig. 104. Number of species of holothurians in relation to depth. The Elasipoda are shown in black.

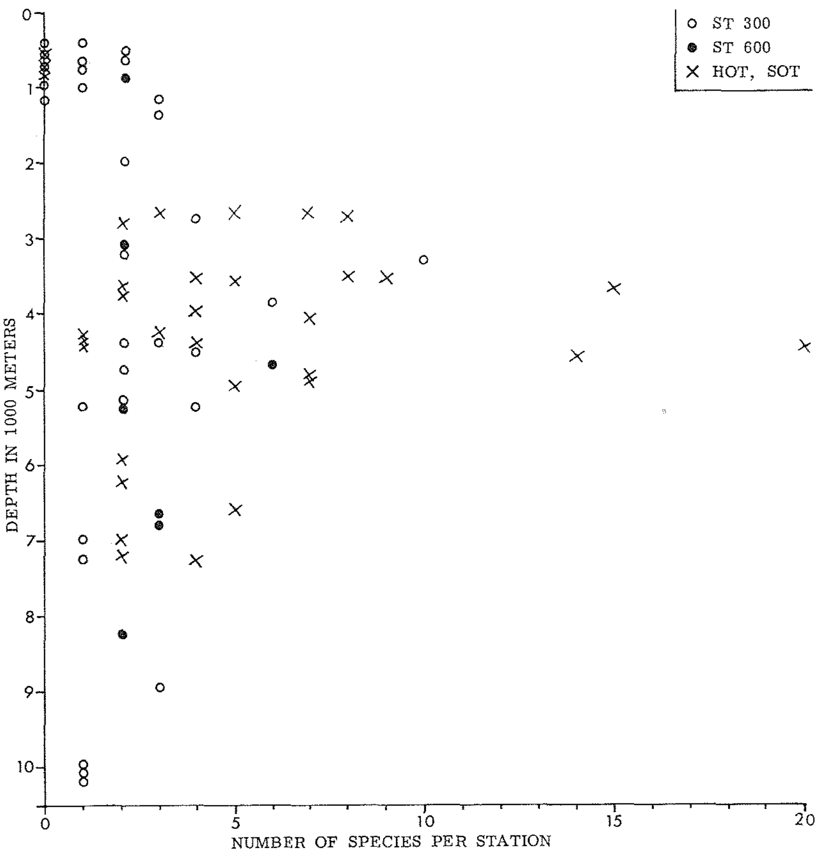


Fig. 105. Number of species of holothurians taken at each trawling-station of the *Galathea.*

cies is, therefore, a measure of the species diversity. The increase in diversity from the bathyal to the abyssal zone takes place in spite of a decrease in total number of species. From the abyssal to the hadal zone there is a decrease both in diversity and in total number of species.

The number of individuals per species shows yet another pattern (Fig. 106). There is a continuous increase in ratio from the bathyal to the hadal zone. The fact that the high number of species at the abyssal stations is accompanied by high numbers of individuals of each species indicates a dominance of holothurians at the expense of other groups. The enormous number of individuals per species at hadal depths may only to a small degree be due to the individuals being distributed on fewer species. A high number of individuals per species is not as a rule found in the hadal animal groups. A dominance of holothurians has been found throughout the hadal zone in all trenches investigated (Wolff 1970). It applies both to the number of specimens and to the biomass. Thus, the Elasipoda constitute 75–90 % of the biomass at a depth of 8000–10000 m in the Kurile-Kamchatka Trench (Zenkevich & Birshtein 1960).

The present findings regarding the number of species and individuals in relation to depth have some bearings on the discussion on the faunal diversity in the deep sea.

Hessler & Sanders (1967) quite remarkably found that the faunal diversity (as defined by the absolute number of species in any single environment) in the deep sea equalled the diversity in equivalent environments from tropical shallow water and greatly surpassed that found in temperate shallow water. Similar results were obtained for Cumacea (Jones & Sanders 1972) and meiobenthic Copepoda (Coull 1972). The authors believed that the high diversity was the result of the great stability of the deep-sea environment throughout the year as well as through geological time.

The presence of a large number of species of holothurians at the abyssal stations is in agreement with the view of a high species diversity in the abyssal zone – although it may to some degree be a consequence of the large number of specimens taken: The higher the density of animals the higher percentage of the total number of species co-existing at a locality will be taken in a single haul. Sanders (1968) developed a "rare-

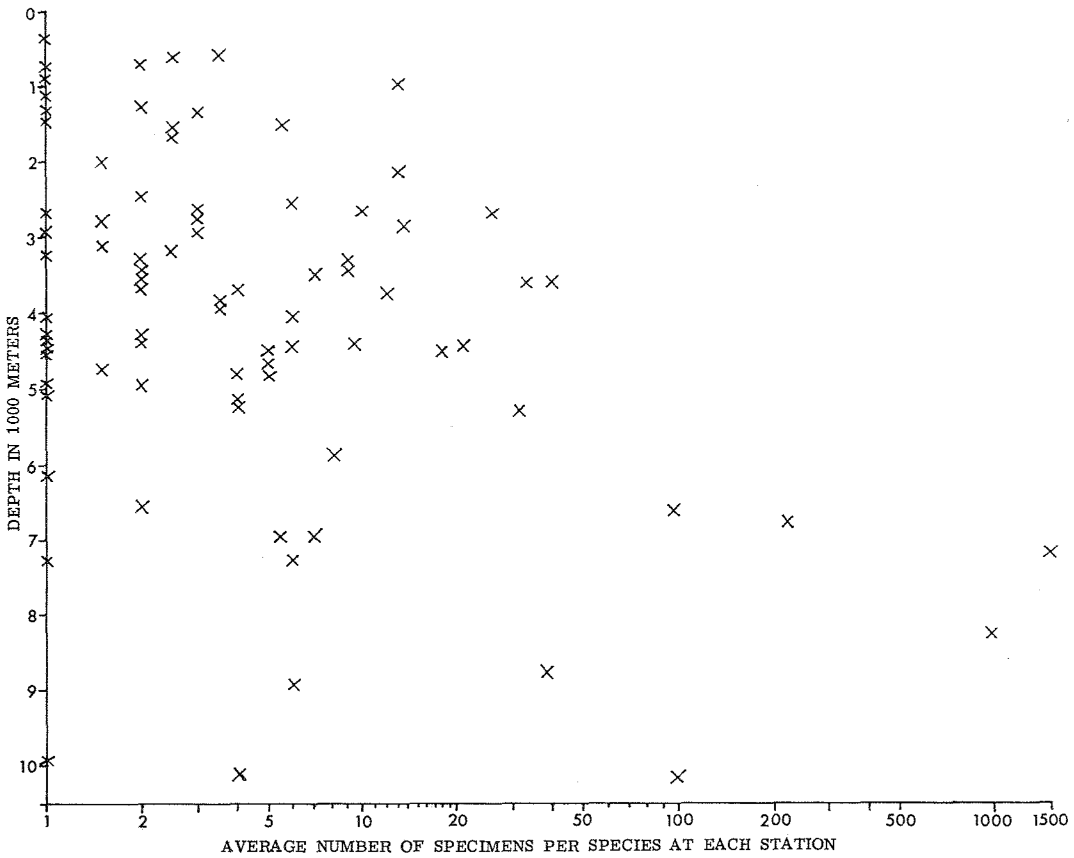


Fig. 106. Average number of specimens per species of holothurians at each trawling-station of the *Galathea*. Abscissa in logarithmic scale.

faction method" to make possible a comparison of the species diversity in samples of different size.

Unfortunately, the bathyal *Galathea* samples are so small that a reasonable estimate of their species diversity is scarcely possible.

The hadal samples, on the other hand, clearly reveal a low species diversity compared to the abyssal samples: The species decrease in number despite the fact that the hadal samples are exceedingly rich in number of individuals.

The low species diversity at hadal depths may not be due to extreme conditions of the environment. Indeed, only the hydrostatic pressure seems to present an increase in the extremeness of the conditions compared to the abyssal zone. The hadal zone, however, differs from the abyssal zone by its more unstable and geologically younger environment (p. 240). The low diversity at hadal depths, like the high diversity at abyssal depths, is thus consistent with the above-mentioned stability-time hypothesis.

A comparative investigation of the species diversity at hadal and abyssal depths, comprising other groups than the extremely dominating holothurians, is desirable.

E. GEOGRAPHIC DISTRIBUTION

The exploration of the different geographic regions

The treatment of a collection originating from all the three main oceans involves a comparison with the materials described from all previous deep-sea expeditions. Such a comparison of faunas from different geographic regions is especially important in view of the fact that reports from regional expeditions often pay too little attention to species described from other oceans.

The degree of exploration varies strikingly from one region to another. The distribution maps of the species (Figs. 109–125) should, therefore, be compared with the maps showing the density of stations in the different geographic regions (Figs. 107–108).

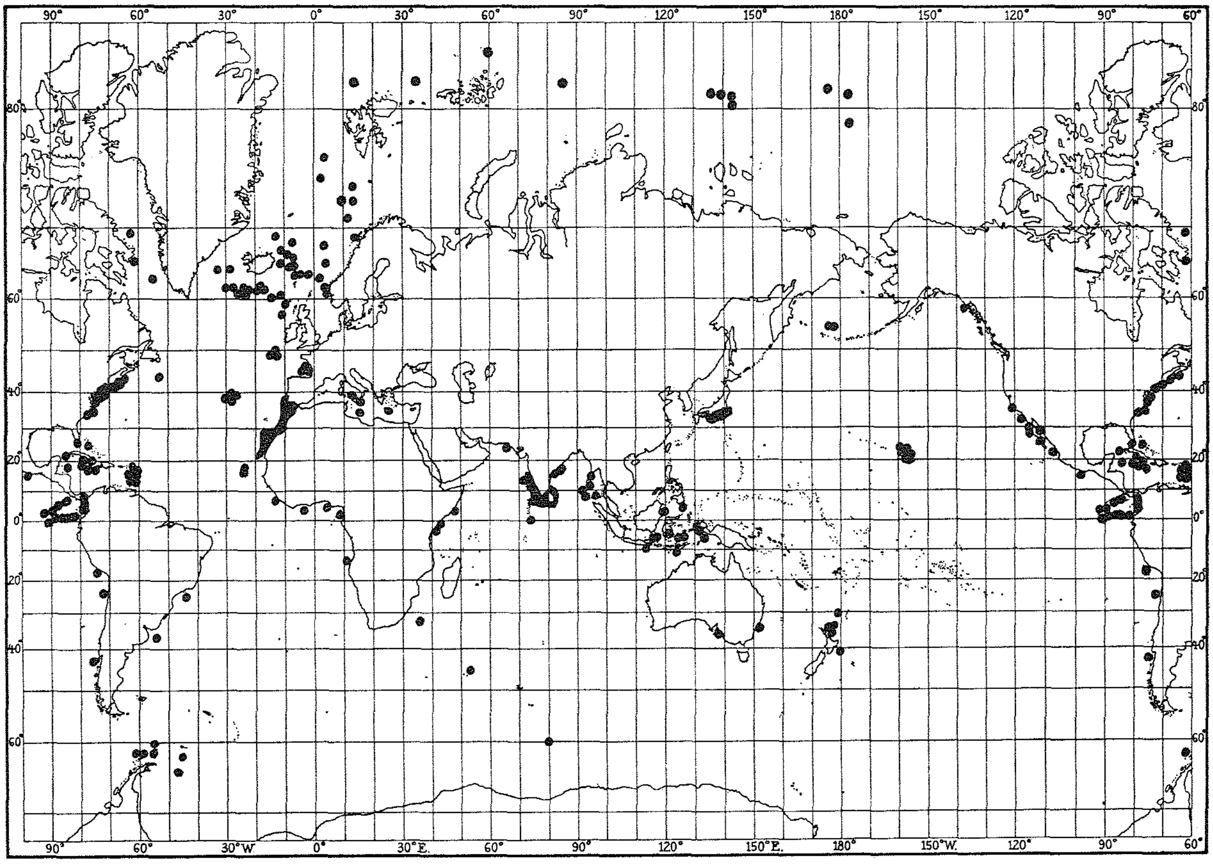


Fig. 107. Distribution of deep-sea stations with published records of holothurians. Depth 1000–2500 m.

The bathyal fauna

This fauna comprises practically all the Laetmogonidae, and the genus *Orphnurgus* in the Deimatidae. The centre of distribution is the archipelago of East Asia where the continental slope is very long and consists of isolated areas round the numerous islands. Three species are endemic to the Indonesian seas: *Benthodytes sibogae, Benthogone abstrusa,* and *Laetmogone interjacens.*

The northern boundary of this rich bathyal fauna lies off Japan in the region of convergence between the Kuroshio and Oyashio Currents. This coincidence suggests that the species have pelagic larvae, the distribution of which is obstructed by the southgoing Oyashio Current (p. 238). Only the deepest living species, *Pannychia moseleyi,* goes beyond this boundary.

To the south, the fauna is to some extent distributed to New Zealand and southern Australia.

The Hawaiian Islands possess four bathyal elasipods. *Orphnurgus vitreus* is endemic. *Pannychia moseleyi* ranges round the coasts of the Pacific. *Orphnurgus glaber* and *Laetmogone biserialis* are also found in southeastern Asia and have their northern boundary at the Kuroshio-Oyashio convergence. The occurrence of *O. glaber* and *L. biserialis* off the Hawaiian Islands may be due to transport of pelagic larvae by bathyal currents running from Japan to the western part of this archipelago (p. 238). *Pannychia moseleyi,* which goes much deeper, may have reached the Hawaiian Islands by way of the chain of submarine mountains which connects these islands with Kamchatka.

The eastern Pacific, in addition to *P. moseleyi,* has only one bathyal elasipod, *Laetmogone scotoeides,* taken off Baja California.

The low number of bathyal elasipods along the eastern coast of the Pacific may be due not only to inability to penetrate north of the Oyashio-Kuroshio convergence, but also to unfavourable conditions for soft-bottom bathyal animals along this steep continental slope.

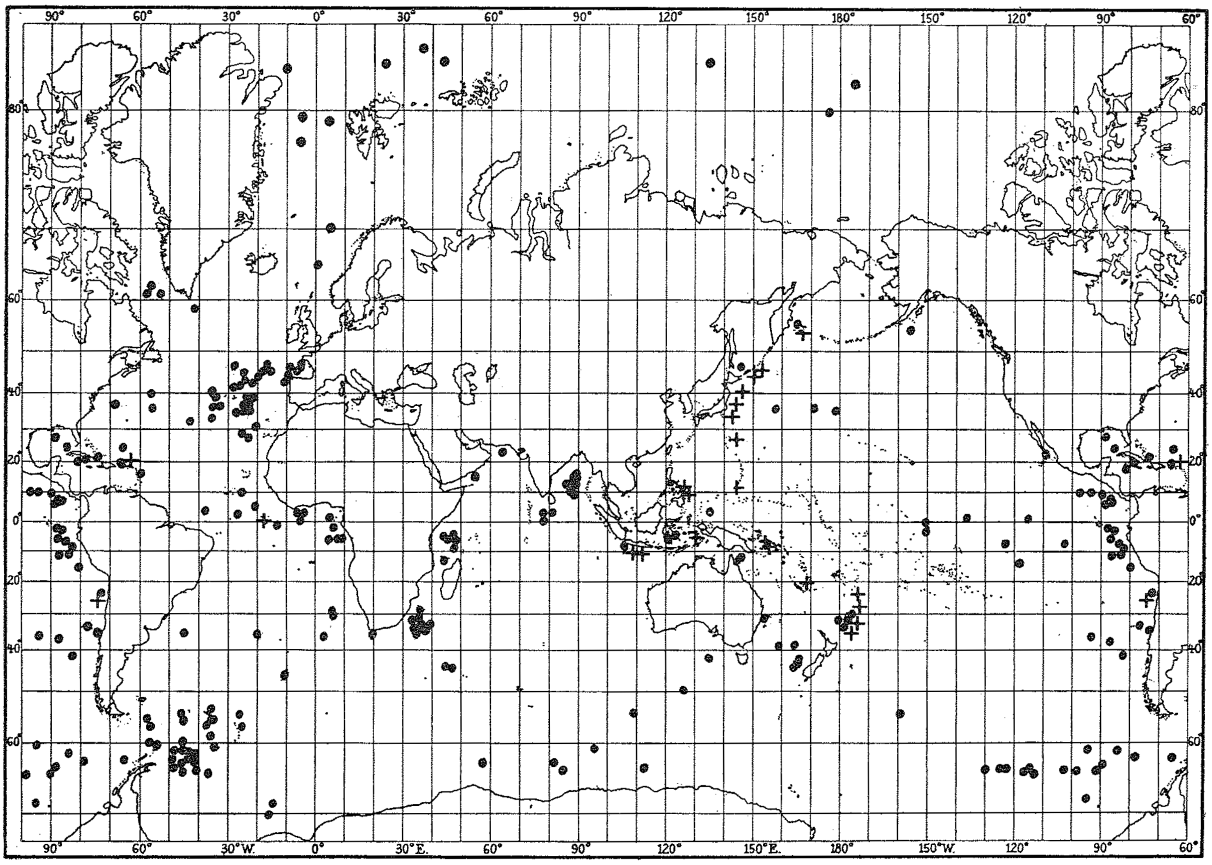


Fig. 108. *Same*. Depth 2500–6000 m (•) and 6000–11000 m (+).

The coasts of southern and equatorial Africa are almost unexplored at bathyal depths, which may explain that only two species have been recorded: *Benthogone rosea* (off East Africa) and *Laetmogone fimbriata* (off Natal).

The two North Atlantic bathyal laetmogonids, *Laetmogone violacea* and *Benthogone rosea,* are both distributed towards the east to Japan and New Zealand. While *B. rosea* has its northern limit of distribution in the North Atlantic west of Ireland, *L. violacea* proceeds along the southern slope of the North Atlantic ridge to west of Greenland. The absence along the east coast of America of this otherwise widely distributed species may be due to adverse currents (p. 238).

The only bathyal elasipod known to occur in the western Atlantic is the West Indian deimatid *Orphnurgus asper.*

The abyssal fauna

The abyssal Elasipoda show no preponderance in number of species in any region, apart from very limited regions such as off the west coast of Central America and the abyssal depths of the Kermadec Trench. Moreover, the various abyssal species have so few distributional features in common that they cannot form the basis of a division of the abyssal zone into larger zoogeographic regions. Distinctive abyssal faunas may be found in basins with low sill depths (as the Mediterranean and the Arctic Basin) but are rare in the remaining deep sea. At the present time only one such region can be pointed out, viz. a narrow region off the west coast of Central America.

Ekman (1953) proposed a division of the abyssal fauna into four major zoogeographic regions: An Arctic, Antarctic, Atlantic, and Indo-pan-Pacific region.

Madsen (1961b) agreed that the Arctic and Antarctic seas are distinct zoogeographic regions. However, he divided the remaining abyssal deep sea into an Atlanto-Indian(-West Pacific) and a main Pacific region, with a transition zone extending from southern Japan to east of New

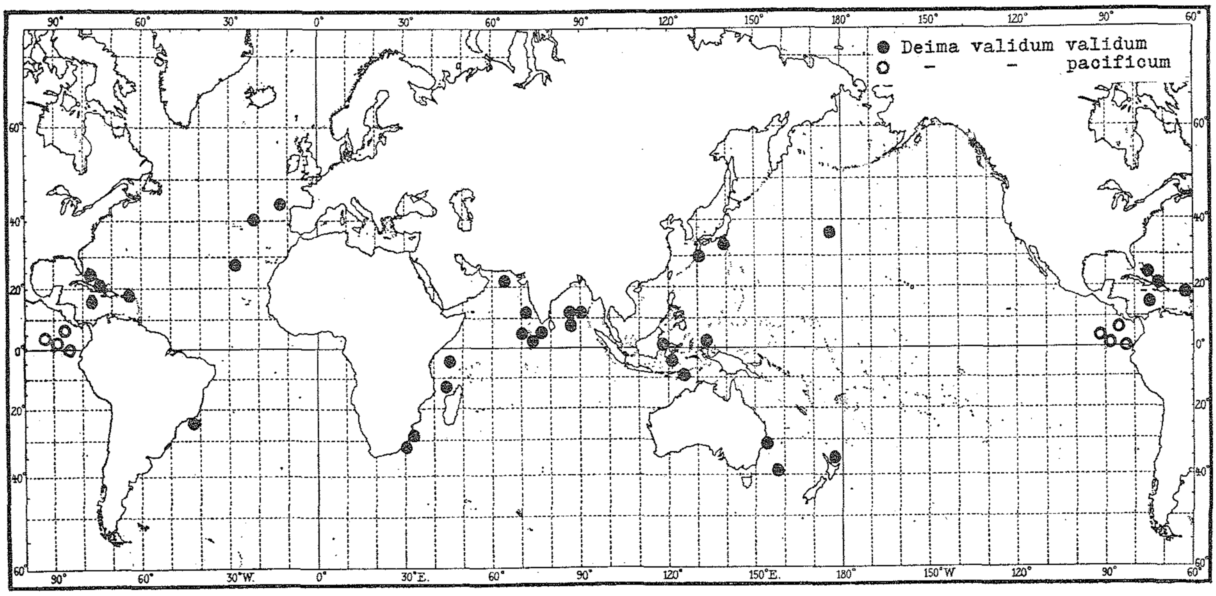


Fig. 109. Records of *Deima validum.*

Zealand. The mid-Pacific deep sea with its sparse food resources was assumed to form the barrier for distribution. Besides, a possible correlation was pointed out between the major abyssal zoogeographic regions and the type of sediment. The Atlanto-Indian region is mainly covered with Globigerina ooze, the main Pacific region with abyssal clay, and the Antarctic region with diatom ooze.

The Elasipoda give no conclusive evidence of the faunal interrelationship of the different oceans. This may in part be due to insufficient exploration. The deep-sea fauna of the South Atlantic is so little known that a comparison of the Atlantic and Indo-Pacific faunas actually means a comparison of the well-explored North Atlantic with the rest of the world ocean. Similarly, the greater part of the abyssal Pacific Ocean

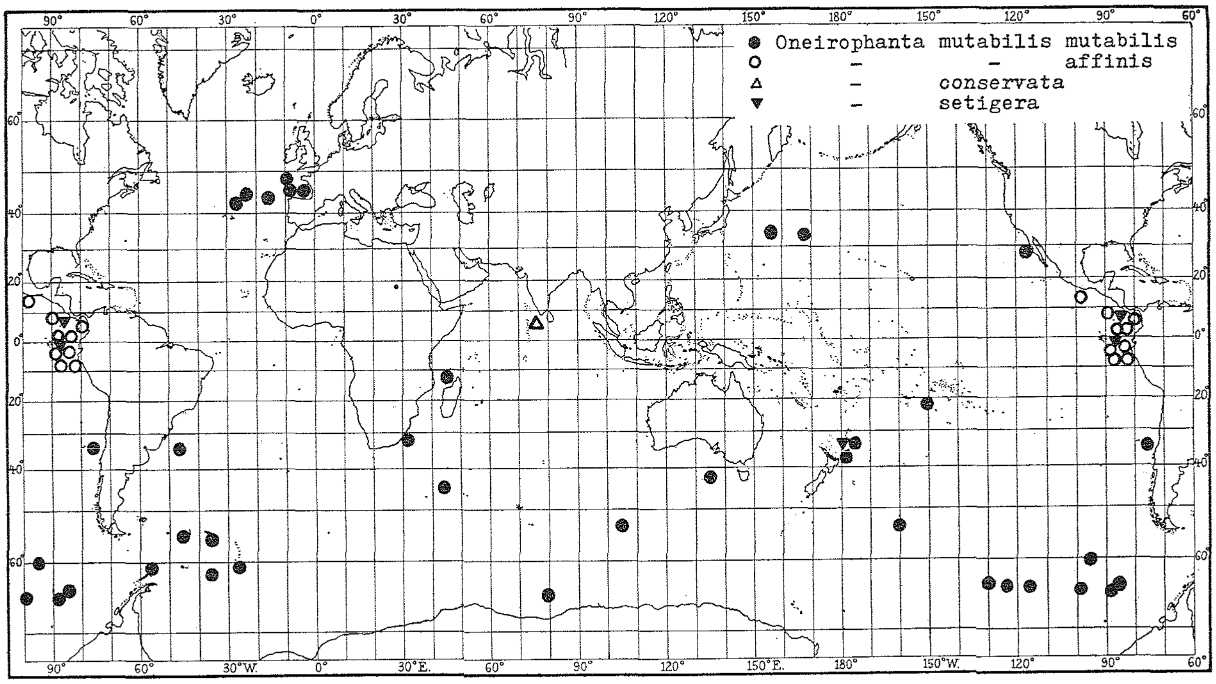


Fig. 110. Records of *Oneirophanta.*

is too little explored to allow conclusions regarding the faunal relationship of this ocean as a whole.

A division of the world ocean into large regions characterized by sediment types finds no support in the distribution of the Elasipoda, which seem to be independent of the usually distinguished types of sediment (p. 235).

The zoogeographic divisions proposed by Vinogradova (1959) are contradicted by the distribution of the Elasipoda. The divisions were largely based on the view that submarine ridges may act as distributional barriers to abyssal animals (p. 238).

The object of the following review of the abyssal elasipod faunas is to point out regions with more or less characteristic faunas, and of underlining similarities and dissimilarities between different faunas and different species.

1. World-wide distributions.
Although the demonstration of synonymy has extended the known range of geographic distribution of many species, it is surprising how few species have a world-wide distribution.

The two most widely distributed species are *Oneirophanta mutabilis* and *Psychropotes longicauda*. The remarkable similarity in the pattern of distribution (Figs. 110 and 118) may be explained by the fact that both have their main vertical range at 3200–6000 m. They have been found in almost every region investigated at these great depths.

The remaining five species with a world-wide distribution seem to be absent in some regions: *Benthodytes typica*, which ranges throughout the abyssal zone, has an almost equally wide distribution as the two above-mentioned species. The absence of records from the Antarctic Ocean is remarkable, as it is known to occur off the coast of South Africa and in the Tasman Sea.

Deima validum seems to be absent from a number of regions, including the Antarctic Ocean. The species shows striking differences in bathymetric distribution from one region to another (p. 17).

Elpidia glacialis is of common occurrence in the Arctic and Antarctic deep sea (in the Kara Sea it ascends to a depth of 70 m). Outside these regions it is confined to the hadal depths of a number of trenches.

Psychropotes depressa, an inhabitant of the deeper bathyal and the upper abyssal zone, may also be world-wide in distribution. The lack of records from the Indian Ocean may be due to insufficient exploration of the depths inhabited by this species.

Scotoplanes globosa occurs in the Southern Ocean, the South Atlantic, and the Pacific, including a number of West Pacific trenches. The absence of records from the North Atlantic is remarkable.

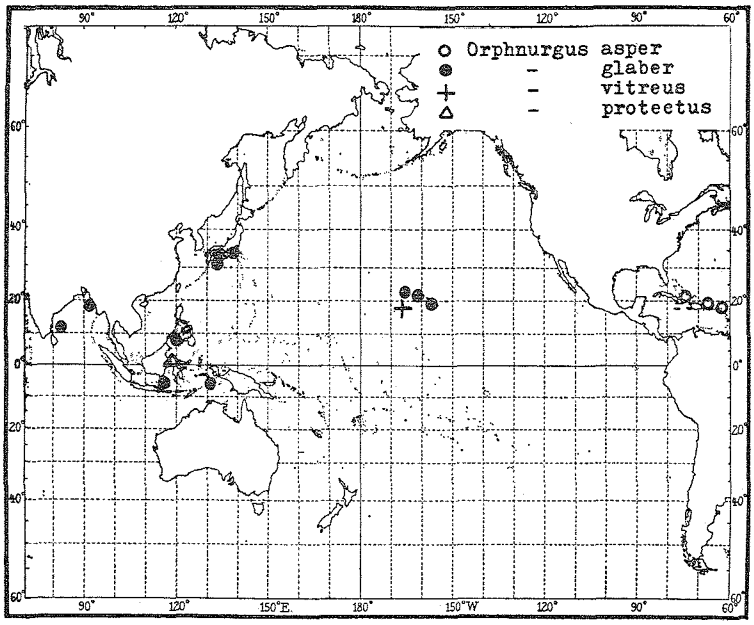


Fig. 111. Records of *Orphnurgus*.

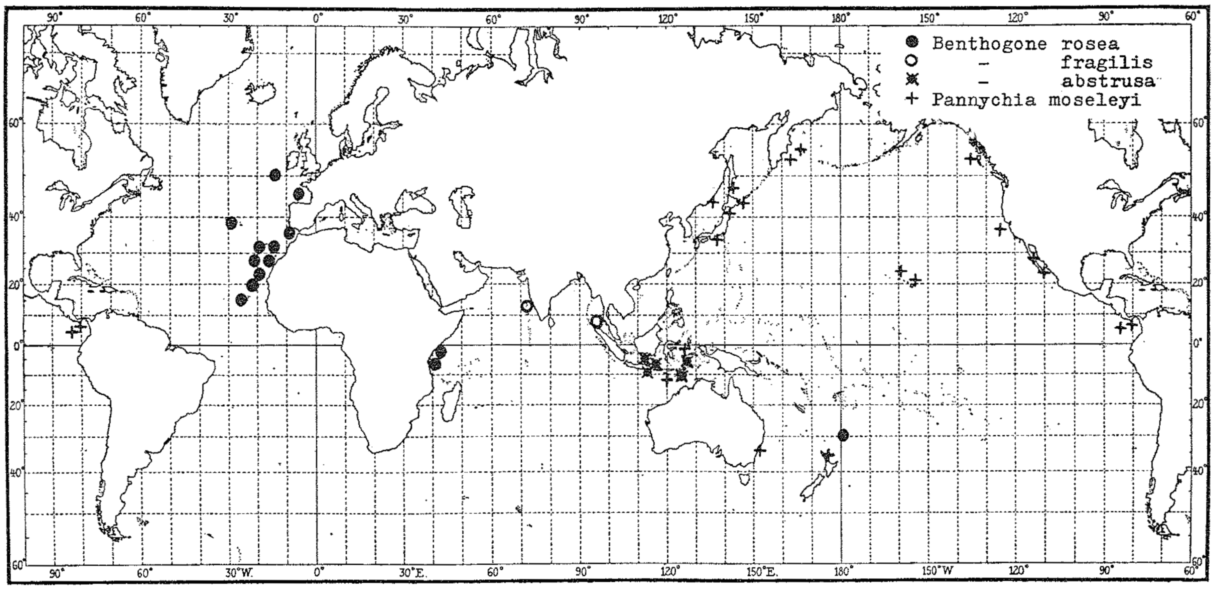


Fig. 112. Records of *Benthogone* and *Pannychia.*

2. The Antarctic Ocean.

Ekman (1953), Vinogradova (1959), and Madsen (1961b) deal with the Antarctic abyssal deep sea as a distinct zoogeographic region. This view finds little support in the distribution of the Elasipoda.

Nine abyssal species of Elasipoda are known only from the Antarctic region. *Peniagone incondita* has been taken on several occasions, while the remaining eight species *(Peniagone mossmani, P. wiltoni, P. affinis, P. incerta, P. willemoesi, Ellipinion facetum, Amperima insignis,* and *Psychropotes scotiae)* are known from one station each.

The Antarctic deep sea is characterized by its low temperature, which in large areas is below zero. But in contrast to the Arctic deep sea there is a gradual transition to regions with normal abyssal temperatures. Thus, although an endemic abyssal fauna dependent on very low temperatures may exist, a well-defined boundary between such a region and the remaining deep sea cannot be expected.

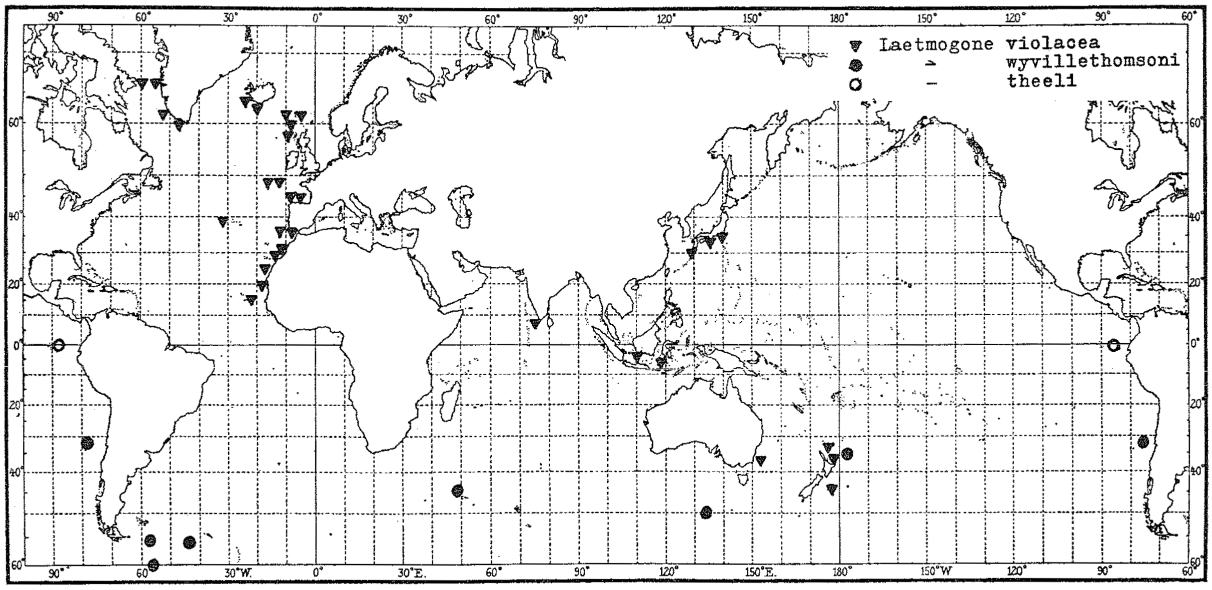
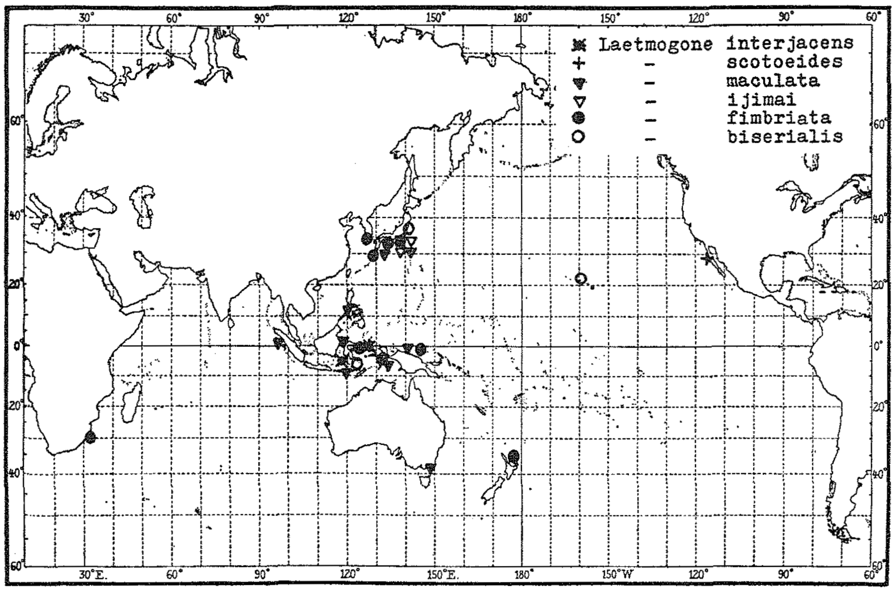


Fig. 113. Records of *Laetmogone* (1).

Fig. 114. Records of *Laetmogone* (2).



Nine species and one subspecies of Antarctic Elasipoda are known also from other seas. *Oneirophanta mutabilis* and *Psychropotes longicauda* are world-wide. *Scotoplanes globosa* occurs also in the South Atlantic and in the western and northern Pacific. *Laetmogone wyvillethomsoni* is known from the Kermadec Trench and from off the coast of Chile; although not exclusively Antarctic, it may be restricted to the Southern Ocean. *Peniagone vitrea* is also known from the Gulf of Panama, *Amperima naresi* from the Gulf of Panama and the Sunda Trench, *A. robusta* from the Kermadec Trench, *Ellipinion papillosum* from the South Atlantic, and *Elpidia glacialis sundensis* from the Sunda Trench. *Kolga hyalina*, also found in the Arctic Basin and the adjoining part of the North Atlantic, is the only example of a bipolar distribution among holothurians.

The problem of the existence of deep-sea elements in the Antarctic sublittoral fauna is considered elsewhere (pp. 233–234).

3. The North Atlantic.

Although the best explored of the oceans, the stations are so unevenly distributed that erroneous

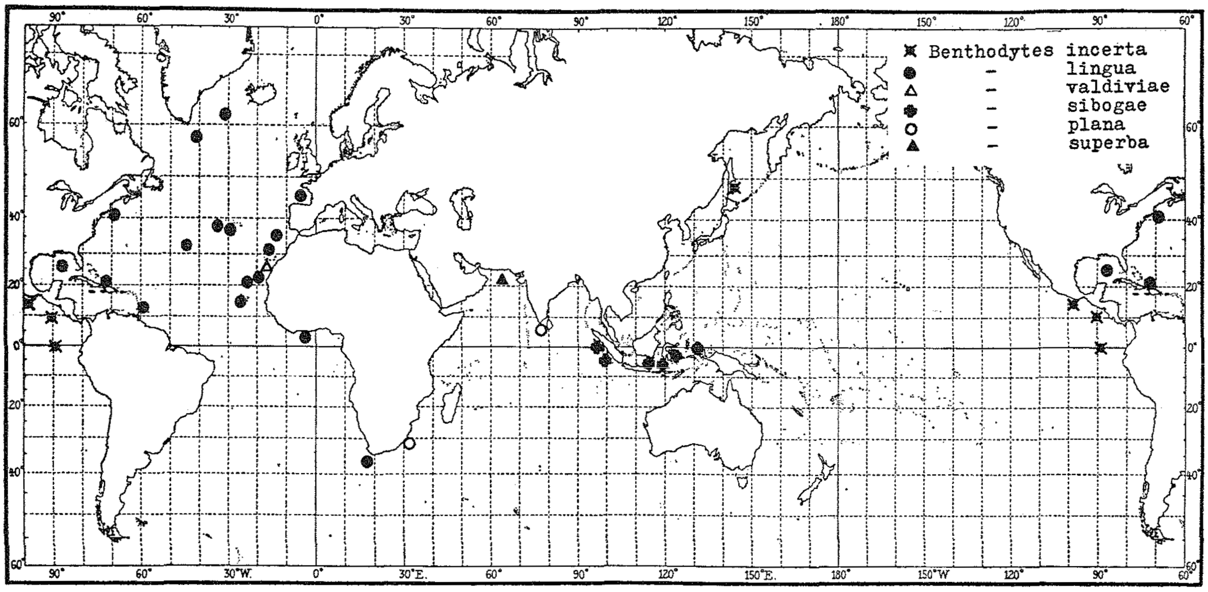


Fig. 115. Records of *Benthodytes* (1).

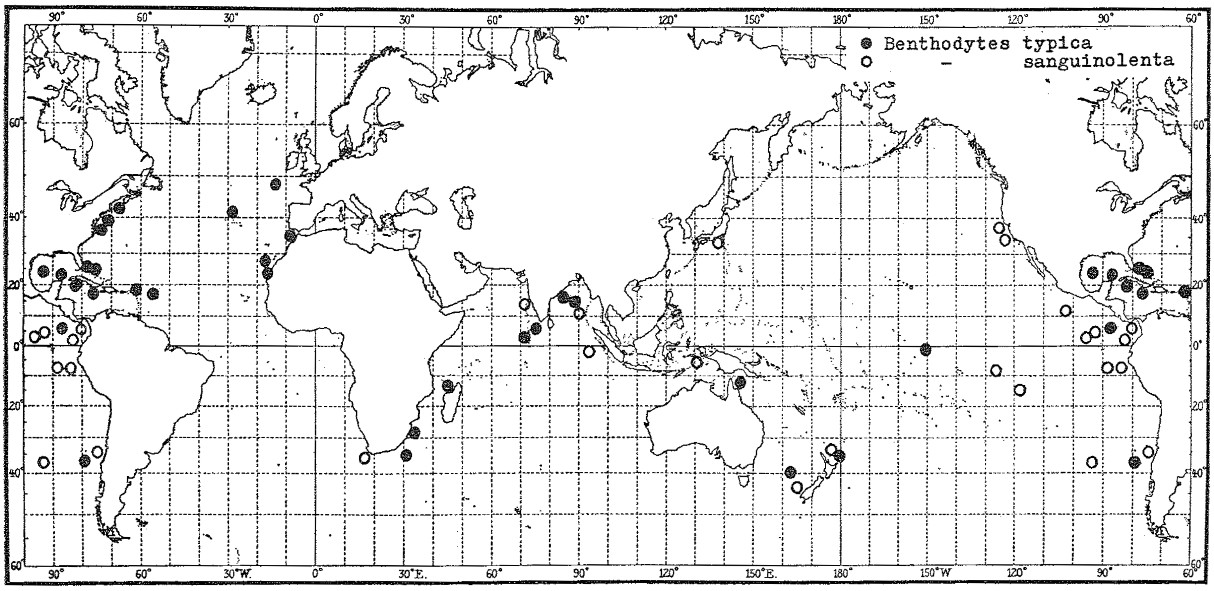


Fig. 116. Records of *Benthodytes* (2).

conclusions regarding the distribution of the species are liable to be drawn. The deeper part of the abyssal zone (3000/4000–6000 m) is well explored only in a region between the Bay of Biscay and the Azores. This might explain why the two otherwise widely distributed deep-abyssal species, *Oneirophanta mutabilis* and *Psychropotes longicauda,* are known only from this part of the Atlantic. The third species of the region, *Amperima rosea,* although not recorded from elsewhere, may have a much wider distribution within the deep-abyssal zone than indicated by the few finds.

Among the species recorded more than once, only two have not been recorded from other oceans. One is the above-mentioned *Amperima rosea,* the other *A. furcata* which is known from two records from the bathyal-abyssal transition zone (1846 and 2320 m).

Of the eleven species which the North Atlantic has in common with other oceans, five (*Oneirophanta mutabilis, Deima validum, Benthodytes*

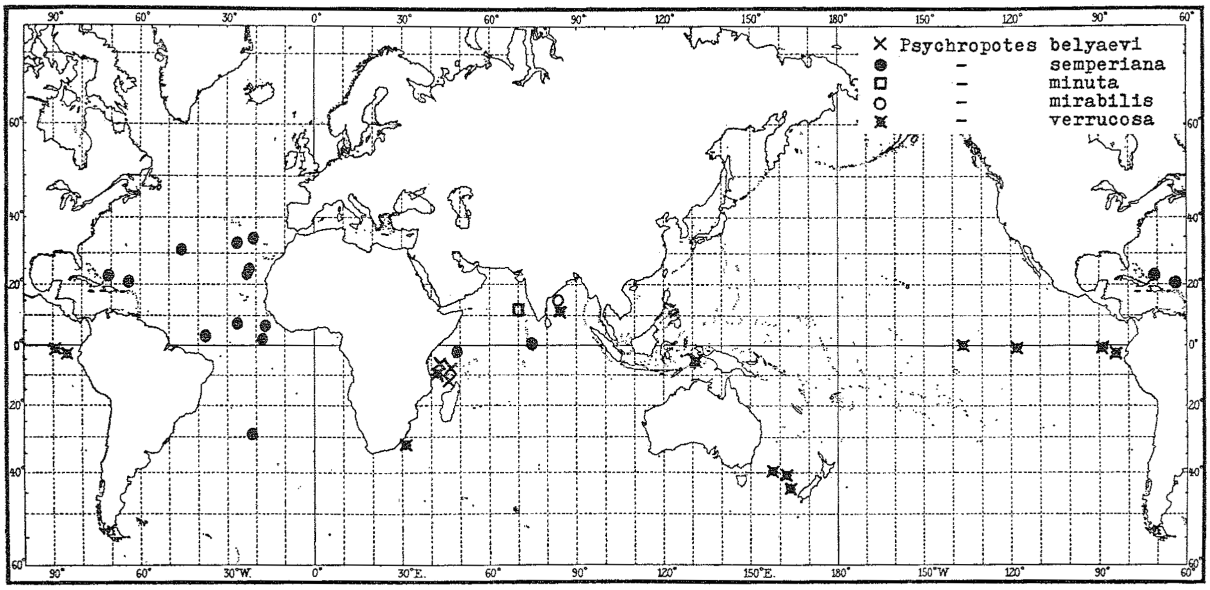


Fig. 117. Records of *Psychropotes* (1).

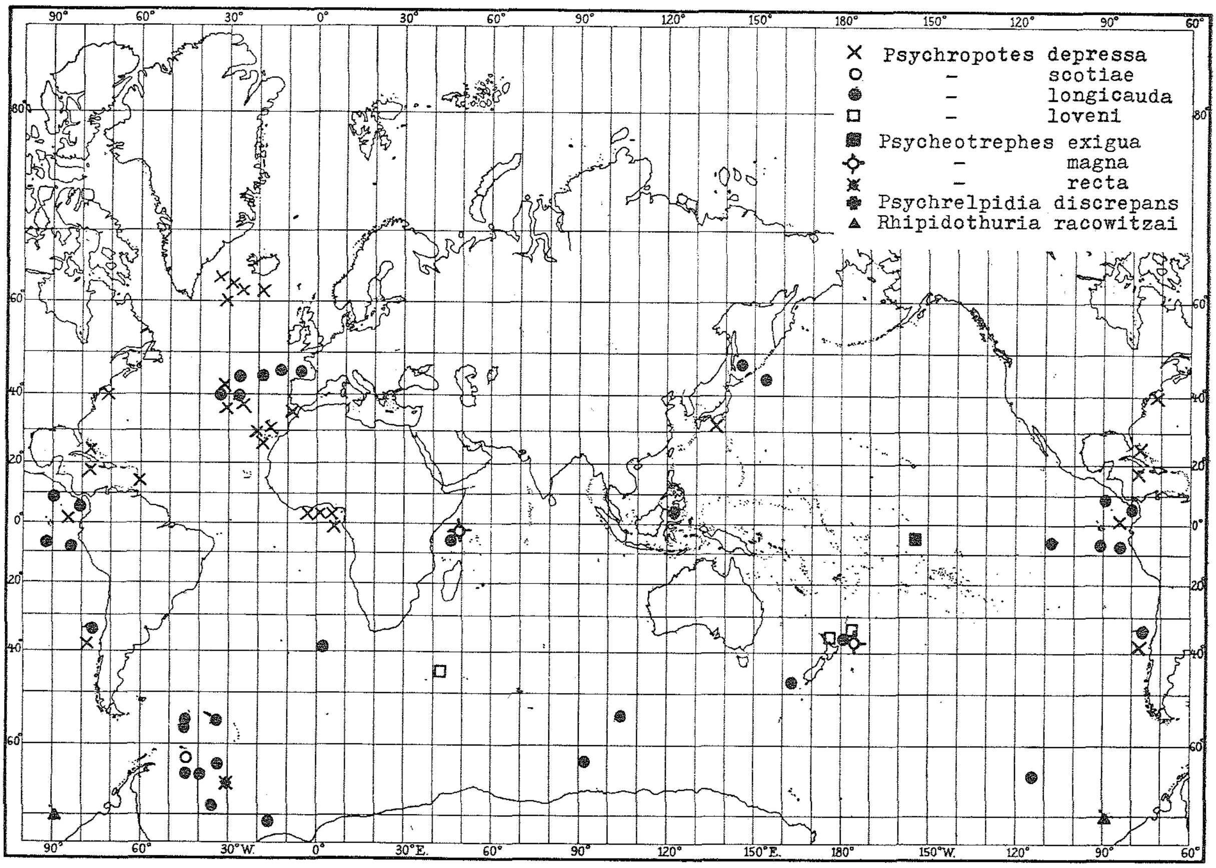


Fig. 118. Records of *Psychropotes* (2), *Psycheotrephes, Psychrelpidia* and *Rhipidothuria.*

typica, Psychropotes longicauda, and *P. depressa)* are world-wide. Three *(Peniagone azorica, P. diaphana,* and *Ellipinion delagei)* range to the southwestern Pacific. *Peniagone wyvillii* is also known from the Central Pacific, *Benthodytes lingua* from the South Atlantic, and *Psychropotes semperiana* from the western Indian Ocean.

The similarities between the holothurian faunas of the North Atlantic and the southwestern Pacific suggest a conveyance of pelagic larvae or juveniles by deep currents (p. 238).

Some otherwise widely distributed species have not been recorded from the North Atlantic *(Amperima naresi, Scotoplanes globosa, Benthodytes sanguinolenta,* and *Psychropotes verrucosa).*

According to Deichmann (1930), deep-sea species of holothurians are usually found at shallower depths in the western than in the eastern North Atlantic. However, the Elasipoda show only two examples: *Deima validum* is bathyal off the West Indies, but exclusively abyssal in the eastern North Atlantic. *Benthodytes typica* is bathyal in the western Atlantic, but otherwise abyssal. No species of the pronouncedly abyssal family Elpidiidae are known to ascend into the West Indian bathyal region.

While the North Atlantic deep sea as a whole differs from the other oceans by few faunistic features, distinctive deep-sea communities might exist in places within this ocean. The remarkable occurrence of a species of *Elpidia* at the base of the continental slope off the coast of North-West Africa indicates unusual conditions, possibly correlated with a rich upwelling (p. 173).

4. The South Atlantic.

A few deep-abyssal stations in the equatorial part and a number of upper-abyssal stations along the coast of the Gulf of Guinea do not permit a discussion of zoogeographic relationships.

5. The Indian Ocean.

Explored at abyssal depths off South and East Africa, as well as in the Arabian Bay and the Bay of Bengal.

Out of a total of 16 species of abyssal Elasipoda recorded from the Indian Ocean, seven have not been found elsewhere. However, only three of these have been recorded more than once: *Psychropotes belyaevi* (3 stations between Madagascar and East Africa), *Benthodytes plana* (southwest of Ceylon and off South Africa), and *Peniagone convexa* (southwest of Ceylon and off East Africa). Of the eight species recorded from other oceans, four are world-wide, two *(Psychropotes verrucosa* and *Benthodytes sanguinolenta)* have wide Indo-Pacific distributions, one *(Peniagone rigida)* is known from the northwestern Pacific, and one *(Psychropotes semperiana)* from the Atlantic.

Deima validum occurs at bathyal and abyssal depths (1224–4320 m) in the northern Indian Ocean. The region has no records of Elpidiidae from less than 3194 m and of Psychropotidae from less than 2738 m.

6. The Indonesian seas.

Explored by stations in the bathyal and the bathyal-abyssal transition zone, and in the hadal zone of the Banda Trench.

The two species recorded from the Banda Trench *(Benthodytes sanguinolenta* and *Psychropotes verrucosa)* are both widely distributed.

Another two are examples of an ascent of abyssal forms into shallower depths: *Deima validum,* recorded from 724–1158 m (Strait of Macassar, south of Celebes, Banda Sea), and a *Peniagone (Scotoanassa incerta* Sluiter) from 538–724 m (Strait of Macassar, southwest of Celebes), an exceptionally shallow occurrence for the genus *Peniagone.*

Mortensen (1923) found that in the region round the Kei Islands "a rich and genuine abyssal fauna", including "various Elasipoda", occurred at only 200–300 m depth. Similar observations were made on the *Challenger* and the *Siboga.* But a study of Mortensen's material showed that the Elasipoda cannot be adduced as evidence of an ascent of deep-sea species to shallow depths in this region. Three species of Elasipoda were taken – *Orphnurgus glaber* (245–352 m), *Laetmogone maculata* (225–245 m), and *L. fimbriata* (245 m). They are, however, upper bathyal also outside this region, and their occurrence off the Kei Islands is not exceptionally shallow.

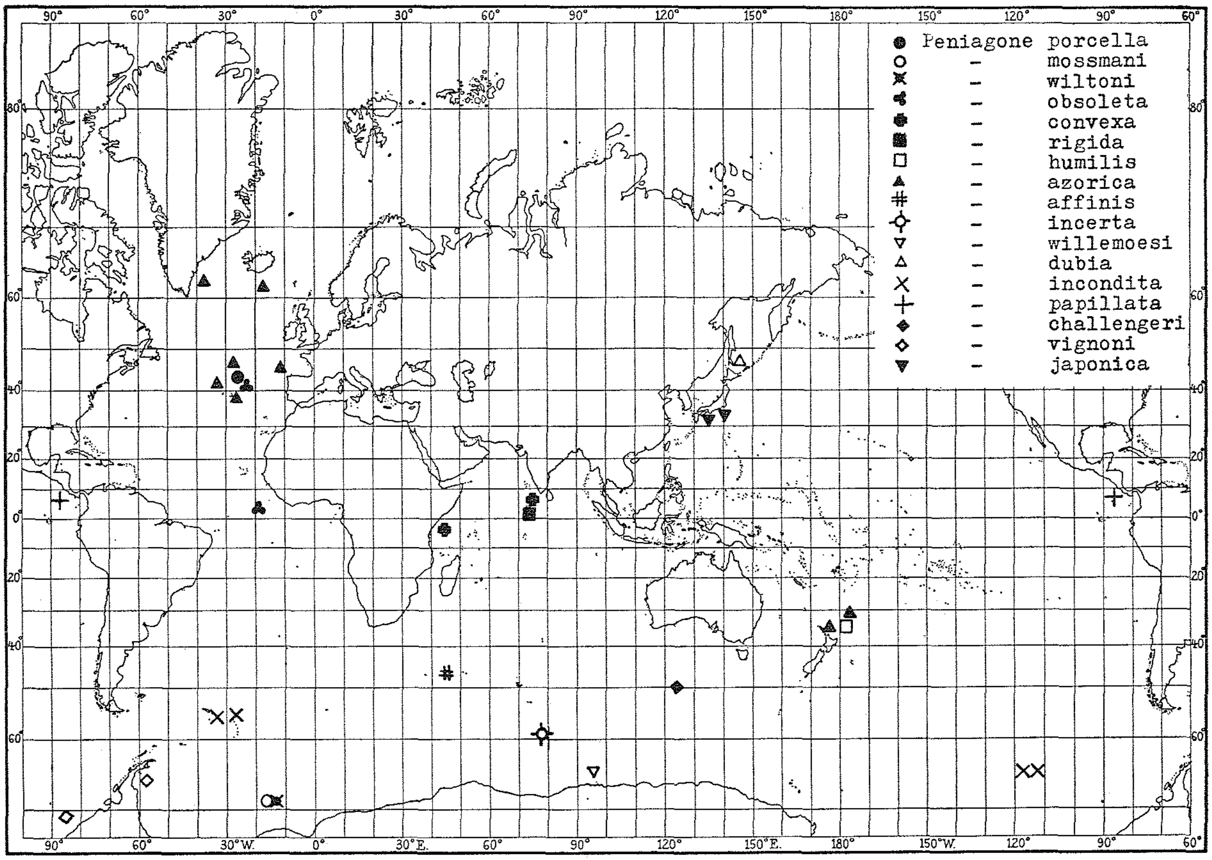


Fig. 119. Records of *Peniagone* (1).

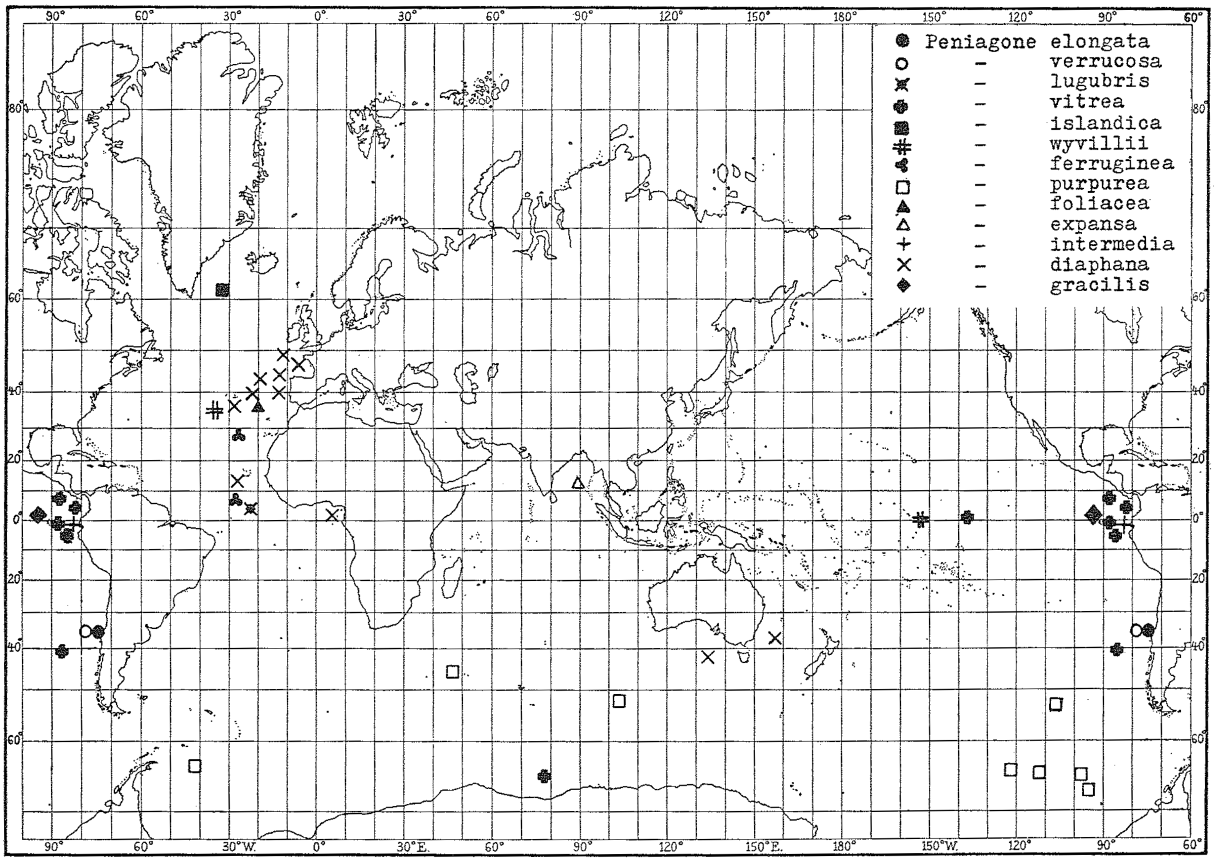


Fig. 120. Records of *Peniagone* (2).

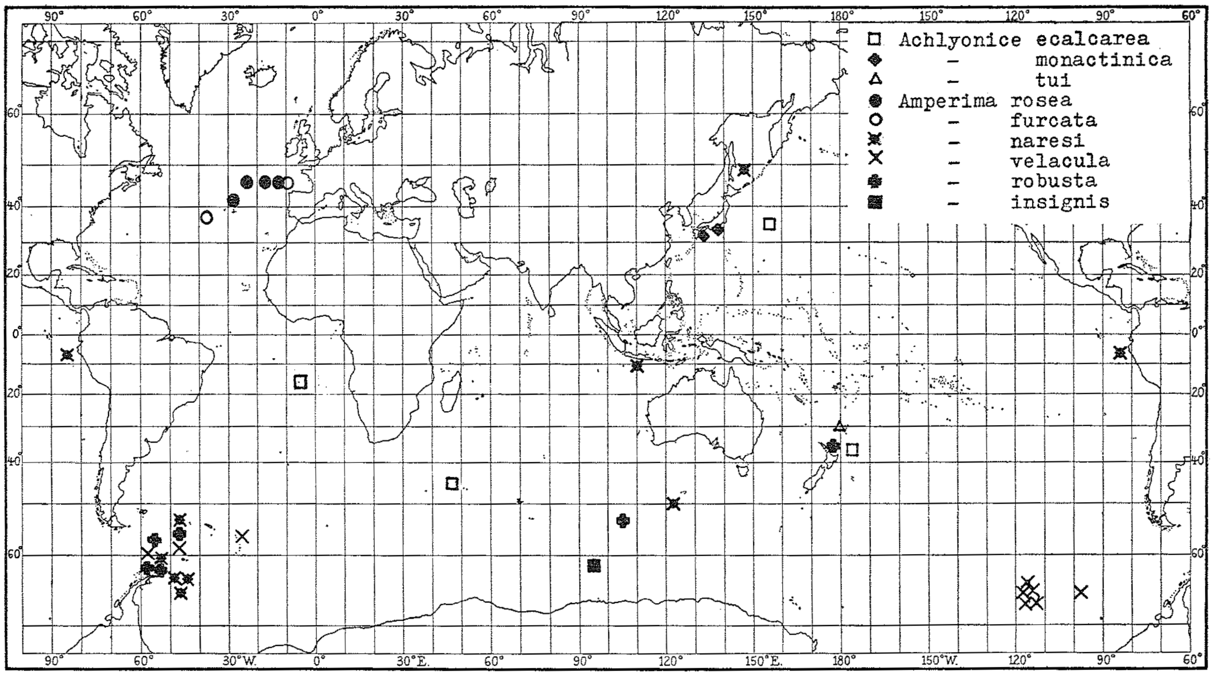


Fig. 121. Records of *Achlyonice* and *Amperima*.

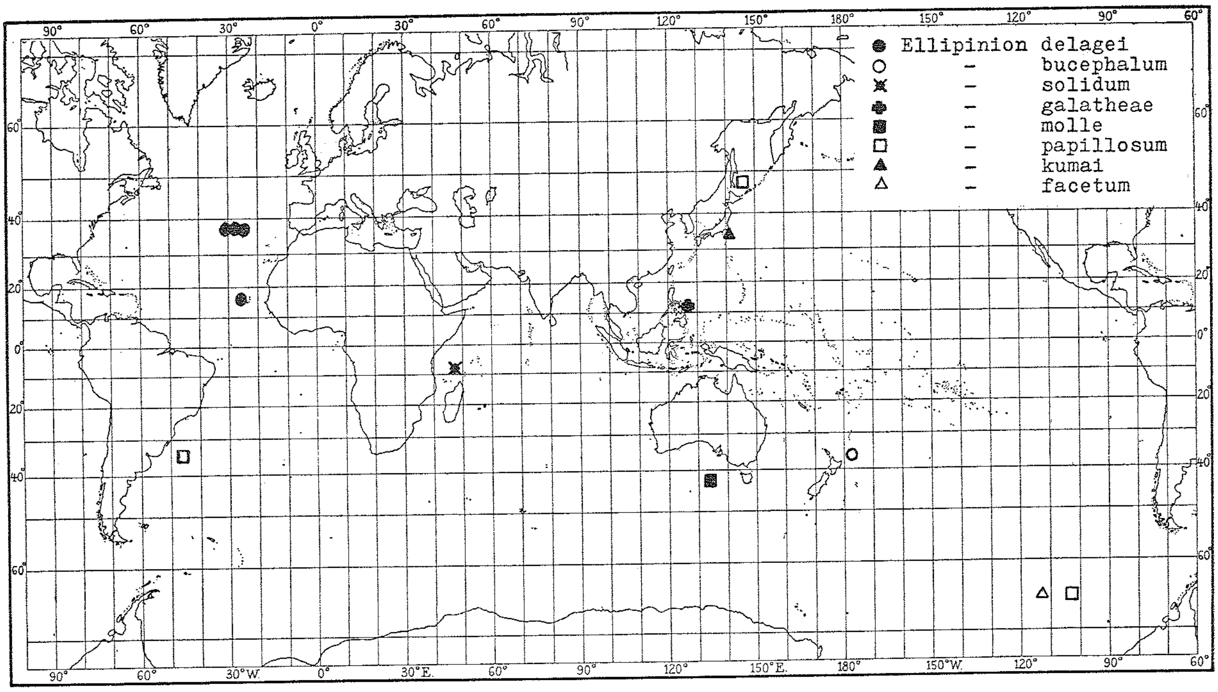


Fig. 122. Records of *Ellipinion.*

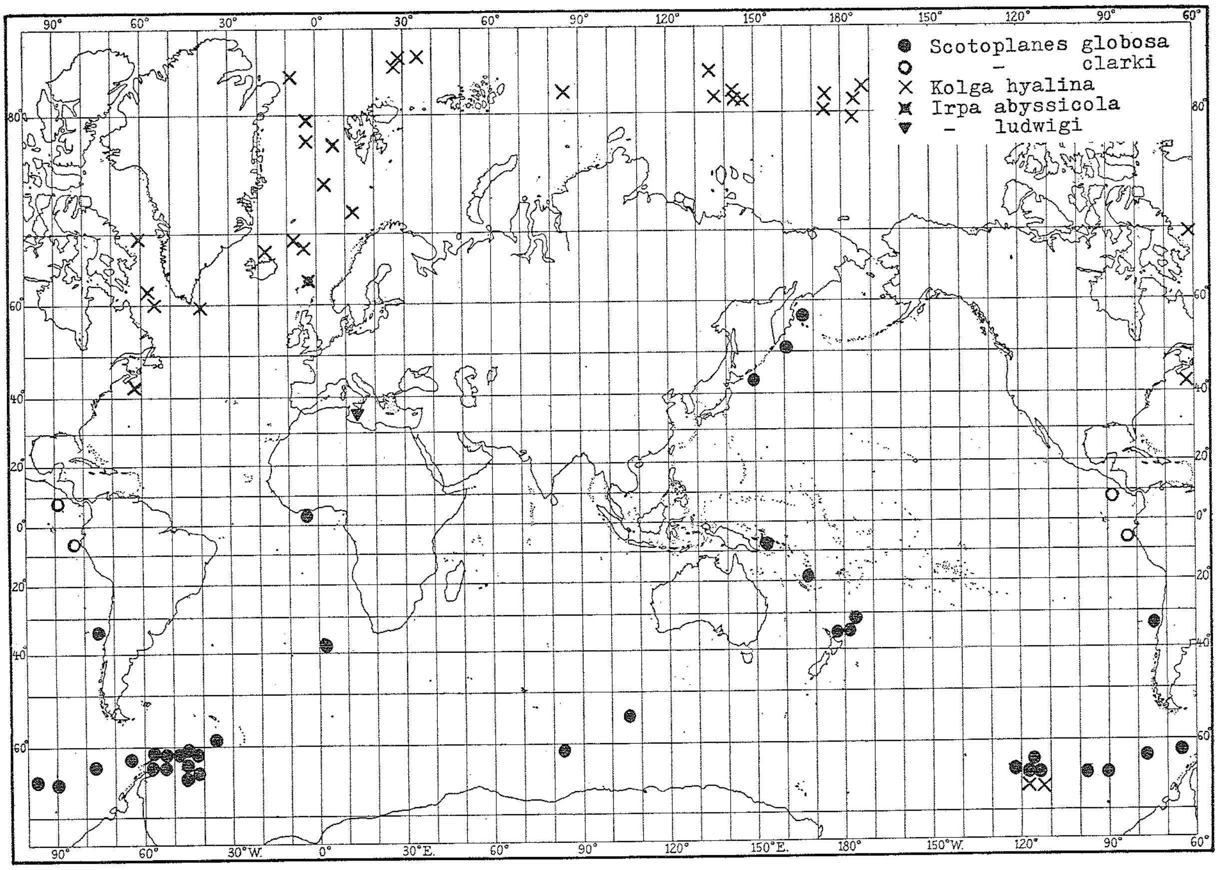


Fig. 123. Records of *Scotoplanes, Kolga* and *Irpa.*

7. The Pacific Ocean.
The abyssal depths are very little explored, apart from the southwestern part (the Tasman Sea and north of New Zealand) and a region extending from California to Peru. A number of trenches have been investigated at abyssal and hadal depths.

The faunal similarities between the southwestern Pacific and the North Atlantic have already been mentioned. Otherwise, the fauna of the southwestern Pacific consists of species with a world-wide or wide Indo-Pacific distribution or with an Antarctic or southern distribution.

The abyssal fauna off the west coast of Central America and northern South America is remarkable for its richness in number of species and individuals, and for its taxonomic relationship. Some widely distributed species are here represented by endemic subspecies or by closely related species (p. 246).

The characteristic features of this fauna are likely to be correlated with the rich supply of nutrient matter caused by upwelling and possibly also by turbidity currents and mud slides due to the steep gradient of the continental slope. The poor food conditions of the Central Pacific may have caused the extinction of species from this region, cutting off the eastern Pacific populations from the main distributional area of the species. In some cases (e. g. *Oneirophanta mutabilis)* the eastern Pacific population may have regained contact with the other populations, although still preserving its characteristic features.

The region extends northward to about 30° N, where it is replaced by a Californian abyssal fauna of a different composition (Parker 1964). Parker suggested that the change in faunal composition was due to convergent deep-sea currents in combination with submarine ridges. The southern boundary of the region has yet to be determined.

Remarkable similarities are found between the abyssal faunas of the eastern Pacific region and the Kermadec Trench. Both regions are rich in number of species as well as in individuals, and the dominating species are often the same, or

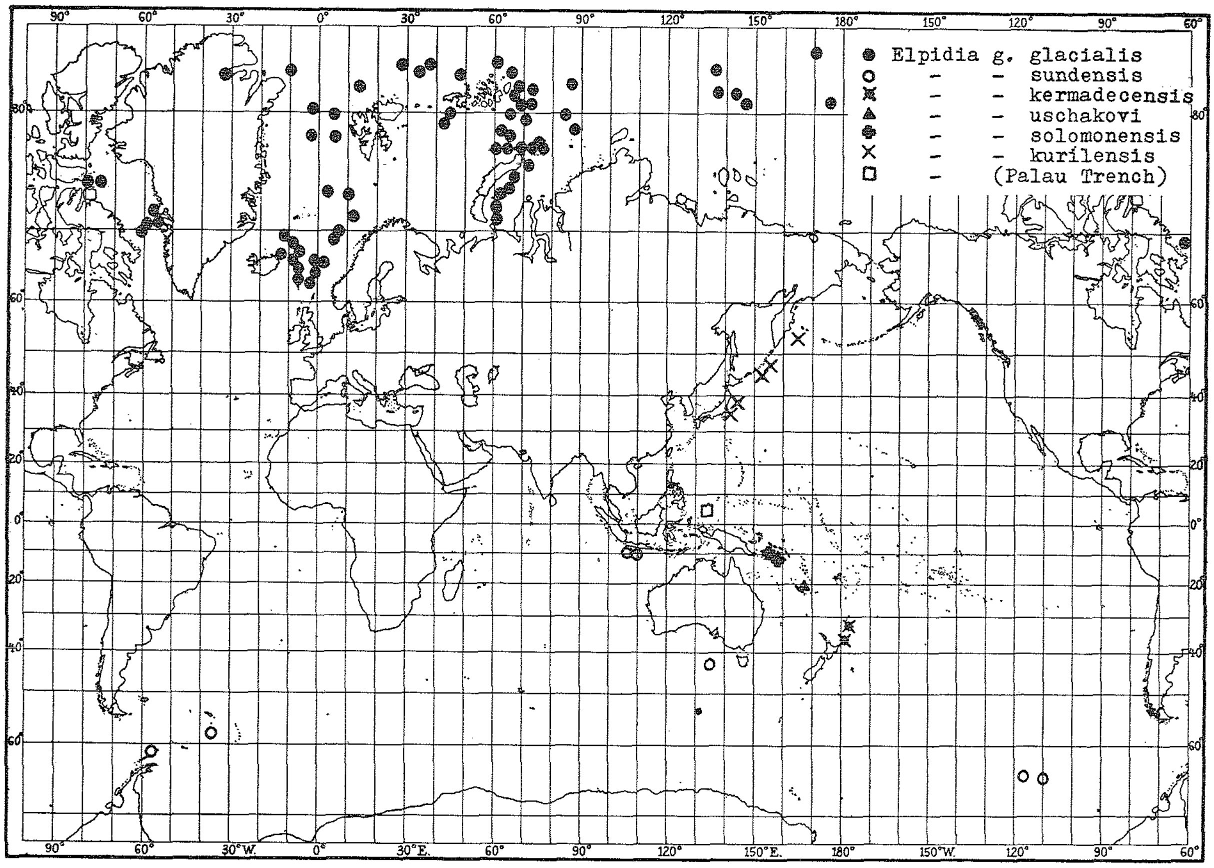


Fig. 124. Records of *Elpidia glacialis.*

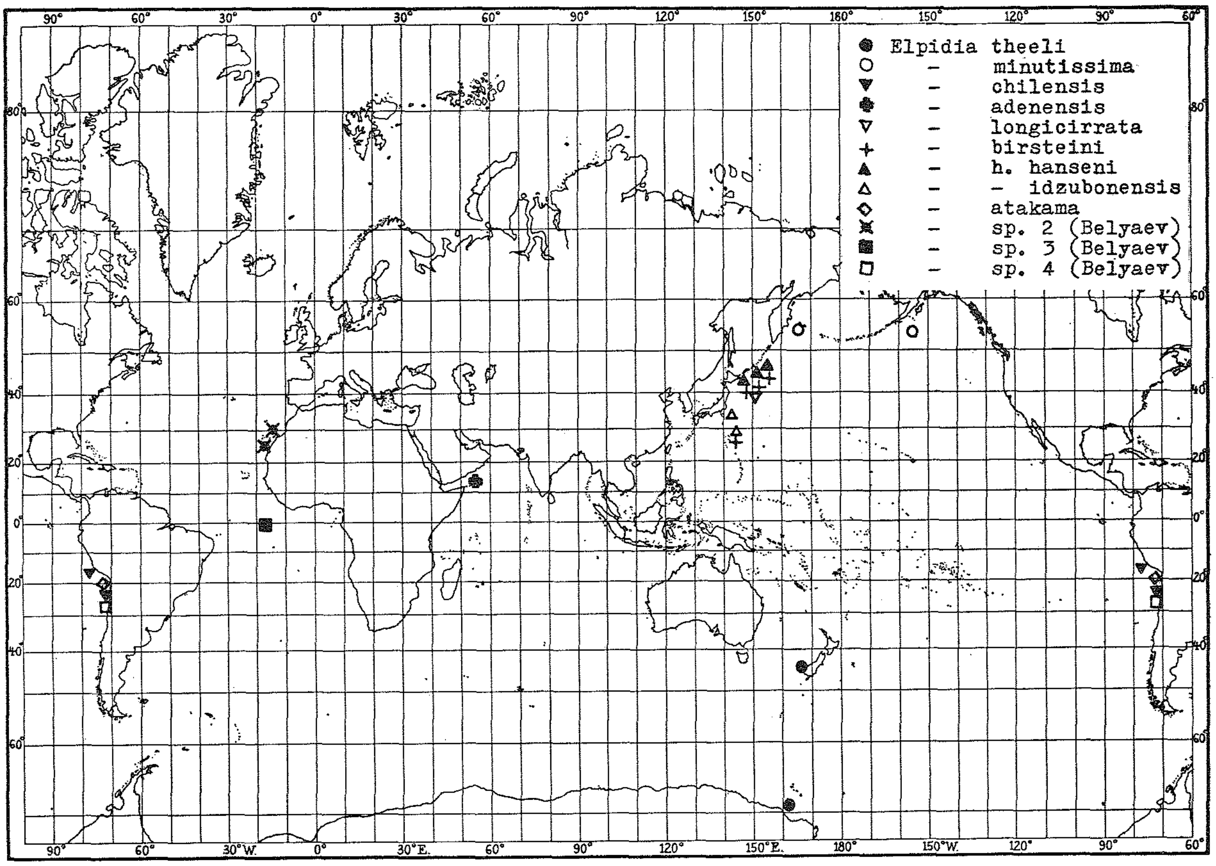


Fig. 125. Records of *Elpidia* (other than *E. glacialis*).

closely related forms. An abyssal fauna of a rather similar composition may be characteristic of the Antarctic region, of which the dominating elasipods are *Oneirophanta mutabilis, Psychropotes longicauda, Scotoplanes globosa,* and *Elpidia glacialis* (Agatep 1967b).

The fact that the dominating species of the three faunas are among the most widely distributed species of Elasipoda indicates that the faunal similarities are ecologically rather than geographically determined. Probably, the similarities are due to a rich supply of nutrient matter in all three regions.

8. The Arctic Basin.

The Arctic Basin (including the Norwegian Sea) is very poor in species. The families Deimatidae and Psychropotidae are absent, and the Elpidiidae is represented by three species only *(Elpidia glacialis, Kolga hyalina, Irpa abyssicola).* The elpidiid genera *Peniagone, Amperima, Ellipinion,* and *Scotoplanes,* all abundantly represented in the remaining deep sea, are absent from the region. It is noteworthy that the three elasipod species of the Arctic Basin belong to closely related genera.

One of the Arctic species *(Irpa abyssicola)* is known only from the type specimen. The other member of the genus *(I. ludwigi)* is known only from the Mediterranean deep sea. *Elpidia glacialis* is represented by the endemic subspecies *E. g. glacialis. Kolga hyalina* occurs also in the northernmost North Atlantic and the Antarctic Ocean.

The Arctic Basin is separated from the Pacific Ocean by extensive sublittoral areas, and from the Atlantic Ocean by the North Atlantic Ridge, with sill depths of about 500 m. The absence of many species and taxa in the Arctic Basin may be due to inability to cross the North Atlantic Ridge, rather than to the negative temperature.

The deep-sea elements in the Arctic sublittoral fauna are considered elsewhere (pp. 234–235).

9. The Mediterranean.

Apart from three dredgings deeper than 3000 m (Marion 1883) the few deep-sea stations are all from less than 1445 m (von Marenzeller 1893b, 1895, Hérouard 1923).

The Mediterranean is separated from the Atlantic by a sill with a depth of about 400 m. The deep water, deriving from the surface, remains constant at c. 13° C. below a depth of c. 1000 m. In spite of this, the Mediterranean deep-sea holothurians belong to the usual deep-sea groups (p. 235).

The ranges of geographic distribution compared with those of other groups

Wide geographic distributions are characteristic not only of holothurians. They have been shown in porcellanasterids (Madsen 1961a) – and may apply to all echinoderm groups – in molluscs (Knudsen 1970), ascidians (Millar 1970), and polychaetes. The polychaete species are probably the most widely distributed of all deep-sea animals, as indicated by the world-wide distribution of many of the hadal species (Kirkegaard 1956).

Restricted distributions appear to be the rule in the Pogonophora, a deep-sea group inhabiting regions close to the coast (Ivanov 1963).

Also some groups of Crustacea have been considered to have remarkably restricted species distributions. Barnard (1961) found this to be the rule in the deep-sea benthic Amphipoda, and proposed the explanation that the species were recent immigrants to the deep sea and/or had a slow rate of dispersion. The species known from widely separated localities proved to be either eurybathic or to have special mechanisms of dispersal.

Wolff (1962) similarly found that the species of the abyssal Isopoda were remarkable for their restricted distributions.

Jones & Sanders (1972) showed that a narrow bathymetric range and a pronounced regional endemism are characteristic of the Cumacea.

F. DISTRIBUTION IN RELATION TO ENVIRONMENTAL FACTORS

In the uniform environment of the deep sea the influence of the physical factors on animal distribution would seem to present a less complicated pattern than in shallow water. It is surprising, therefore, that the geographic and bathymetric distribution of the Elasipoda can hardly ever be correlated with parameters of the physical environment.

Temperature

The temperature has generally been regarded as the main factor determining the bathymetric distribution of deep-sea animals. This view was also held by Bruun (1957), who pointed out that the abrupt change in temperature between the warm thermosphere and the cold psychrosphere agrees fairly well with the change in faunal composition from the sublittoral to the bathyal zone. The change in temperature usually takes place at about 10° C.

According to Bruun, also the bathyal-abyssal boundary was mainly determined by the temperature, coinciding with the isotherm of 4° C. The abysso-hadal boundary, on the other hand, does not coincide with a change in temperature. Due to adiabatic heating the temperature in the hadal zone shows a slight increase with depth.

The fact that the sublittoral-bathyal and the bathyal-abyssal boundaries largely coincide with isotherms does not imply that the faunal changes are determined by the temperature. In order to examine a possible influence of the temperature, the bathymetric distribution of the species should be investigated in regions where the said isotherms are closer to the surface (Antarctic and Arctic seas) or are entirely absent (the Mediterranean).

1. Faunal similarities between the polar sublittoral regions and the deep sea.

(1) The Antarctic. A number of sublittoral and abyssal stations have been operated, while the bathyal depths are almost unexplored. A possible ascent of deep-sea species has to be concluded from the existence of bathyal and abyssal elements in the sublittoral Antarctic fauna.

The present investigation confirms the view held by Ekman (1925) that the Antarctic sublittoral echinoderm fauna contains very few deep-sea elements. In the Antarctic seas, at depths less than 600 m, the deep-sea groups of holothurians are represented by the following species:

Elasipoda. *Peniagone vignoni*, taken at 400 m in the Antarctic, is the shallowest recorded member of the genus. Its close relative, *P. japonica,* is the next shallowest recorded species (Japan, 1135–1669 m; temp. 2.6–3.4° C.).

Amperima velacula is known only from the Antarctic (131–4850 m). It is the shallowest recorded member of the genus.

Apodogaster alcocki, taken at 385 m in the Antarctic, is otherwise known from the Bay of Bengal at 1026 m and 7.2° C. The shallow occurrence in the Antarctic is apparently not determined by the low temperature.

Aspidochirota. Three species of the family Synallactidae have been recorded from the Antarctic sublittoral. (A fourth species, *Synallactes carthagei* Hérouard, in my opinion is a synonym of the dendrochirote, *Ekmocucumis turqueti).*

Pseudostichopus mollis Théel is known from the Antarctic and southern Chile at 137–400 m. It is otherwise recorded from the eastern Pacific (Gulf of Panama to California) at 245–3436 m and 2.2–12.7° C., which indicates that the shallow Antarctic occurrence is not due to low temperature.

Bathyplotes moseleyi (Théel) has been recorded from the Antarctic and southern Chile at 100–627 m, and from off Japan at 127–805 m and 1.8–13.5° C. These widely separated areas are not likely to be connected through a deep-sea occurrence. (Apart from the record of *B. reptans* from 2212 m off the Canary Islands, no member of the genus has been taken deeper than 1300 m). Probably, the northern and southern records of *B. moseleyi* refer to different species.

Mesothuria bifurcata Hérouard is recorded from a juvenile Antarctic specimen taken at about 450 m. A specimen from 2337 m depth south of Iceland was only tentatively referred to the same species (Heding 1942). The record at 450 m is not especially shallow in the genus.

Molpadonia. *Molpadia antarctica* (Théel) was recorded from off southern Chile at 220–631 m. The depth range is not unusual in this predominantly bathyal genus.

Dendrochirota. *Abyssocucumis abyssorum* (Théel) is a widely distributed abyssal species, recorded from depths of 1645–4064 m. The Antarctic record from 385 m (Ekman 1927) refers to a juvenile specimen (4 mm long) which might have been misidentified.

The two Antarctic sublittoral dendrochirotes, *Staurocucumis liouvillei* (Vaney) and *Ekmocucumis turqueti* (Vaney), both belonging to monotypic genera, are most closely related to the abyssal genus *Abyssocucumis.*

Apoda. The Antarctic sublittoral members of Apoda are not related to deep-sea forms.

(2) The Arctic. The absence in the Arctic Basin of practically all the abyssal holothurians of the North Atlantic indicates that in high latitudes abyssal species in general do not ascend to shallow depths. The temperature (c. 4° C.) at the top of the North Atlantic Ridge would not prevent a migration of North Atlantic deep-sea species into the Arctic Basin.

The Arctic sublittoral has one species *(Elpidia glacialis)* in common with the Arctic deep sea. However, it is remarkable that the sublittoral records are from the Kara Sea, a region where special conditions prevail (p. 173). Usually, the species in the Arctic does not ascend to depths smaller than 400 m.

The following deep-sea holothurians ascend to shallow depths in northern latitudes:

Laetmogone violacea ranges from 256–1804 m and from 2.2–10.2° C. All records from less than 654 m are from Greenland waters.

Psychropotes depressa. The shallowest record is from south of Iceland (957 m). The temperature was probably 3–4° C., which is in the warmer part of its normal range (1.6–4.2° C.). The next shallowest record (1158 m) is from the eastern Atlantic at about 7° C. – the only known occurrence of the species at temperatures higher than 4.2° C. Thus, the shallow records do not coincide with low temperatures.

Scotoplanes globosa has been recorded twice from depths of less than 2000 m off Japan (545 and 970 m), both stations with "abyssal" temperatures (2.2° and 1.6° C.). However, bathyscaphe observations of *Scotoplanes globosa* (or the closely related abyssal species, *S. clarki)* in the San Diego Trough (depths 1060 and 1243 m, temp. 3.0° C.) indicate that the ascent of *Scotoplanes* to shallow depth depends primarily on sedimentary conditions (p. 196).

Bathyplotes natans, which in the eastern North Atlantic occurs at 600–1600 m, ascends along the Norwegian coast to 200 m. This is the only example of a synallactid ascending to shallower depths in northern latitudes.

No deep-sea species of Dendrochirota, Molpadonia, or Apoda ascend to shallower depths in northern latitudes.

A taxonomic relationship between the deep sea and the Arctic sublittoral is shown by the Myriotrochidae (order Apoda), which occur at shallow depths only in high northern latitudes (p. 216).

(3) Conclusion. Almost no deep-sea holothurians are known to ascend to shallower depths in polar seas.

A faunal relationship between the polar sublittoral regions and the deep sea is shown at a higher taxonomic level. Two species of Antarctic sublittoral Dendrochirota are closest related to deep-sea forms, and the species of Myriotrochidae are found either in the Arctic sublittoral or in the deep sea.

The fact that the deep-sea fauna has entirely different relationships to the sublittoral faunas of the Arctic and Antarctic indicates that the migration was from sublittoral depths into the deep sea, and not the opposite way. An ascent of deep-sea species to shallow depths would probably have resulted in similarities in the representation of deep-sea elements in the Arctic and Antarctic sublittoral faunas.

2. Penetration of species into the Mediterranean deep sea.

The constant temperature prevailing below a depth of 1000 m in this sea would make it possible to eliminate the temperature factor in the study of the vertical zonation of the deep-sea fauna. Unfortunately, the Mediterranean deep-sea fauna is practically unexplored apart from that of the upper bathyal zone (pp. 232–233).

The Mediterranean deep sea has one endemic holothurian, the elasipod *Irpa ludwigi*. The other five species known from the Mediterranean deep sea occur also in the North Atlantic deep sea. The known depth ranges are:

Mesothuria verrilli (Théel). Mediterranean: 280–1103 m. Atlantic Ocean: 618–4165 m.

Mesothuria intestinalis (Ascanius). Mediterranean: 390–1445 m. Atlantic Ocean: 20–1400 m.

Pseudostichopus occultatus v. Marenzeller. Mediterranean 415–3624 m. Atlantic Ocean: 232–2984 m.

Stichopus regalis (Cuvier). Mediterranean: 5–834 m. Atlantic Ocean: 30–470 m.

Molpadia musculus (Risso). Mediterranean: 50–200 m. Cosmopolitan: 36–3580 m.

Thus, only *S. regalis* is known to penetrate deeper in the Mediterranean than in the Atlantic Ocean. Strangely enough, the opposite holds good of *M. musculus* which seems to be restricted to the sublittoral zone in the Mediterranean, while in other regions it penetrates into the abyssal zone.

3. Comparison with other groups.

A general lack of dependence on temperature in the vertical distribution of the species is not confined to exclusive deep-sea groups, such as the various taxa of deep-sea holothurians. The bivalves, in which the sublittoral species are apparently rather easily adapted to the deep-sea environment, show no preference for a descent into the deep sea in Arctic or Antarctic regions (Knudsen 1970).

Wolff (1962), on the other hand, found that in the Isopoda the bathyal-abyssal boundary was indistinct in high latitudes, owing to the presence of many eurybathic cold water species.

Sediments and nutrient conditions

The vertical zonation of the sea according to biological principles agrees fairly well with the commonly used zonation according to type of sediment. While the littoral and sublittoral zones are covered with terrigenous sediments and the abyssal zone with pelagic sediments, the bathyal zone is covered with a transitional type, the hemipelagic sediments, which contain a decreasing amount of terrigenous material towards the abyssal zone.

Nevertheless, it is doubtful whether a causal relationship exists between the usually distinguished sediment types (terrigenous sediments, Globigerina ooze, diatom ooze, pteropod ooze, abyssal clay) and the vertical and horizontal distribution of animal species. No elasipods known from more than one station have been recorded only from diatom ooze, pteropod ooze, or abyssal clay. Even the most widely distributed abyssal sediment, the Globigerina ooze, shows only three species with more than one record which have not been recorded from other types of sediment as well: *Benthodytes plana* (two stations), *Psychropotes belyaevi* (four stations close to each other), and *Amperima rosea* (three stations close to each other).

This absence of correlation suggests that the usually distinguished sediment types are based on criteria which are biologically irrelevant.

Investigations on animal communities from shallow water confirm that the relationship between animal distributions and sediment types is not of a simple nature. Sanders (1958) found that the occurrence of the two dominating species, *Nucula proxima* and *Nephthys incisa,* in a sediment-eating association in Buzzards Bay depended on a clay content of 10–20 % in the sediment, rather than on the texture of the sediment as a whole. The organic matter bound to the clay particles (which are less than two microns in diameter) appeared in this sediment to be presented in a way which agreed with the feeding biology of these particular species.

Ursin (1960) showed that the distribution of echinoderm species in the North Sea only to a small degree depended on the texture of the sediment. Buchanan (1963) similarly found that the distribution of three animal communities off the Northumberland coast was poorly correlated with the texture of the sediments: Similar sediments could be associated with very different faunas, and conversely, a mixture of sediment types was not necessarily accompanied by a mixing-up of the animal communities.

Ekman (1947), on the other hand, found that the distribution of various invertebrates in the Gullmarfjord and the Skagerrak was partly correlated with the compactness of the sediments.

Sanders *et al.* (1965), studying the faunal assemblages along the transect from Gay Head (Massachusetts) to Bermuda, found that the density of animals on the sea floor showed no clear correlation with the content of organic matter in the sediment. This was ascribed to the fact that the analytical techniques (Kjeldahl analysis and determination of organic carbon) did not differentiate between labile and refractory organic matter. The abyssal sediments with their smaller supply of organic matter, according to the authors, might show a higher percentage of refractory matter than the bathyal sediments. Furthermore, the greater faunal density in the bathyal zone might lead to a greater mixing of the sediments and thus to a quicker burial of refractory matter.

Thus, neither grain size nor organic content of the sediment seem to directly influence the distribution of animal species. The features on which they depend are more complicated. As almost nothing is known of the vertical and horizontal distribution of these features in the deep sea, it is not to be expected that usual expedition materials should reveal correlations between sediment types and animal distributions.

While the organic content of the sediments is a doubtful indicator of their nutritive value, a better indication of the food conditions might be gained through a knowledge of the amount of organic matter supplied from the euphotic zone. Sokolova (1972), based on organic surface productivity, divided the world ocean into eutrophic and oligotrophic regions. Eutrophic conditions prevail in the peripheral and equatorial parts of the oceans. Vast oligotrophic regions are found in the northern and southern Pacific.

The supply of organic matter is especially high in places where upwelling occurs. The rich fauna at St. 716, situated beneath the Costa Rica Dome, is likely to be conditioned by a rich surface production due to upwelling. The only known instance of brood protection in deep-sea holothurians (in *Oneirophanta mutabilis)* is from this station. The young seem to be developed during the upwelling season. This suggests that seasonal variations in the surface production may be reflected to a depth of at least 3600 m (p. 200).

Turbidity currents and mud slides may in some regions play a major role in the food supply to the deep-sea bottom. Heezen *et al.* (1955) suggested that they may not only convey large quantities of nutritive matter for the abyssal fauna, but that they may also involve mass burial of animals on the abyssal sea floor, which again may lead to oil-forming deposits. An indication that turbidity currents exert a great influence on animal life in restricted localities is provided by the investigations of Griggs *et al.* (1969) in the Cascadia Channel off the Oregon coast. The channel, which is richly supplied with terrestrial detritus conveyed by turbidity currents, has an animal density four times higher than the surrounding abyssal plain. Besides, the turbidity currents could be shown at times to have led to a complete destruction and burial of the benthic fauna.

Turbidites may be responsible for the formation of the smooth "abyssal plains" (Johnson 1964), and both turbidites and sediments derived from mud slides are probably brought to the bottom of the trenches in large quantities down their steep slopes (p. 240). Thus, Anikouchine & Ling (1967) demonstrated that the sediments of the Java and Mindanao Trenches are mostly turbidites, and that even the sediments of the oceanic Mariana Trench contain significant additions of turbidites.

An abundant supply of sediments to the trenches probably forms the basis of the rich fauna of Elpidiidae at hadal depths (pp. 195–196).

The similarity in species composition of the rich abyssal holothurian faunas of the eastern Pacific region, the Antarctic, and the Kermadec Trench may be due to a rich supply of organic matter in all three regions (pp. 231–232).

If a region with an abundant food supply is bordered by barren regions, a geographic isolation of species may result. The distinctive features of the eastern Pacific region (p. 231) may be due to such type of isolation.

Russian workers (Vinogradova 1962b, Zenkevich *et al.* 1971) have done an extensive work in mapping the distribution of biomass in the oceans. An analysis of the species composition in relation to the variations in biomass might yield interesting results. It should, however, be emphasized that the biomass, or standing crop, is not a direct measure of the organic production. In shallow water communities a high biomass may represent many years' production, while a smaller biomass composed of short-lived species may be combined with a high organic production.

While variations in the food supply to the bottom seem to exert a great influence on the geographic distribution of deep-sea species, an influence on the bathymetric distribution seems more doubtful. It might be assumed that deep-sea species ascend to shallower depths in regions with a poor food supply, while in regions with a rich supply shallow water species would penetrate deeper. However, no such correlation can be demonstrated in the bathymetric distribution of the Elasipoda. Thus, in the barren region off the West Indies only two species of Elasipoda, *Benthodytes typica* and *Deima validum,* ascend to shallower depths. The occurrence of *D. validum* at equally shallow depths in the rich eastern Pacific region suggests that the range of bathymetric distribution in this species is not determined by food conditions alone.

The rich eastern Pacific region shows no example of holothurians descending to unusually great depths.

Deep-sea species of holothurians thus generally remain at their preferred depths also in regions where the temperature or food conditions might induce them to extend their distribution to other bathymetric zones. This does not, however, prevent that the two factors in combination exert an influence on the bathymetric distribution of many species.

The possibility that the abyssal fauna is conditioned by a combination of low temperature and poor food supply might be checked in cold regions with a poor food supply. An example of an Arctic region with poor food conditions is provided by the Kara Sea, where many deep-sea forms (including *Elpidia glacialis)* ascend to shallow water. But the Kara Sea is also remarkable for the darkness of its water (p. 173). Actually already Moseley (1880) suggested that the occurrence of deep-sea animals at shallow depth in the Arctic is not only due to the low temperature, but also to the darkness of the water during most of the year.

Hydrostatic pressure

A number of physiological and biochemical reactions have been observed in the laboratory when shallow water organisms were exposed to high hydrostatic pressure: Changes in protoplasmic viscosity, pseudopodia formation, ciliary movement, cell division, enzyme activity, etc.

Knight-Jones & Morgan (1966) maintained that the influence of high hydrostatic pressure on living systems is so profound that it is not surprising that the hadal fauna is poor in species. Flügel & Schlieper (1970) similarly regarded the high pressure as one of the factors responsible for the absence of some invertebrate groups at depths exceeding 4000 m. Wolff (1970), in his recent review of the hadal fauna, maintained that the gradual change in faunal composition at depths exceeding 6000 m is primarily caused by increased hydrostatic pressure.

It should be emphasized that the laboratory experiments deal with the pressure reactions of single specimens and have little bearing on the problem whether a species through a multitude of generations may develop genetic adaptations to increased pressure. Actually, there is no indication that inability to pressure adaption has prevented animal groups from penetrating into the deep sea. The few groups which are absent or poorly represented at the greatest depths seem to be prevented by their feeding habits. The low species diversity at hadal depths may be due to the low geological age of the trenches rather than to unfavourable conditions of life at the great depths (p. 219).

The significance of the hydrostatic pressure for the bathymetric distribution of animals is still obscure.

Currents

The distribution of some bathyal and a few abyssal species of Elasipoda seems to be related to ocean currents. This suggests the presence of a pelagic phase in their development, or a faculty of leaving the bottom as adults.

Juvenile and adult benthic holothurians have sometimes been taken in pelagic nets (pp. 204–205). On the other hand, there is no proof of a special, pelagic larval stage of benthic deep-sea holothurians. The eggs in all the families of Elasipoda are so large that possible pelagic larvae are likely to be independent of the plankton for food uptake – thus serving only the dispersal of the species.

Current-dependent distributions are suggested in the following cases:

(1) In the region of Newfoundland where north- and southgoing currents meet. The northgoing currents, which can be traced to a depth of 4000–5000 m, would seem to present an effective barrier to a southward migration of bathyal species with pelagic larvae.

Laetmogone violacea (Fig. 113), which is of common occurrence along the northern and eastern continental slopes of the North Atlantic, might have been obstructed in its southward migration in the western Atlantic by this barrier.

(2) Off Japan a similar boundary exists between north- and southgoing currents, comprising the water masses of the upper 1500 m (Sverdrup *et al.* 1942, fig. 205). The boundary may form a distributional barrier to bathyal species with pelagic larvae or juveniles.

Laetmogone violacea, L. maculata, L. fimbriata, L. biserialis, and *Orphnurgus glaber* are known from Japan up to this boundary, while they have never been taken along the northern and eastern coast of the Pacific. Two of the species *(L. biserialis* and *O. glaber)* have reached the Hawaiian Islands, possibly by way of pelagic larvae or juveniles conveyed by bathyal currents from Japan. It is noteworthy that the Hawaiian specimens of *O. glaber* are more similar to those from Japan than to those from South-East Asia.

Of the bathyal species of Elasipoda known from the western Pacific, only the deepest living, *Pannychia moseleyi* (Fig. 112), extends north of this point of convergence. It has been found down to 2600 m.

(3) The existence of some degree of similarity between the abyssal holothurian faunas of the North Atlantic and the southwestern Pacific (p. 227) recalls a pattern of distribution demonstrated by Sewell (1948) for pelagic deep-sea Copepoda. Sewell pointed out that the faunal similarities might be due to transport by deep ocean currents. At depths of 1500–4000 m, the water moves from the North Atlantic southward, giving off a water mass that flows eastward south of the Cape of Good Hope and proceeds across the southern part of the Indian Ocean to the southwestern Pacific.

Three of the species of Elasipoda common to the two regions *(Benthodytes typica, Psychropotes longicauda,* and *Peniagone diaphana)* have been taken as juveniles in pelagic nets.

Topography

Vinogradova (1959) distinguished a number of zoogeographic regions and subregions in the deep sea, separated to a great extent by submarine ridges. The importance of these ridges as distributional barriers, according to Vinogradova, was shown by the existence of an inverse correlation between the depth of the habitat of the species and the wideness of their geographic range. The deep-sea species with most restricted distributions (apart from the trench species) were held to be the stenobathic abyssal species.

The justification of Vinogradova's conclusions cannot be fully evaluated owing to lack of detailed information on the distribution and taxonomic status of the total of 1031 species on which they were based. The present revision of the Elasipoda, however, led to completely different zoogeographic conclusions. The two stenobathic deep-abyssal species, *Oneirophanta mutabilis* and *Psychropotes longicauda,* belong to the very few cosmopolitan species of Elasipoda, while even the most widely distributed bathyal species are far from being cosmopolitan.

The topography of the ocean floor at abyssal depths seems to have very little influence on the distribution of the Elasipoda. The faunal composition of some deep-sea basins which are separated from the main ocean by ridges or elevations with low sill depths may partly be determined by inability of some species to cross the topographical barrier. However, the fact that these ridges at the same time exert a pronounced influence on the hydrographic conditions in the basin, makes it difficult to demonstrate a direct influence of the topography on the distribution. Thus, a possible absence in the Mediterranean of a North Atlantic abyssal species may be due to the high temperature of the Mediterranean deep sea, rather than to inability of the species to cross the barrier at the entrance.

On the other hand, the absence in the Arctic Basin of practically all the Elasipoda of the North Atlantic is not likely to be due to failure to adapt themselves to the negative temperatures of this basin. Equally low temperatures prevail in the Antarctic deep sea which has a diversified fauna of Elasipoda. Apparently, the North Atlantic Ridge forms an insurmountable barrier to the species.

Conclusion

The known distribution of the Elasipoda can only to a very small extent be correlated with parameters of the physical environment. The deep-sea environment is so uniform that it is difficult to imagine distributional barriers for the species. Yet, hardly two species have the same distribution, and only few species approach a cosmopolitan distribution.

The influence of the physical environment on the distribution of the species probably consists in changing the conditions of competition. Absence of a species from certain regions is apparently due to inability to compete successfully rather than to inability to exist under the particular physical conditions. However, our present knowledge does not permit a discussion of the distribution of the species in terms of biological relationship. The zoogeography of the deep-sea holothurians (as of other deep-sea groups) is still little beyond the descriptive stage.

G. THE HADAL FAUNA

The term *hadal* was introduced by Bruun (1956) to designate the depths of 6000–11000 m. Apart from some ocean basins with depths slightly exceeding 6000 m, hadal depths are found only in the deep-sea trenches. Bruun regarded the hadal depths as an ecological zone equal in rank to the bathyal and abyssal zones. Wolff (1960), speaking of "the hadal community", adhered to the same view; he found that the hadal fauna differed from the abyssal fauna not only in its composition, but also in a number of morphological peculiarities of its species. Although summarizing the knowledge of all the species occurring deeper than 6000 m, Wolff (l. c.) held that the abysso-hadal boundary would be more correctly placed at 6800–7000 m. (A lowering of the abysso-hadal boundary from 6000 m to 6800–7000 m increases the number of exclusively hadal species from 58 % to 74 %).

Belyaev (1966) again reviewed the fauna living deeper than 6000 m (by Russian workers termed the *ultra-abyssal* fauna) and discussed its specific features.

Menzies & George (1967) questioned that the fauna of the hadal depths differed from the abyssal fauna by any morphological or biological features. The term *trench floor fauna* was preferred, because it did not imply the existence of a biological zone comparable to the abyssal and bathyal zones.

Wolff (1970), induced by the criticism advanced by Menzies & George, provided further arguments in support of his views. Both Wolff and Menzies & George based their views especially on a study of Isopoda, a fact which makes their different opinions even more remarkable.

In the following, the composition of the hadal fauna and the characteristics of its species is reviewed with special regard to the holothurians. The investigation confirmed the existence of a number of features peculiar to the hadal fauna. The features are probably not related to the depth, but rather to the topographical, geological, and sedimentary conditions of the trench environment.

The hadal environment

The hadal zone is characterized by the following features:

(1) Small total area. While 78.4 % of the sea has depths of 2000–6000 m, only 1.3 % has depths of 6000–11000 m. The abrupt decrease in area takes place in the interval of 6000–7000 m.

(2) Geographic discontinuity. While the abyssal

depths, with few exceptions, form a continuous geographic unit, the hadal depths consist of a number of geographically isolated trenches and basins.

(3) Geological instability. In contrast to the stable and uniform abyssal environment the deep-sea trenches are influenced by tectonic instability and, in coastal trenches, by an often high rate of sedimentation. Thus, Moore (1972) presented evidence that a deep-sea trench bordering the continental shelf of the eastern Bering Sea was uplifted during Cretaceous to be superceded by the Aleutian Trench in the earliest Tertiary.

There is evidence that a fairly recent (possibly Quaternary) decrease in depth of the Japan Trench has led to the extermination of three deep-hadal species of holothurians (p. 242).

(4) Ecological conditions. Most of the trenches are situated close to the coast and may benefit from the rich production of the coastal plankton. In addition, the steep slopes allow turbidity currents and mud slides to reach the bottom of the trenches, conveying a supply of organic material (p. 236). The rich accumulation of sediments in the trenches may be the most important ecological factor distinguishing the hadal from the abyssal zone.

The temperature in the trenches is usually between 1.5° and 2.5° C. Due to adiabatic heating the temperature increases by about 1° C. from 5000 to 10000 m.

The water renewal is probably sufficient to ensure that oxygen is no limiting factor for hadal animal life.

The undersaturation of the water with calcium at depths beyond 5000 m has not prevented the existence of strongly calcified forms at hadal depths (p. 241).

The high hydrostatic pressure is still of unknown importance to the bathymetric distribution of deep-sea animals (pp. 237–238).

General features of the hadal fauna

A comparison between the hadal and the bathyal-abyssal faunas involves a number of questions. In the following these are considered in relation to the physiographical and ecological conditions in the hadal zone.

(1) Number of species per locality. The present investigation indicates that the hadal zone has a low faunal diversity compared to the abyssal zone. This may be due to the unstable and geologically young environment, rather than to extreme conditions of life at great depths (p. 219).

(2) Number of species per trench. A low faunal diversity in the hadal zone will tend to reduce the number of species occurring in each trench. This may to some degree be counterbalanced by the considerable diversity of habitats due to the irregular topography of the slopes.

(3) Total number of hadal species. The division of the hadal zone into geographically isolated trenches tends to increase the total number of hadal species. Nevertheless, the species number decreases abruptly at 6000–7000 m. This may be due to the abrupt decrease in area at this depth and to a low faunal diversity in the hadal zone.

(4) Number of individuals per species. The fact that holothurians (Elasipoda in particular) are highly adapted for life at great depths, combined with their low species diversity in the hadal zone, has led to exceptionally high numbers of individuals per species, compared to other groups (p. 218).

(5) Composition of the hadal fauna. Concurrently with the increasing abundance of the holothurians with depth a change takes place also in the relative representation of other groups. Wolff (1960, 1970) pointed out that the hadal fauna is characterized by the absence (Decapoda, Brachiopoda) or poor representation (fishes, Cirripedia, Bryozoa) of some groups, while other groups (Polychaeta, Holothurioidea, Isopoda) are dominant. These faunal changes indicate an increasing dominance of deposit feeders at the expense of filter feeders and carnivores. The poor representation of carnivores is not unexpected. The large biomass in the trenches is accounted for by elpidiids, which have a very low food value.

The decrease in number of filter feeders may to some degree be apparent only. Sokolova (1959) pointed out that the slopes of the trenches in some places are swept by currents which may create favourable conditions for filter-feeding animals. This has been confirmed by deep-sea photographs revealing a rather rich representation of crinoids and other filter feeders in places with hard bottom at hadal depths (Lemche *et al.* in press). Due to difficulties in fishing on this type of bottom the filter-feeding fauna of the trenches is little known. No filter-feeding holothurians are known from hadal depths.

Menzies & George (1967) rightly pointed out that the groups which are poorly represented at hadal depths are also poorly represented at abyssal depths. The change in faunal composition is gradual with depth, and, therefore, cannot motivate the distinction of an abysso-hadal boundary.

The authors further held that the dominant groups are not the same in different trenches, or at different levels in each trench. But actually, the holothurians are dominant at all levels in all trenches (p. 218).

Menzies & George (1967) also pointed out that the nomination of a group to be dominant depends very much on the mesh-size of the gear. With fine-meshed gear the isopods would increase in dominance and with even finer meshes the Foraminifera would be the dominant group. However, this does not invalidate the finding that the holothurians increase in dominance with depth compared to other groups of similar body size.

(6) Morphological characteristics. Birshtein (1957) and Wolff (1956a, b, 1960, 1962, 1970) found that gigantism in Crustacea is most often met with in the deep sea, and in particular in the hadal zone. Menzies & George (1967), on the contrary, held that gigantism in the Isopoda is not correlated with depth.

The holothurians lend no support for the view of deep-sea gigantism. Although the abyssal species are often large-sized, they are generally not larger than the bathyal and sublittoral species. The hadal species of holothurians, as a rule, are smaller in size than the abyssal species. Thus, none of the large-sized species from the abyssal stations in the Kermadec Trench *(Oneirophanta mutabilis, Psychropotes longicauda, Psycheotrephes magna, Mesothuria candelabri, Abyssocucumis abyssorum, Molpadia blakei)* descend into the hadal zone. This decrease in average size, however, has no direct relation to the depth. It is due to the fact that the dominance of the holothurians at hadal depths is accounted for, in particular, by the Elpidiidae.

The only hadal example of a change in morphological features with depth is shown by the genus *Elpidia* in which there is a tendency to increasing calcification with depth. This is the more remarkable as the high hydrostatic pressure and the low temperature cause dissolution of calcium in the sediments at depths beyond 5000 m. Evidently, undersaturation of the water with calcium does not prevent animals from storing large amounts of calcium in their skeletons. This was also noted by Zenkevich (1963) who pointed to the fact that the echinoderms are extremely abundant in the brown mud of the Kara Sea, in spite of the total dissolution of calcium in this sediment.

An increased calcification with depth is also found in *Deima validum,* in which the deposits are more robust and strongly calcified in abyssal than in bathyal specimens.

(7) Endemism in the trenches. Belyaev (1966) stated that of the known hadal species 68 % had so far never been taken outside the hadal zone.

Menzies & George (1967) argued that this percentage was not at all remarkable. Comparing the isopod faunas of two abyssal localities which were rather close to each other and not separated by any topographic barrier they found that both localities had a higher percentage of "endemic" species than that distinguishing the hadal zone from the remaining deep sea. According to these authors a species is "endemic" to locality A if absent in locality B, irrespective of its remaining distribution. However, this type of "endemism" has no bearing on the problem in question, which deals with the percentage of hadal species that have not been found outside the hadal zone in any part of the world ocean.

In order to avoid confusion of terms, the word "endemic" in the present work is used in the meaning "endemic to one trench system". Species recorded from the hadal zone only (whether from one or from several trenches) are called "exclusively hadal".

Out of the total of 22 species of holothurians known from the hadal zone, 13 are exclusively hadal.

Nine exclusively hadal species are endemic to one trench system:

Ellipinion galatheae: Philippine Trench (9820–10000 m).

Elpidia longicirrata: Kurile-Kamchatka Trench (8035–8345 m).

Elpidia atakama: Peru-Chile Trench (7720 m).

Paroriza grevei: Banda Trench (6650–7280 m).

Myriotrochus kurilensis: Kurile-Kamchatka Trench (7795–8430 m).

Myriotrochus longissimus: Japan and Idzu-Bonin Trenches (6475–7190 m).

Myriotrochus mitis: Kermadec Trench (8927–9174 m).

Myriotrochus kermadecensis: Kermadec Trench (8927–9174 m).

Hadalothuria wolffi: New Britain Trench (8920 m).

There is photographic evidence (Lemche *et al.* in press) of the occurrence *Hadalothuria (wolffi?)* in the New Hebrides Trench.

Three exclusively hadal species are common to the Kurile-Kamchatka and Idzu-Bonin Trenches, but seem to be absent in the interjacent Japan Trench: *Elpidia hanseni* (8610–9735 m), *E. birsteini* (8060–9345 m), and *Myriotrochus zenkevitchi* (8135–9715 m). Only one of the species *(E. hanseni)* has developed subspecific differences between the two populations. As pointed out by Belyaev (1971), this suggests that in fairly recent time (possibly as late as the Quaternary) the Japan Trench was deep enough to permit a continuous distribution of these deep-hadal species. At present, the Japan Trench is less than 8000 m deep, with the exception of a local deep (8412 m) in its southern part.

One exclusively hadal species, *Myriotrochus bruuni,* is common to several trenches: Philippine, Japan, Mariana, New Britain-Bougainville, Kermadec, Tonga, and Sunda Trenches. Total depth range 6458–10710 m.

The example of *M. bruuni* is remarkable, since species exclusive to the hadal zone are otherwise with almost no exception restricted to one single trench system (Belyaev 1966). However, the absence of taxonomic differences between the trench populations of *M. bruuni* (Cherbonnier 1964, Belyaev 1970) suggests that the populations are, in actual fact, connected through an abyssal occurrence. The species, therefore, may constitute no exception to the rule.

The non-exclusively hadal species of holothurians often penetrate into several trenches. Thus, the four non-exclusively hadal species of holothurians from the Kermadec Trench all seem to occur in other trenches as well. *Elpidia glacialis* has been dredged in a number of trenches, and there is photographic evidence (Lemche *et al.* in press) that also the other three species occur in additional trenches: *Peniagone azorica* (New Britain and Romanche Trenches), *Scotoplanes globosa* (New Britain and New Hebrides Trenches), and *Pseudostichopus villosus* (New Britain Trench).

The Banda Trench provides an exception, as none of its four non-exclusively hadal species of holothurians are known to penetrate to hadal depths in other trenches (Hansen 1956). This may be due to ecological and zoogeographic conditions particular to this isolated trench which is completely surrounded by shallow seas.

Apart from the species of the Banda Trench, only one non-exclusively hadal holothurian seems to penetrate into one trench only *(Amperima naresi* in the Sunda Trench).

(8) Evolution in the trenches. A species which has become restricted to hadal depths in a number of trenches may be subject to a divergent evolution. In the course of time, a geographic subspeciation or even speciation may result, leading to endemic trench species.

Examples of geographic subspeciation due to isolation in trenches are provided by the hadal populations of *Elpidia glacialis.* This species had probably a wide abyssal distribution during the Glacial Age. The subsequent extinction of the species at abyssal depths outside the polar regions resulted in its isolation in a number of trenches, where it developed into endemic subspecies. *Elpidia atakama* from the Peru-Chile Trench may represent one such population which has reached species level.

A geographic subspeciation has also taken place in *Elpidia hanseni,* in which, according to Belyaev (1971), the populations of the Kurile-Kamchatka and Idzu-Bonin Trenches differ at the subspecies level.

The fact that the exclusively hadal species are almost all endemic to one trench system suggests that the evolution in the trenches has often proceeded to species level. On the other hand, the present restriction of a species to the hadal depths of a single trench is no proof of its origin *in situ.* It may represent a relict occurrence of a former abysso-hadal distribution. An indication that isolation in trenches has led to speciation might be found in cases in which hadal species from different trenches together form a superspecies. As yet, such superspecies have not been described for any group. Among the holothurians, a hadal species pair, as mentioned, may be represented by *Elpidia glacialis,* inhabiting the trenches of the western Pacific, and *E. atakama* from the Peru-Chile Trench.

(9) Taxonomic variation within trench populations. The irregular topography of the trenches

may lead to isolation and taxonomic segregation of populations. Four species of the Kermadec Trench exhibit a pronounced local variation. In *Oneirophanta mutabilis* the specimens from St. 654 have very peculiar features in common, indicating a pronouncedly stationary population. *Psychropotes longicauda* shows differences in body colour between the specimens from St. 663 and those from St. 664. In the two abysso-hadal species, *Scotoplanes globosa* and *Peniagone azorica,* a correlation is indicated between taxonomic variation and bathymetric occurrence.

Belyaev distinguished four species of *Elpidia* in the Kurile-Kamchatka Trench. The shallowest living, *Elpidia kurilensis* (= *E. glacialis kurilensis*) (6710–8100 m), was regarded as the ancestor of the deep-hadal *E. longicirrata* (8035–8345 m) and *E. birsteini* (8060–9345 m). The deepest living, *E. hanseni* (8610–9530 m), is likely to be of the same ancestry. The four species differ in number and size of the dorsal papillae. Besides, they show an increasing calcification with depth.

The existence in the Kurile-Kamchatka Trench of four closely related species of *Elpidia* suggests that populations isolated in parts of a trench may develop into subspecies and even species.

Conclusion. The features which characterize the hadal fauna are correlated with the trench environment, rather than with the great depths. In point of fact, there would be no reason to distinguish a particular zone for the depths of 6000–11000 m if these depths were not restricted to trenches.

A large supply of sediments forms the basis of the overwhelming abundance of holothurians (elpidiids in particular) and may be the most important ecological factor in the hadal zone.

Geological instability and low age may have permitted only a low faunal diversity, as indicated by the low number of species per station in the hadal holothurians.

The small total area combined with a low faunal diversity may explain the abrupt decrease in total number of species at the abysso-hadal transition.

Geographic discontinuity has led to subspeciation, and probably speciation, in former abysso-hadal species which have become restricted to a series of trenches. This may to some degree counterbalance the low total number of species in the hadal zone.

The irregular topography may bring about isolation and taxonomic segregation of populations within the single trenches. The existence in the Kurile-Kamchatka Trench of four closely related species of *Elpidia* raises the question whether such populations may evolve further into distinct species.

H. EVOLUTIONARY ASPECTS

The deep-sea environment, apart from the trenches, is characterized by its great uniformity from one region to another, and its stability throughout the year and through geological time. Three consequences of evolutionary significance have already been considered: The low total number of species in the deep sea due to the geographic uniformity, the high faunal diversity in abyssal communities due to the stability of the environment, and the low holothurian (and probably faunal) diversity in the unstable hadal environment.

The present chapter deals with the evolutionary processes in the deep-sea fauna, as revealed by the taxonomy and distribution of the Elasipoda. A thorough knowledge of the taxonomy of a group is indispensable to such a study. A group should preferably be revised on a world-wide basis to minimize the risk that regional faunas are described with too little attention being paid to the faunas of other geographic regions.

The hadal zone in several respects offers conditions for its fauna which are different from those of the abyssal and bathyal zones. The evolutionary problems in the hadal zone were, therefore, discussed in connection with the other problems of the hadal fauna (pp. 239–243).

Evolution within the deep sea versus immigration from shallower depths

New species may be added to the deep-sea fauna either through speciation within the deep sea or through immigration from the sublittoral zone. The relative role played by the two phenomena differs greatly from one animal group to another. In groups which have been restricted to the deep sea during a long geological time the species have probably arisen mainly through speciation within the deep sea. In groups where the deep-sea species are closely related to sublittoral forms new species may also have been added to the deep-sea fauna through a relatively recent immigration from sublittoral depths. Groups restricted to the deep sea are especially well suited for the study of the conditions of evolution in this environment. It has already been emphasized that the holothurians constitute a pronounced example of such a group, and that at least one of the elasipod suborders, Psychropotina, seems to have evolved entirely within the deep sea (p. 209).

The echinoderms have produced several exclusive deep-sea groups (stalked crinoids, the families Porcellanasteridae, Benthopectinidae, Brisingidae, and Zoroasteridae among the Asteroidea, the Echinothuridae and Aspidodiadematidae among the Echinoidea). At least some of these groups do not follow the rule of the holothurians that the relationship is closest between species from the same bathymetric zone. Thus, Alton (1966) found that in Goniasteridae and Zoroasteridae "the replacement of species belonging to the same genus with depth was strongly exhibited". As examples were mentioned bathyal species which were replaced by closely related abyssal species.

No polychaete families are restricted to the deep sea. The molluscs (apart from the Monoplacophora) possess only one family restricted to the deep sea, the bivalve family Galatheavalvidae. The only species of the family, *Galatheavalva holothuriae* Knudsen, 1970, lives as a commensal in the oral cavity of *Psychropotes belyaevi.*

Some families of crustaceans are restricted to the deep sea (Neotanaidae among the Tanaidacea, Eryonidae and Homolodromiidae among the Decapoda). In general, however, the crustaceans of the deep sea seem to exhibit a close relationship to sublittoral forms. This has been stressed both for Amphipoda Gammaridea (Barnard 1961) and Isopoda (Wolff 1962).

Geographic variation

It is generally agreed that in terrestrial animals speciation is almost exclusively brought about by geographic isolation (Mayr 1963). There is less evidence of the importance of geographic isolation for speciation in marine animals, although polytypic sublittoral species are known from a number of groups (Rensch 1947, Mayr 1954).

Hardly anything is known about the types of geographic variation in deep-sea animals. Yet it would be highly desirable to acquire a knowledge of the conditions of geographic speciation in the stable and uniform environment of the deep sea, with its remarkable absence of distributional barriers or abrupt changes in ecological conditions.

The omnipresence of geographic variation in marine animals is revealed almost whenever a sufficient number of specimens are examined from different localities. A striking example among sublittoral echinoderms was provided by Vasseur (1952), who studied populations of the sea-urchins *Strongylocentrotus droebachiensis* and *S. pallidus* from three localities along the Norwegian coast. A geographic variation was present in all the characters examined: Colour of the test, colour and structure of the spines, number of ocular plates reaching the periproct, shape of the pedicellariae, number of pore-pairs, relative weight of the lantern, ecology, and sperm agglutination.

Madsen (1961a), in his revision of the deep-sea Porcellanasteridae, also found that the species differed taxonomically from one population to another.

Knudsen (1970), on the other hand, found that the abyssal bivalves showed a remarkable lack of geographic variation.

The existence of a geographic variation has often been obscured due to the tendency of taxonomists to describe specimens from widely separated localities as distinct species, even when they are only slightly different. Thus, Clark (1907, p. 69) stated that "on *a priori* grounds, it is to be assumed that a species from the Atlantic Ocean is distinct from its nearest allies in the western Pacific. Even slight differences, if they are constant, may be used to distinguish species from widely separated areas". This subjective element in species determination was also pointed out by Madsen (1961b, p. 204), who illustrated it by the example of his own decision (Madsen 1956) to erect a new species, *Primnoella krampi,* for a gorgonarian from the Kermadec Trench. The species so much resembles the North Atlantic species *P. jungerseni* that "had they been found in the same area there should have been little objection in considering them individual variants of the same species".

These cautious measures taken by taxonomists have the advantage that premature conclusions regarding synonymies and types of geographic variation are avoided. On the other hand, it is important that a specialist calls attention to the species in his material which might represent geographic forms of other species, and to the part of the intraspecific variation which might prove to be of a geographic type. Usually, only a specialist will be able to point out such possibilities.

A material from a large number of stations is required to make out whether a character changes gradually with distance or by abrupt changes at definite boundaries. With our present limited knowledge such an analysis is tentative only, even in the case of the most well-investigated species.

In the following is discussed the role played by the different types of geographic variation in the better-known species of Elasipoda.

1. Clines.

Clines, or character-gradients, are known to be wide-spread in continental species (Mayr 1963). They arise as adaptations to changes in the environment, and are smoothed through the action of gene flow. The widely distributed species of the deep sea, living in an environment which gradually changes with distance, are likely to show this type of geographic variation.

In *Orphnurgus glaber* the extensive variation in number of dorsal papillae and in shape of the deposits seems primarily to be of a clinal nature.

2. Local variation.

While a clinal variation is difficult to demonstrate, the presence of marked differences between closely situated populations is more easily recognized. Almost every species known from a reasonably large number of specimens could be shown to vary taxonomically from one locality to another. A pronounced local variation may develop in trenches, apparently due to their irregular topography (pp. 242–243).

3. Polytypic species.

The fact that geographic segregation plays a major role in speciation lends a special interest to the demonstration of discontinuous geographic variation. The description of this type of variation in terms of polytypic species serves the dual purpose of clarifying the presentation of geographic variation and of pointing out geographic regions with characteristic populations which may eventually evolve into new species.

The usefulness of the subspecies concept in describing intraspecific geographic variation has been questioned by various taxonomists. It has been held that the application of subspecific names to local populations encumbers the literature with nomenclature and tends to confuse rather than clarify the presentation of geographic variation, and, furthermore, that division of a gradually changing species into subspecies gives a false impression of discontinuity in the variation.

However, although the subspecies concept is not adequate in describing all types of geographic variation, it has the advantage of pointing out, also to the non-specialist, regions inhabited by especially characteristic populations. Comparison of taxonomic works on different groups may in this way reveal geographic regions which are, or have been, centres of species formation.

Subspecific names have been used only to a very small extent in the description of benthic deep-sea invertebrates, and in most cases only to designate specimens which, in one or more respects, differ from the "typical" form of the species. Actually, the subspecific name often replaces the "variety" of older descriptions, and is not intended to cover a distinct geographic form of the species. These subspecies are usually known from too few specimens to allow a decision as to their taxonomic status.

The subspecies concept has here been applied to three species, *Oneirophanta mutabilis, Deima validum*, and *Elpidia glacialis*. The subspecies erected conform with the 75 % rule proposed by Mayr *et al.* (1953, p. 145): The overlap is so small that at least 75 % of the specimens of subspecies A are distinguishable from 97 % of the specimens of subspecies B.

The subspecies of *Elpidia glacialis* are probably geographically isolated from each other. The eastern Pacific subspecies of *Deima validum* may be geographically isolated at the present time, the nearest finds of the main subspecies being off Japan. The two subspecies of *Oneirophanta mutabilis* apparently adjoin each other by a narrow zone of intergradation; possibly, they have met subsequent to a former isolation.

The only example of geographic subspeciation in abyssal bivalves similarly comprises a widely distributed and an eastern Pacific subspecies (Knudsen 1970).

4. Superspecies.
The region off the Pacific coast of Central America and northern South America not only possesses endemic geographic subspecies, but also endemic species which replace closely related species from other regions. *Scotoplanes clarki* in this region apparently replaces the closely related and widely distributed *S. globosa*. A similar example may be provided by the widely distributed *Laetmogone wyvillethomsoni* and the eastern Pacific *L. theeli*, the only two abyssal species of the genus.

The Molpadonia present a species pair with a similar distribution. *Molpadia blakei* (Théel, 1886b), previously known from the North Atlantic, was taken by the *Galathea* in the South Atlantic, the Indian Ocean, the Tasman Sea, and the Kermadec Trench. The closely related *M. granulata* (Ludwig, 1894) seems to be confined to the eastern Pacific. The specimens which Sluiter (1901b) and Koehler & Vaney (1905) referred to this species (i. e. to *Trochostoma granulatum)* were probably misidentified. The two species are the only true abyssal species of *Molpadia*. They are more closely related to each other than to any of the bathyal species of the genus (p. 216).

Knudsen (1970) mentioned two examples of geographic replacement in abyssal species of bivalves. Both comprise a widely distributed species and a closely related species from the eastern Pacific region.

The alleged antiquity of the deep-sea fauna

Since the beginning of deep-sea exploration it has been widely believed that the great depths of the ocean have acted as a refuge for primitive animal groups. As examples of ancient survivors have, in particular, been cited animal groups which are restricted to, or are dominant, in the deep sea.

In recent time this view has been opposed by various authors (Menzies & Imbrie 1958, Menzies *et al.* 1961, Madsen 1961b, Clarke 1962). On the other hand, Zenkevich & Birshtein (1956, 1960) maintain that the deep sea is dominated by ancient (i. e. mesozoic) groups.

The Elasipoda are among the groups which have been cited as evidence of great antiquity. But this view finds no support in the present investigation. The features peculiar to the Elasipoda are either adaptations to life in the deep sea (pp. 207–208) or they are paedomorphic, like various features of the Elpidiidae (p. 207). Nor is there any evidence that the deep-sea representatives of the four other holothurian orders are more primitive than their shallow-water relatives.

The view that the deep sea harbours exceptionally many ancient and primitive groups has been based not only on the supposed phylogenetic relationship of the deep-sea groups, but also on theoretical considerations regarding the influence of the deep-sea environment on the evolutionary processes.

It has been argued (Zenkevich & Birshtein 1960, Carter 1961, Friedrich 1965) that the great stability and homogeneity of the environment has delayed the process of evolution and thereby made possible a survival of ancient groups. However, although the evolutionary processes may be slow in the stable deep-sea communities, it should be remembered that the deep sea is not a closed environment. Shallow water groups which are able to develop the necessary adaptations may continually introduce new species into the deep sea to compete with the "ancient" groups. In actual fact, there is evidence that the stable and homogeneous abyssal environment has led to the development of highly diversified communities with a keen competition between the species (p. 218).

The idea of a low level of competition in deep-sea communities led Parker (1961) to the view that groups which are no longer able to compete successfully in shallow water may avoid extinction through emigration to the deep sea. However, there is no reason why a group should postpone its penetration into the deep sea until it can no longer survive in shallow water.

A less keen competition in the less diversified hadal communities might seem to provide better conditions for the survival of primitive forms. However, the low faunal diversity at hadal depths seems to be connected with a low geological age of the environment (p. 219), which in itself prevents the trenches from being refuges for ancient forms. Actually, the hadal fauna bears no primitive or ancient stamp.

In short, there is no evidence that the deep-sea environment is especially favourable for the survival of ancient and primitive forms. The composition of the deep-sea fauna, like that of the sublittoral fauna, is determined by the ability of the species to compete successfully under the particular conditions. Thus, the increasing dominance of the holothurians at great depths, which Zenkevich & Birshtein (1960) regarded as one of the indications of the antiquity of this group in the deep sea, is rather due to their highly evolved adaptation to the deep-sea environment.

Bruun (1956) and Bruun & Wolff (1961) held that the bathyal fauna includes a number of ancient animal groups, whereas the present abyssal fauna is on the whole of a fairly recent date. A cooling of the abyssal zone due to the formation of the polar ice caps during the Pleistocene glaciation was believed to have exterminated the Tertiary abyssal fauna, with the exception of eurybathic and eurythermic species. The bathyal zone, which at the present time has temperatures similar to those of the Tertiary abyssal zone, on the contrary offered conditions for the survival of an ancient deep-sea fauna.

As examples of ancient bathyal groups were mentioned the stalked crinoids, the hexactinellid sponges, the eryonid crustaceans, and the coelacanth fish *Latimeria* (which, however, is sublittoral). The two first-mentioned groups are filter feeders and thus poorly adapted for abyssal life. The eryonid crustaceans are represented in the abyssal zone by the genus *Willemoesia* and are thus not strictly bathyal.

A post-Tertiary origin of recent bathyal and abyssal faunas may apply to groups in which there is a close taxonomic relationship between the faunas of the different bathymetric zones. The absence of such a relationship in the Holothurioidea points to an evolution within the bathyal and abyssal zones of a magnitude which could hardly have been brought about since Tertiary time.

Moreover, the fact that the temperature does not seem to be of paramount importance for the bathymetric distribution of the holothurians makes it unlikely that the extremely slow process of cooling at the end of the Tertiary should have exterminated the abyssal fauna of this group.

The stable deep-sea environment has been thought to favour not only the survival of ancient forms but also the evolution of extreme specializations which would be dangerous in a more changing environment. As an example has been adduced the Elasipoda with their "fantastic modications of the form of the body" (Carter 1961).

However, it seems very doubtful whether there is any correlation between the great array of body forms in the Elasipoda and the stability of the environment. The modifications of the body are caused by the peculiar development of the ambulacral appendages, notably the papillae of the dorsal and ventrolateral ambulacra. In the absence of respiratory trees the papillae have taken over the respiratory function. It seems quite natural that this function has been fulfilled in different ways: By increase in number or size, or by excessive delopment of some of the papillae. The great variation in number, size, and arrangement of the papillae is not surprising in animals which have their whole body surface exposed to the water and in which the papillae act as respiratory organs. A similar evolution has taken place in the shallow water opisthobranch molluscs, in which an excessive development of the body appendages is combined with absence of mantle cavity and true gills. Apparently, this evolution may take place both in a stable and in a changing environment.

Thus, the Elasipoda do not support the view that the deep-sea environment has favoured the survival of primitive groups or the evolution of groups with extreme specializations.

The influence of the deep-sea environment on the rate of evolution cannot be illustrated by the example of the Elasipoda. Although at least the suborder Psychropotina probably evolved exclusively within the deep sea, its geological age is unknown due to lack of fossil records from the deep-sea bottom (p. 209).

IV. SUMMARY

The class Holothurioidea comprises about 1100 species, 380 of which are from the deep sea, i. e. from depths exceeding 200–400 m. Among the five orders, the Elasipoda are unique in being confined to the deep sea.

The knowledge of the Elasipoda was founded by the Challenger Expedition 1872–1876 (Théel 1882). Also the subsequent exploration of the group was based on the collections from the great deep-sea expeditions.

The material collected by the Galathea Expedition 1950–52 is larger than that of any previous expedition. This is due to the use of large collecting gear, as Herring Otter Trawl, and Sledge Trawls with 3 and 6 m wide openings. Large gear is especially suited for the catch of holothurians, which, owing to their high buoyancy, often escape the openings of smaller nets. Its effectiveness is shown by the fact that only one out of a total of 80 soft-bottom stations at depths greater than 1000 m failed to bring up holothurians.

The present work describes the Elasipoda collected by the *Galathea,* as well as a small number of Elasipoda collected by the late Dr. Th. Mortensen. In addition, the work is based on a re-examination of the material from most of the previous deep-sea expeditions.

The Systematic Part includes all the known species of the four benthic families of Elasipoda (the pelagic family, Pelagothuriidae, is omitted). The number of recognized species is reduced from 165 to 106, despite the erection of 11 new species. The order is being divided into two suborders, Deimatina and Psychropotina, the foundations of which are presented in the General Part.

The General Part deals with the morphology, biology, and distribution of the Elasipoda. Special chapters are devoted to the problems of the hadal fauna and to the evolutionary processes in the deep sea, as viewed from our present knowledge of the Elasipoda.

A. The taxonomic characters and their variation

The *calcareous deposits* (sclerites, spicules) of the skin as a rule provide the best species characters, although they may be almost identical in species belonging to different genera, or even families. A geographic or local variation is often present.

The present investigation contradicts the views of Hérouard (1923) and Ekman (1926) regarding the phylogeny of the deposits. Instead, it is pointed out that in the Psychropotidae and Elpidiidae the deposits have a feature in common which is unique among holothurians: They completely lack dichotomous ramifications, apart from the two bifurcations of the primary cross proper.

The *calcareous ring* in the Elpidiidae consists of five star-shaped pieces and resembles the embryonic ring in other holothurians. The most original state is represented by the ring of *Psychrelpidia, Peniagone,* and *Achlyonice,* in which the pieces are small, separate, and composed of a varying number of arms. From this type may be derived the firm and continuous ring of *Elpidia* and *Irpa.* In these genera the ring pieces possess four pairs of arms only, two pairs of which are joined to the corresponding arms of the neighbouring pieces. The reduction and fixation of the arm number probably happened subsequent to the re-attainment of a firm and functional structure of the ring. In *Amperima, Ellipinion,* and *Scotoplanes* each piece likewise has four pairs of arms, but the pieces are small and isolated from each other. This type of ring may be derived from the *Elpidia-Irpa* type through reduction of the five pieces.

Thus, the morphology of the calcareous ring in the Elpidiidae bears evidence not only of a paedomorphic origin of the family, but also of the interrelationship of its genera.

The ring in the Deimatidae, Laetmogonidae, and Psychropotidae is of the usual holothurian type, apart from its low degree of calcification. Due to its soft consistency the ring is changeable in shape and, therefore, of hardly any taxonomic value.

The *tubefeet* in the Psychropotidae are small and usually fused. The other three benthic families have large tubefeet which are usually few in number. They communicate with large water-vascular cavities of the ventral skin, a unique feature connected with a peculiar type of walking (see below).

The *papillae* are often large, numerous, and of a peculiar shape. The unpaired appendage in *Psychropotes* and the velum in the Elpidiidae consist of fused dorsal papillae. The velum seems to be an original feature in the Elpidiidae.

The abundant development of the papillae, like the absence of respiratory trees, is a feature connected with the surface-dwelling habit. In animals with the whole body surface exposed to the water it seems more natural to make use of the body appendages for respiratory purposes than to use intestinal respiration. A similar evolution is known from the shallow water opisthobranch molluscs, in which the abundant development of the body appendages is connected with the absence of mantle cavity and true gills.

Differences in number of tubefeet and papillae are important to the study of intraspecific variation. The geographic subspecies of *Elpidia glacialis, Deima validum,* and *Oneirophanta mutabilis* are based in part on such differences.

Circum-oral papillae are present in all species of *Deima, Benthogone,* and *Benthodytes* (*B. sanguinolenta* has only post-oral papillae), which represent three different families. A contractile membrane, which may completely cover the tentacle crown, is in all three genera present inside the ring of circum-oral papillae.

The *tentacles* show a variation of taxonomic significance both in number and shape.

The *alimentary canal* is in most genera of the Elpidiidae provided with a large rectal caecum. Its absence in the primitive genera *Psychrelpidia* and *Peniagone* indicates that it is not a rudimentary respiratory tree but an organ originating in the Elpidiidae. The mud-filled caecum may act as a ballast tank, increasing and regulating the specific gravity of these extremely buoyant animals.

The *mesentery* in the Elasipoda, contrary to other holothurians, has a dorsal attachment throughout its length. This is apparently an adaptive feature connected with the peculiar mechanism of protraction of the tubefeet (see below).

Ekman (1926) held that differences in the course of the attachment of the mesentery on the body wall might characterize species, and even genera. But in *Oneirophanta mutabilis* it was found that even at a single station the variation may approach the highest possible for a mesentery with an entirely dorsal attachment.

The *external morphology of the gonads* may contribute to the characterization of genera, and even higher categories.

B. Biology

Feeding. The Elasipoda subsist on the surface layer of the substratum, which they graze by means of their ventrally turned tentacle crown. A different degree of selective feeding is indicated by the considerable variation in the shape of the tentacle discs. In *Elpidia* the highly specialized tentacles are combined with a very slender intestine, both features indicating a high degree of selective feeding. Two other dominant genera of the hadal zone, *Scotoplanes* and *Amperima,* have feebly differentiated tentacle discs and a heavily filled intestine.

Differences in gut content related to the different tentacle types could, however, not be demonstrated.

Reproduction. The larval development of the Elasipoda is unknown. However, even the smallest eggs (0.2 mm in diameter in the Elpidiidae) are so large that a lecitotrophic development is to be expected. Pelagic larvae, if any, will thus be independent of food uptake from the plankton, at least in their initial stages.

The largest eggs (1.7–4.4 mm in diameter) were found in the Psychropotidae. In bulk, they surpass the largest hitherto known echinoderm eggs by up to 85 times. The large size seems to be correlated with a long pelagic life of the juveniles. Thus, *Psychropotes longicauda* (egg diameter 4.4 mm) is known to spend its life in the plankton up to a body length of at least 32 mm.

A positive correlation between egg size and depth occurrence was found in the Laetmogonidae and Psychropotidae.

Brood protection was found in a population of *Oneirophanta mutabilis affinis* from 3570 m off the Pacific coast of Central America. The young are retained in the ovaries up to a length of 30 mm, representing one-third to almost half the length of the mother. The fact that the young are born at the end of a period of rich phytoplankton production suggests that a seasonal variation in the surface production may induce a reproductive periodicity at abyssal depths.

A reproductive periodicity is also indicated in abyssal populations of *Deima v. validum* from the western Indian Ocean. A definite proof of reproductive periodicity, however, requires samples from the same locality at different seasons of the year. The phenomenon may be more widespread in the deep sea than indicated by the two examples.

The gonads of the Deimatidae and Psychropotidae contained a nutritive-phagocytic tissue similar to that previously known from a number of sublittoral echinoids and asteroids. The cells ingest the sperm and ova which remain after each spawning, and later transfer nutrients to the next batch of sexual products. The tissue is abundantly developed in the Psychropotidae and in the brood-protecting *Oneirophanta mutabilis affinis.*

Hermaphroditic specimens have not been found, and there was no indication of a change of sex.

Swimming and floating. Many psychropotids and synallactids probably have the power of swimming over the bottom by means of undulatory movements of the body. The synallactid *Galatheathuria* swims in the free water masses, apparently by means of undulatory movements of the brim. Juvenile specimens of some psychropotids and elpidiids have likewise been caught a great distance above the bottom.

Function of the water-vascular dermal cavities. The water-vascular ampullae of the tubefeet and papillae are in the Deimatidae, Laetmogonidae, and Elpidiidae replaced by large water-vascular, dermal cavities. These are emptied into the tubefeet and papillae by means of peristaltic movements of the muscles of the body wall. Photographs show that the protracted tubefeet may act as stilts which raise the ventral surface of the walking animal above the substratum. Walking on stilt legs is otherwise known from various abyssal crustaceans and pycnogonids. The papillae of the velum have been observed, in some species of *Peniagone,* to be extended sufficiently to reach the substratum in front of the animal, thus acting as tactile organs.

The pumping action of the cavities may also further the circulation of fluid in the tubefeet and papillae, thus increasing the respiratory exchange through the skin.

C. Systematics, relationship, and adaptation

Monophyletic origin. The absence of respiratory trees and the exclusively dorsal attachment of the mesentery are common to all Elasipoda. Further indications of a monophyletic origin are found in three features shared by families or genera belonging to each of the two suborders: (1) Large tubefeet connected with water-vascular dermal cavities are common to the Deimatidae, Laetmogonidae, and Elpidiidae. (2) Circum-oral papillae in combination with a sphincter muscle are found in one genus of each of the families Deimatidae, Laetmogonidae, and Psychropotidae. (3) The wheel-shaped deposits found in some species of Elpidiidae are of the type otherwise characteristic of the Laetmogonidae.

Evolutionary trends. The Elasipoda appear to have separated at an early stage into two evolutionary trends, here proposed as the suborders Deimatina and Psychropotina.

Deimatina, comprising the families Deimatidae and Laetmogonidae, are, with few exceptions, characterized by their numerous and often long papillae. The two families differ distinctly in their calcareous deposits. The Deimatidae have reticulated plates (or derivatives of such plates), the most primitive type of holothurian deposit. The Laetmogonidae have wheels of a type otherwise found only as rare, accessory deposits in a few species of Elpidiidae and may represent a retained larval feature.

Psychropotina comprises the families Psychropotidae, Elpidiidae, and Pelagothuriidae. A common descent is indicated partly by the very specific similarity between the deposits of the Psychropotidae and those of the Elpidiidae (absent in the Pelagothuriidae), and partly by the fact that *Psychrelpidia* (here reckoned among the Elpidiidae) combines features of all three families.

The Elpidiidae and Pelagothuriidae are probably paedomorphic. Paedomorphic features in the Elpidiidae include the ovoid body form, the few and large tubefeet, the number of ten tentacles, the structure of the calcareous ring, and the occasional presence of scattered wheel-shaped deposits. The Pelagothuriidae may originate from pelagic juveniles of some benthic Psychropotina.

The most primitive elpidiid genus (apart from *Psychrelpidia)* is *Peniagone,* which possesses the basic elpidiid type of deposits and calcareous ring.

The adaptation of the Elasipoda to the deep-sea environment. The present investigation contradicts the view of the Elasipoda being primitive survivors in the deep sea. The majority of the features peculiar to the Elasipoda are adaptations to the particular environment of the deep sea. Some features are highly specialized, none appear to be primitive. Alleged primitive features of the Elpidiidae are paedomorphic rather than primitive.

The dominance of the holothurians in the deep sea is determined above all by their feeding-biology. Their faculty of ingesting large amounts of sediment, combined with a low food requirement due to their low content of organic matter, makes them well-fitted for subsisting on the nutrient-poor deep-sea sediments.

The surface-dwelling habit of the Elasipoda, which may be conditioned by the scarcity of carnivores (fishes in particular) in the deep sea, represents a further advantage. The food, which is confined to a thin surface layer of the bottom, becomes more easily accessible, and an extensive area may be searched by the animals.

Features correlated with the surface-dwelling habit are the flat ventral sole, the ventrally turned tentacle crown, the absence of respiratory trees, and the utilization of the papillae for respiratory purposes.

The peculiar mechanism of protraction of the tubefeet in three of the families is an adaptation to walking over the soft bottom. Part of the same mechanism is the entirely dorsal attachment of the mesentery, which prevents the intestine from interfering with the function of the ventral water-vascular cavities.

The elpidiids have among all holothurians the lowest content of organic matter in relation to body size. This makes them so buoyant that even slight water movements may sweep them off the bottom. As suggested above, the rectal caecum may be an organ compensating for the low specific gravity of the body.

A further adaptation to the deep-sea environment is the enormous eggs of the Psychropotidae, which apparently permit the juveniles to spend a long pelagic life independent of food uptake from the meagre deep-sea plankton.

The calcareous deposits of the Psychropotina are highly specialized, in spite of their simple structure.

The paedomorphic evolution of the Elpidiidae included the development of a unique and specialized calcareous ring.

The high degree of adaptation to the deep-sea environment and the absence of primitive features indicate that the Elasipoda originated in the deep sea and never occurred in shallow water.

The evidence of paleontology. Fossil deposits referable with certainty to Elasipoda are not known. Deposits of the fossil family Protocaudinidae (Devonian to Jurassic) resemble those of the recent Laetmogonidae. However, similar deposits occur in the Dendrochirota.

The deposits of the Psychropotina are sufficiently specific to permit a reliable identification of fossil remains. Their absence in fossil sediments confirms that at least this suborder never occurred in shallow water.

Relationship to other orders of the Holothurioidea. There is only doubtful evidence of the position of the Elasipoda within Holothurioidea. Relationship to the Aspidochirota is indicated by external features only, the deposits being entirely different.

D. Bathymetric distribution

Bathymetric distribution of the species. In Figs. 99 and 101–103 each record of a species is indicated by a line. This method of representation gives some idea of depth preferences, if the different degree of exploration is taken into account (Fig. 98).

Bathymetric zonation of the deep sea. A division of the sea into bathymetric faunal zones should be based on changes in faunal composition and not on changes in environmental factors of supposed biological significance. A transition between two zones may be indicated by a concentration of upper and lower limits of distribution of species and by a change in dominance of larger groups.

The upper and lower distributional limits of the species of Elasipoda (Fig. 100) supports the distinction of an abyssal zone with an upper limit at 1800–2600 m and a lower limit at 5000–6000 m. A bathyal zone, on the contrary, is not clearly delimited. Due to the more varied ecological conditions at these depths, the species exhibit considerable differences in bathymetric distribution, and few species range from the lower limit of the sublittoral to the upper limit of the abyssal zone.

The scarcity of lower limits at depths exceeding 6000 m may, in part, be due to the fact that not all abyssal species have the opportunity to go any deeper. However, only few of the many abyssal holothurians of the Kermadec Trench descend into the hadal zone, which indicates that there is also a change in ecological conditions.

The replacement of larger taxonomic units is most strongly exhibited at the sublittoral-bathyal transition. This is the upper boundary of the Elasipoda and the Synallactidae, which together comprise the greater part of the known species of deep-sea holothurians.

Bathymetric distribution and taxonomic relationship. In holothurians the taxonomic relationship is generally closest between forms living in the same bathymetric zone. Apparently, the sublittoral, bathyal, and abyssal zones developed their own groups of holothurians with little admixture of species from other zones.

Number of species and individuals in relation to depth. While the Elasipoda show a maximum in number of species in the abyssal zone, the holothurians as a whole continuously decrease in species number with depth (Fig. 104).

The number of species per station is highest in the abyssal zone (Fig. 105). This agrees with the view advanced by Hessler & Sanders (1967) that the stable abyssal environment has favoured the evolution of a high faunal diversity. Conversely, the low number of species per station in the hadal zone may be due to a young geological age and a lack of stability of the hadal environment.

The number of individuals per species (Fig. 106) continuously increase from the bathyal zone to the bottom of the trenches. The combination in the abyssal zone of a high number of individuals per species and a high number of species per station indicates a dominance of holothurians at the expense of other groups. This dominance is even more pronounced in the hadal zone where, in spite of the decrease in number of species, the total number of individuals per station is much higher than in the abyssal zone.

E. Geographic distribution

The *bathyal species* include almost all laetmogonids and the species of the deimatid genus *Orphnurgus*. None of the bathyal species even approach a cosmopolitan distribution.

The *abyssal species* are often widely distributed, although few are world-wide. The ranges of geographic distribution increase with depth throughout the bathyal and abyssal zones.

Due to the many individual differences in the geographic distribution of the species, the Elasipoda lend no support to a division of the deep sea into larger zoogeographic regions. Characteristic faunas are found in basins with a low sill depth (e. g. the Arctic Basin). A zoogeographic abyssal region may be distinguished along the Pacific coast of Central America.

F. Distribution in relation to environmental factors

In the uniform deep-sea environment the influence of physical parameters on animal distribution would seem to present a less complicated pattern than in shallow water. Nevertheless, the geographic and bathymetric distribution of the Elasipoda can hardly ever be correlated with variations in the physical environment.

Temperature has usually been regarded as the main factor determining the bathymetric distribution of deep-sea animals and the zonation of the deep sea. However, no sublittoral holothurians are known to descend into the Mediterranean deep sea, in spite of its high temperature (c. 13° C.). Similarly, the great majority of deep-sea holothurians remain within their usual depth range in the polar seas where the isotherms approach the surface.

A faunal relationship between the deep sea and the polar sublittoral regions is shown at a higher taxonomic level. *Myriotrochus* (order Apoda) is common to the deep sea and the Arctic sublittoral, and the monotypic, abyssal genus *Abyssocucumis* (order Dendrochirota) is closest related to two monotypic genera of the Antarctic sublittoral. The fact that the two polar regions exhibit completely different types of relationship with the deep sea indicates that the migration was from sublittoral depths into the deep sea, and not the opposite way. A migration from the deep sea would probably have resulted in some degree of similarity between the deep-sea elements of the Arctic and Antarctic sublittoral faunas.

Sediments and nutrient conditions. The distribution of the Elasipoda seems to be independent of the usually distinguished types of deep-sea sediment. This is hardly surprising as investigations in shallow water have shown that there is no simple correlation between animal distributions and the structure and organic content of the sediments.

A correlation is rather to be expected between animal distributions and the amount of nutrients supplied to the deep-sea floor through downsinking from the surface and through turbidity currents and mud slides. The similarities between the faunas along the west coast of Central America, the Antarctic, and the Kermadec Trench may be due to an abundant supply of nutrients in the three areas. The similarity is shown by the presence of identical or closely related species, as well as by the richness in number of individuals.

A correlation between bathymetric distribution and food supply could not be demonstrated. There is no indication that species descend to greater depths in regions with an abundant supply of food, or that deep-sea species ascend to shallower depths in nutrient-poor regions.

Although the bathymetric distribution of the holothurians seems to be largely independent of both temperature and nutrient conditions, the two factors in combination may exert an influence: The deep-sea fauna may depend on a combination of low temperature and poor food supply.

Hydrostatic pressure. Numerous observations have been made on the physiological and biochemical reactions of animals to increased hydrostatic pressure. These observations, however, do not throw light on the question whether a species through a multitude of generations is able to adapt itself to an increased pressure.

Almost all marine animal groups are represented in the deep sea. The poor representation of some groups, and the dominance of others, may be explained without introducing the hypothetical factor of pressure adaptation.

Currents. The distribution of a few bathyal and abyssal species shows a dependency on ocean currents, which indicates that they possess a pelagic larval or juvenile phase, or that they may leave the bottom as adults. In actual fact, juvenile and adult benthic Elasipoda were on a few occasions taken in pelagic nets.

A zoogeographic boundary for bathyal species may exist off Newfoundland where north- and southgoing currents meet. The northgoing current possibly prevented *Laetmogone violacea* from migrating southward along the east coast of North America.

A similar boundary off Japan seems to coincide with the northern limit of a number of bathyal species, including *L. violacea*.

Similarities between the abyssal elasipod faunas of the North Atlantic and the southwestern Pacific may be due to conveyance of pelagic stages with deep currents.

Submarine ridges, according to Vinogradova (1959), may act as distributional barriers, in particular to the deep-abyssal fauna. The present investigation, on the contrary, showed that the most widely distributed species are those of the deeper part of the abyssal zone.

G. The hadal fauna

The present study of the Elasipoda confirmed the justification of distinguishing a hadal zone comprising the depths exceeding 6000 m, but at the same time showed that the characteristic features of the zone are all connected with the fact that it consists almost exclusively of trenches.

The abundant accumulation of sediments in the trenches forms the basis of the enormous dominance of holothurians (elpidiids in particular) and is probably the most important ecological factor in the hadal zone.

A lack of stability and a comparatively low geological age may have led to a low faunal diversity in the trenches, as indicated by the low number of species of holothurians at the hadal stations.

The small total area occupied by the trenches, combined with a low faunal diversity, may explain the abrupt decrease in total number of species at the abysso-hadal transition.

The division of the hadal environment into a number of geographically isolated trenches may lead to the formation of polytypic species if an abysso-hadal species becomes extinct at abyssal depths in the intervening regions. An example is provided by *Elpidia glacialis* which, in a number of West Pacific trenches, is represented by endemic subspecies.

As yet, there is no evidence that this divergent evolution has proceeded further to the formation of superspecies. But the fact that the exclusively hadal species of animals are almost without exception endemic to one trench suggests that isolated trench populations have in many cases diverged to species level.

The irregular topography in the trenches may bring about isolation and taxonomic segregation, as evidenced by the pronounced local variation in four species of the Kermadec Trench. The existence in the Kurile-Kamchatka Trench of four closely related species of *Elpidia* raises the question whether such segregation may lead to species formation.

H. Evolutionary aspects

The insignificant role played by immigration from shallower depths in the evolution of the deep-sea holothurians makes this group well suited for a study of the conditions of species formation in the deep sea.

The importance of geographic isolation for species formation has long been recognized for well-investigated groups of terrestrial animals. The deep sea, however, with its uniform and stable environment and its almost complete absence of geographic barriers, seems to offer few possibilities of geographic isolation, apart from the discontinuous environment of the hadal zone.

The distribution and geographic variation of a number of species of holothurians suggest that geographic isolation with a subsequent subspecies and species formation has taken place in an abyssal region along the Pacific coast of Central America and northern South America. Two widely distributed species, *Deima validum* and *Oneirophanta mutabilis,* are in this area represented by geographic subspecies. Two other widely distributed species, *Scotoplanes globosa* and *Molpadia blakei,* are in the same area replaced by the closely related species, *S. clarki* and *M. granulata.*

A clinal variation is present in the deimatid *Orphnurgus glaber,* which ranges from the Bay of Bengal to the Hawaiian Islands.

The deep sea has sometimes been regarded as a refuge for ancient animal groups which are no longer able to stand the competition at shallow depths. This view of a low degree of competition is hardly compatible with the high faunal diversity recently found in abyssal communities.

The existence and dominance of an animal group in the deep sea depend on its ability to compete successfully in this particular environment. The Elasipoda is a pronounced example of a group which owes its dominance to its highly evolved adaptation to life in the deep sea.

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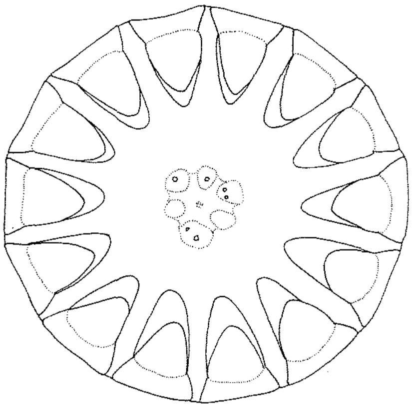
VI. INDEX TO NAMES OF GENERA AND SPECIES

Main entries in *italics*. Generic names preceded by * refer to non-Elasipoda. Specific names in keys, diagrams of bathymetric distribution, and maps of geographic distribution are not included (see main entry to generic name).



Additions and corrections

P. 76, right column, line 6 from below: Koehler & Vaney, 1905 .... *Read* Vaney, 1908.
P. 127, left column, line 3 from below: Théel, 1879 .... *Read* Théel, 1882.
P. 235, left column. With regard to the penetration of species into the Mediterranean deep sea the following information from E. Tortonese 1965 (Fauna d'Italia, 6) should be noted: (1) *Mesothuria verrilli* may not occur in the Mediterranean, the recorded specimens probably belonging to *M. intestinalis*. (2) *Molpadia musculus* penetrates to at least 820 m. (3) The molpadonian *Hedingia mediterranea* is known from the type specimen only (Tyrrhenian Sea: 800–1005 m). The species is likely to be identical with *H. albicans* (North Atlantic, Bay of Bengal, southwestern Pacific: 491–3200 m).