## 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  $4 \, 0/_0$  formalin neutralized with borax, or in 70  $0/_0$  alcohol. The former specimens were transferred to 70  $0/_0$  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<sub>3</sub> 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 sions. 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, spindleshaped, 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 circumoral 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. Intraovarian 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)

- 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  $1227 \text{ m} (3.3^{\circ} \text{ C.})$  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 sub-

species 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- $2.9^{\circ}$  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 *Challen*ger 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- Iateral tubefeet	Ventro- Dorsal lateral papillae tubefeet	
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 ("Oneirophantalike"), 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. Preanal 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. Preanal 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. mo*saicum 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 manylayered 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 3layered 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, singlelayered 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  $10 \times 4$  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  $9 \times 3.5$  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 starshaped.

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  $8 \times 4$  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 papillaein 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
- 1	0	7.0	13-12	3	5 - 5	54
- 1	1	7.5	12-12	3	5 - 5	4-4
- 1	2	7.5	13–13	4	5 - 5	5 - 5
- 1	3	7.5	13-12	4	7-7	6-6
- 1	4	9.0	14–13	4	7-7	77

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 preanal 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 largeholed 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 reexamined, 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



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.

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.

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

Deposits of body wall exclusively spatulated crosses. Papillae always rigid from	
the densely crowded cluster of spatulated rods protectus	(p. 47)
Deposits of body wall differently developed, but spatulated crosses always rare.	
Papillae usually flexible	
Deposits of body wall small spinous rods asper	(p. 38)
Deposits of body wall varying greatly, but never small, spinous rods 3	
Deposits dorsally slender, spatulated rods, ventrally small rods with a few dicho-	
tomous ramifications vitreus	(p. 46)
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)
	Deposits of body wall exclusively spatulated crosses. Papillae always rigid from the densely crowded cluster of spatulated rods protectus Deposits of body wall differently developed, but spatulated crosses always rare. Papillae usually flexible

## 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 rodshaped, 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.

51.52(5405,152501),55211.-1 specificit.

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  $7.5 \times 1.5$  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 suck-ing-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  $7 \times 1.5$  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  $7.5 \times$  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 spindleshaped 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  $15 \times 3.5$  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  $9 \times 4.5$  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 speci-

men 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, mid-

ventral tubefeet, and on each side about 30 double-rowed ventrolateral tubefeet and 30 double-rowed dorsal papillae. The other specimen (72 cm long) had 26 rudimentary, mid-ventral 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 doublerowed (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 spindleshaped, 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 pro-

nounced 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.	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. Midventral 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)
- 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.

8	9	10	11	12	13	14	15	16	17	18	19
4	12	32	39	13							
-	5	14	32	43	4	2					_
13	28	30	18	11	_		_	_	_	_	_
3	23	20	29	18	5	2		-		-	
-	1	3	5	24	22	20	14	8	1	-	2
	8 4 - 13 3 -	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$ \begin{vmatrix} 8 & 9 & 10 & 11 \\ 4 & 12 & 32 & 39 \\ - & 5 & 14 & 32 \\ 13 & 28 & 30 & 18 \\ 3 & 23 & 20 & 29 \\ - & 1 & 3 & 5 \end{vmatrix} $	$ \begin{vmatrix} 8 & 9 & 10 & 11 & 12 \\ 4 & 12 & 32 & 39 & 13 \\ - & 5 & 14 & 32 & 43 \\ 13 & 28 & 30 & 18 & 11 \\ 3 & 23 & 20 & 29 & 18 \\ - & 1 & 3 & 5 & 24 \end{vmatrix} $	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$ \begin{vmatrix} 8 & 9 & 10 & 11 & 12 & 13 & 14 \\ 4 & 12 & 32 & 39 & 13 & - & - \\ - & 5 & 14 & 32 & 43 & 4 & 2 \\ 13 & 28 & 30 & 18 & 11 & - & - \\ 3 & 23 & 20 & 29 & 18 & 5 & 2 \\ - & 1 & 3 & 5 & 24 & 22 & 20 \end{vmatrix} $	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$

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

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 circumoral 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 *Tra*vailleur 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 papil-

lae. 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



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

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.

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 *Laet*mogone 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 wheelshaped 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. Ten-	
	tacles 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 (oc-	
	casionally 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.	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	
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	
5.	Rosette-shaped deposits present. Some of the wheels of the large type with a tri-	
	angular 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.	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 suckingdiscs 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.				Spok	es	
mm	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).

Diam.		Spokes										
mm	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 5. Galathea.

Table 6. Challenger.

Diam.					Sp	okes			
mm	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

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.

Diam.					Spokes								
mm	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 7. Challenger.

### Table 8. Challenger.

Diam.		Spokes											
mm	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			

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) trom 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 reexamined 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. wyvillethom*soni. 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 reTable 9. Laetmogone theeli. Number of spokes and diameter of 100 wheels from the dorsal skin in a specimen from Albatross St. 3400. (The ven-

Diam.					Spok	es		
mm	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

tral wheels show a similar distribution).

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.

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

Table 10. Laetmogone violacea

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.

Diam.	Cen	tral	rays						Spo	kes			
mm	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

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.

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.					S	poke	s			
mm	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. wyville*- thomsoni 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. wyvillethom*soni 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 suckingdiscs. 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.

Diam.	Central rays	Spokes	
mm	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	22	
0.08	21	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 -	-153-1 10	
0.14	- 8 1 -	- 3 2 1 3 - 9	
0.15	- 6 1 1	-1133-8	
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 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.

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.	Centr	al rays					SI	ooke	3		
mm	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 XLVI: 1; Sluiter 1901b, pp. 66–67, pl. II: 2; Heding 1940, pp. 369–370, fig. 19.

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,

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. Rosetteshaped 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 lslands (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 reexamined. 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

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	_	_

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

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 rosetteshaped 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, Laetmogone 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 suckingdiscs.

Synonymy: *Pannychia moseleyi* was taken in two specimens by the *Challenger*, one wellpreserved 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  $P.\ m.\ vir$ gulifera 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 singlerowed. 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 Apodo-gaster (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. lies. 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).

Remarks: The suborder comprises three fami-

#### 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 pres-

ent. 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)
- 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	
1.	Deposits rod-shaped or absent. Dorsal papillae minute	
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	<b>u</b> 7
	brim fused throughout their length	
3.	Crosses of two types, both with a bipartite apophysis; in the large type the apo-	
	physis 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 <i>B. incerta</i>	<b>`</b>
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	( <b>I</b> )
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 adjoin-	
	ing 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 crossshaped 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 doublesized 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 simi-

lar 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 whitishtransparent. 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.



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 rodshaped, 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.

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Fig. 31. Benthodytes valdiviae. Valdivia St. 33. 1–4, crosses from dorsum; 5, rod from ventrum.

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



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.

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.

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 watervascular 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.



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 circumoral 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 *Benthody*tes, it could be seen that the deposits were crossshaped.

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 circumoral 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 abovementioned 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 en-

tirely 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.	Tentacles 10 exigua	(p. 96)
2.	Tentacles 16–18 magna	(p. 97)

Psycheotrephes exigua Théel, 1882	<i>lenger</i> at a depth of 5029 m in the Central Pacific $(7^{\circ}25'S, 152^{\circ}15'W)$ .	
Théel 1882, pp. 92–93, pls. VIII: 8, XXXV: 12,		
XLIV: 1.	The species may represent a juvenile stage of	
One specimen, 2.5 cm long, taken by the Chal-	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	· <b>-</b>
5.	Dorsal appendage at least $1/3$ length of the body	
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 $\frac{1}{3}-\frac{1}{1}$ length of the body, placed on the most	· <b>_</b> /
	elevated part of the body. Arm spines of deposits not arranged in rings 8	

- 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 1/3-1/2body 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 character-

istic 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 onethird 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 "holo-thurid" 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 anchorshaped 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 ( $22^{\circ}47$ 'N,  $80^{\circ}24$ '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 onethird 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  $40^{\circ}N$ ). 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



Fig. 44. Psychropotes depressa. Number of tentacles in relation to body length in 25 North Atlantic specimens taken by the Ingolf and the Thor.

a variation of 10-18 tentacles, largely increasing with the size of the specimens (Fig. 44).

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 reexamined 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  $0.05-0.10 \text{ mm} \log a \text{ arms}$ . 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 detect). 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 irregular-

ly 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 wellspaced 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 brownishviolet, 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. longi*cauda 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 tube-feet.

Free, ventrolateral tubefeet 14-15 pairs, large and well spaced.

Posterior brim composed of 2-3 pairs of tube-feet.

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 tube-feet.

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 yellowbrown 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 reexamined 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



Fig. 53. Psychropotes longicauda. Dorsal deposits. Challenger St. 157 (the 8 cm long specimen in MNHN).

often much higher than the other spines (Fig. 53). The deposits resembled those found in North Atlantic specimens.

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 point-

ed, 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 ofpairs 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	26	10-13	721	2-4
Eastern Pacific	5–7	9–24	7-12	5-7
Japan	48	1214	79	-

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 Pacifis, 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