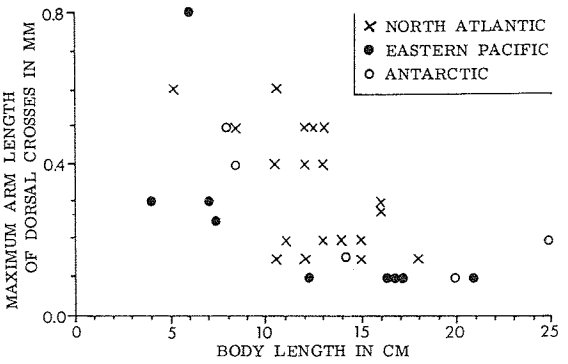


Fig. 54. *Psychropotes longicauda.* Maximum arm length of dorsal crosses in relation to body length.

This may represent a geographic or local variation; deposits with more than four arms have not otherwise been found in *P. longicauda.*

The ventral deposits probably show no geographic variation. In the Kermadec Trench the variation in shape comprised the whole variation found in the species.

An age variation is present in the size of the crosses. In the specimens from the North Atlantic, the Antarctic, the Kermadec Trench, and the eastern Pacific the maximum arm length of the dorsal crosses decreases on an average with the size of the specimens (Fig. 54).

The ventral crosses belong to two size groups. Crosses with arms smaller than 0.1 mm are abundant in all the specimens, and are usually the only deposits present. (One specimen from St. 664 in the Kermadec Trench, however, had only rod-shaped deposits in the ventrum). Large scattered crosses, with arm lengths of 0.2–0.3 mm, are found mainly in smaller specimens.

Conclusion. A *geographic variation* is shown by the shape of the dorsal crosses, by the number of free ventrolateral and fused posterior tubefeet, and by the presence or absence of radial elevations on the head. The variation in each feature is largely independent. A division of the species into geographic subspecies cannot be made on the basis of our present knowledge.

A *local variation* in body colour was found between specimens from two *Galathea* stations in the Kermadec Trench.

An *age variation* is shown by the presence of large, juvenile crosses both in dorsum and ventrum, and by the fact that the tubefeet in specimens up to 5–6 cm in length are fused to form a continuous brim. A number of 12 tentacles was present in the 3.2 cm long specimen from St. 663; already at a body length of 5–6 cm the full number of 18 tentacles is attained.

Relationships: A large unpaired dorsal appendage placed close to the posterior end of the body is found also in *P. loveni* which possibly represents a juvenile stage of *P. longicauda.* No other species can be pointed out as being particularly close to *P. longicauda.*

Distribution: Cosmopolitan, 2210–5173 m.

Type: BM, labelled "Type".
Type locality: *Challenger* St. 157 (53°55'S, 108°35'E).

Psychropotes loveni Théel, 1882
Fig. 55

Théel 1882, p. 100, pls. XXVII: 2–4, XXXV: 1–3.

Diagnosis: Tentacles 10–12. Dorsal papillae minute. Unpaired dorsal appendage large and placed close to posterior end of body; base of appendage as broad as the body. Brim continuous round the body. Dorsal deposits with a high and smooth central apophysis; arms up to 0.5 mm long, and usually with only one large spine on each arm. Ventral deposits with a low and spinous central apophysis, or with no apophysis; arms up to 0.2 mm long, with small spines only.

Material:
St. 668, Kermadec Trench (36°23'S, 177°41'W), 2640 m. – 2 specimens.

Description: The two specimens are 2.5 and 2.0 cm long, and very defective. The unpaired appendage as well as large parts of the skin are lacking.

Skin whitish and soft.

Tentacles 12 in both specimens. Discs with about 20 marginal knobs. On all the tentacles most or all of the knobs are retracted.

Brim (preserved in patches only) continuous round the body.

Midventral tubefeet very small but present throughout length of ventral sole.

Deposits (Fig. 55). Dorsal crosses very uniform in appearance, with a high and smooth central

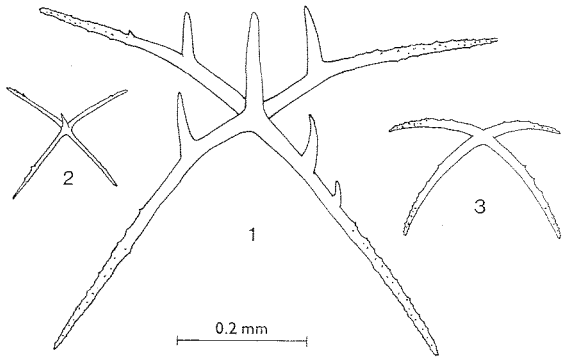


Fig. 55. *Psychropotes loveni.* Deposits. St. 668. 1–2, dorsum; 3, ventrum.

apophysis, and four high and smooth arm spines; additional spines rarely present. Arms up to 0.5 mm long. Ventral crosses (preserved in one of the specimens only) with regularly curved and tapered arms which are up to 0.2 mm long; central apophysis absent; arm spines very small.

Remarks: The reference to *Psychropotes loveni* is based primarily on the dorsal crosses which are of the same characteristic shape (although almost twice as large) as those in the *Challenger* specimen (the type). The ventral crosses differ by the complete absence of a central apophysis.

The small size of the specimens and the low number of tentacles (the type is about 5 cm long and has 10 tentacles) suggest that all the known specimens of *P. loveni* are juveniles.

In external features the specimens resemble the 3.2 cm long juvenile of *P. longicauda* from St. 663. However, the deposits in *P. loveni* are outside the known variation of *P. longicauda.*

Distribution: Southwestern Indian Ocean, 2514 m. Kermadec Trench, 2640 m.

Psychropotes sp.

St. 217. One specimen, 7.5 cm long and 1.5 cm broad. Tentacles 18. Brim continuous round the body. Unpaired appendage 0.5 cm long, close to posterior end of body. Skin gelatinous, light violet, ventral side of head dark violet. Deposits strongly corroded.

Family **ELPIDIIDAE** Théel, 1879

Diagnosis: Tentacles 10–12. Ventrolateral tubefeet large, well spaced, and usually few. Midventral tubefeet absent. Calcareous ring consisting of five star-shaped pieces.

Taxonomy: The taxonomic position of the family is considered in the General Part (pp. 206–207), where the view is advanced that the family represents a paedomorphic trend of evolution.

In the present section only the subdivision of the family is discussed. The question of the correct basis of this subdivision has been subject to divergent opinions by earlier authors. This was partly due to the fact that divisions based on the external characters were difficult to reconcile with divisions based on the deposits, and partly to different opinions regarding the phylogeny of the deposits.

The views presented here with regard to the phylogeny of the deposits (pp. 183–185) and the calcareous ring (pp. 187–189) in the Elpidiidae lead to a new evaluation of the interrelationship of the genera.

1. – Earlier systems of the Elpidiidae. Théel (1882), who established the original system for the family, based the genera mainly on external characters. *Peniagone* was defined by the large velum (an anterior, dorsal appendage composed of two or three pairs of fused papillae); *Parelpidia* by the elongated, *Synapta*-shaped body and the reduced dorsal papillae; *Scotoanassa* by the depressed body form; and *Achlyonice* by the number of 12 tentacles.

Théel regarded the deposits as less important taxonomically. *Peniagone* included species with four-armed deposits and one species *(Amperima naresi)* with three-armed deposits. Other species with four-armed deposits were referred to *Elpidia,* despite the fact that the type species of this genus *(E. glacialis)* had completely different deposits.

The genera *Kolga* and *Irpa* were separated by an anatomical feature, the stone canal in *Kolga* opening to the exterior, in *Irpa* to the body cavity.

The genus *Enypniastes* was characterized by the large anterior brim composed of both dorsal and ventrolateral papillae, and by the presence of 20 tentacles.

R. Perrier (1902) primarily based his system on the deposits and thereby attained a more natural grouping of the species. He reserved the genus *Elpidia* for the species *E. glacialis* which possesses spicules of a type otherwise unknown in the

holothurians. He defined *Scotoplanes* by the presence of rods in addition to C-shaped spicules, and united species simultaneously possessing C-shaped and tripartite spicules into a new genus, *Periamma*. (Pawson (1965a) pointed out that the name *Periamma* was preoccupied and changed it to *Amperima)*. The genera *Scotoplanes* and *Periamma (=Amperima)* together embraced all Elpidiidae with C-shaped spicules.

Species with four-armed spicules were by Perrier collected into four closely related genera, distinguished by the shape of the body, and by the presence or absence of a velum. Of these genera, *Parelpidia* and *Scotoanassa* were defined in accordance with Théel, whereas *Peniagone* was given another content – being no longer defined by the presence of a particularly large velum. In Perrier's system this genus included species with four-armed spicules, an elongatedly oval body, and a velum (whether or not the latter was large), while species having a similar body form, but with separate dorsal papillae, were referred to a new genus, *Elpidiogone*.

Hérouard (1902) proposed a system based exclusively on external characters. This constituted no improvement of Théel's system and needs no comment – particularly since Hérouard himself later replaced it by another system which, similar to that of Perrier, was primarily based on the deposits.

In his new system, Hérouard (1923) adopted most of Perrier's generic definitions. However, the presence or absence of a velum was discarded as a generic character. The genus *Elpidiogone* was accordingly regarded as a synonym of *Peniagone*. On the other hand, the genus *Scotoplanes* was restricted to species possessing both anterior and posterior dorsal papillae, whereas species in which all the papillae were anteriorly placed (whether or not the papillae were fused into a velum) were referred to a new genus, *Ellipinion*.

The genus *Rhipidothuria* Hérouard, 1901, with the single species *R. racowitzai*, was regarded as closely related to *Peniagone* – differing only in having small papillae throughout the length of the dorsal radii.

Enypniastes Théel, 1882, and *Euriplastes* Koehler & Vaney, 1905, together with *Pelagothuria* Ludwig, 1894, were united to form the family Cyclioninae. As pointed out by Ekman (1926) the correct name of this family is Pelagothuriidae Ludwig, 1894. The family is not included in the present work.

Although Hérouard's revised division of the family into genera did not differ essentially from that of Perrier, he did advance an entirely new idea concerning the generic interrelationship. Based on theoretical considerations on the phylogeny of the deposits, the genera were regarded as belonging to two evolutionary trends – one comprising the genera with four-armed deposits, the other all the remaining genera, the deposits of the latter being derived from a single, "trinary" type.

Ekman (1926) replaced Hérouard's theory by yet another, contending that some holothurian deposits are derivatives of a primary cross, while others are derived directly from a primary rod. Based on this theory, he divided the Elpidiidae into two subfamilies, Elpidiinae and Peniagoninae. Although based on completely different theoretical considerations, these subfamilies were identical to the two evolutionary trends assumed by Hérouard.

The Elpidiinae (comprising the genera *Elpidia, Kolga, Irpa, Scotoplanes, Ellipinion, Amperima,* and *Achlyonice)* were characterized by the absence of primary cross derivatives (apart from the occasional presence of wheel-shaped deposits in some species).

The Peniagoninae (comprising the genera *Peniagone, Parelpidia, Scotoanassa, Elpidiogone, Psychrelpidia,* and, with some doubt, *Rhipidothuria)* were characterized by the presence of both primary cross and primary rod derivatives.

Ekman's theory, along with Hérouard's, is contradicted in the present investigation (pp. 183–185). No support was found of the idea that the genera of the Elpidiidae represent two evolutionary lines.

2. – Taxonomic characters. The shape of the body, used to characterize the genera *Parelpidia* and *Scotoanassa,* would appear to be unfit for generic distinctions. In actual fact, these genera merely represent two extremes in the variation of the genus *Peniagone,* being interconnected with typical representatives of the latter genus by species intermediate in shape. Accordingly, *Parelpidia* and *Scotoanassa* are regarded here as synonyms of *Peniagone*.

The following features provide information on the interrelationship of the genera:

(1) *The deposits.* The finding (p. 184) that the tripartite and rod-shaped spicules are reductional stages of primary crosses, and not representing a separate line of evolution, reduces the taxonomic importance of the different types of spicule. However, although the deposits do not justify a division of the family into two subfamilies, they remain of primary importance in characterizing the genera and also provide information on intergeneric relationships.

Psychrelpidia, Rhipidothuria, and *Peniagone* possess primary crosses (or crosses with reduced stem). Also in other respects they occupy an original position within the family.

Achlyonice and *Amperima* have tripartite spicules, while *Ellipinion* and *Scotoplanes* have rods. The three latter genera have in common the presence of C-es, a spicule type related to the curved rods found in *Kolga* and *Irpa.*

Among the spicules occurring in the family, those of *Elpidia* are the most deviating, representing a specialized development from rod-shaped spicules.

Wheel-shaped deposits occur scatteredly in a few, mutually unrelated species of the family (pp. 185–186; Fig. 93).

(2) *The calcareous ring* (Fig. 95). The view that the Elpidiidae represent a paedomorphic trend of evolution is based, in particular, on a study of the calcareous ring. However, the unique development which has taken place in the calcareous ring within this family not only supplies information on the derivation of the family as a whole but also provides a means of distinguishing between primitive and specialized genera, analogous to the conditions found in the deposits. The genera of the Elpidiidae may be divided into three groups of relationship according to the structure of the calcareous ring (pp. 187–189).

(3) *The velum* is in all probability an original feature in the family (p. 190).

(4) *The tentacles.* Deviations from the number of 10 tentacles are found in the genus *Achlyonice* (10–12) and in *Peniagone islandica* (8).

Differences in the shape of the tentacle discs may characterize genera and species (p. 192).

(5) *The gonads.* The presence of paired gonads is one of the primitive features of *Psychrelpidia* and *Peniagone.* Differences in the external morphology of the gonads are of little taxonomic importance in the family (pp. 194–195).

(6) *The rectal caecum.* The absence in the primitive genera *Psychrelpidia* and *Peniagone* of a rectal caecum indicates that the latter is an organ developed within this particular family (p. 192).

3. – Interrelationship of the genera. The above considerations on the taxonomic characters within the family lead to a reduction in the number of genera from 13 to 10.

(1) *Psychrelpidia* Hérouard forms a link between the three families which are united here to form the suborder Psychropotina (pp. 206–207).

(2) *Rhipidothuria* Hérouard, with the single species *R. racowitzai,* has four-armed deposits, a similarity to *Psychrelpidia* and *Peniagone.* Papillae are present throughout the length of the dorsal radii. The two anteriormost pairs, which are placed close together on an elevation of the skin, apparently represent a velum. The difference between *Rhipidothuria* and *Peniagone* thus consists in presence or absence of papillae on the posterior part of the dorsum. The structure of the calcareous ring is unknown.

(3) *Peniagone* Théel includes *Parelpidia* Théel, *Scotoanassa* Théel, and *Elpidiogone* R. Perrier as synonyms. These genera were distinguished from *Peniagone* by external features which show a gradual transition to those of *Peniagone.*

Four-armed spicules are common to all the genera synonymized. Among these spicules, those having an unreduced primary rod (the primary crosses) are the most primitive – representing the prototype of spicule within the suborder Psychropotina.

The calcareous ring resembles the embryonic ring of other holothurians, and represents a type from which the rings of the other genera may be derived. The paired gonads and probably also the absence of a rectal caecum (both features shared with *Psychrelpidia)* are further primitive features.

(4) *Achlyonice* Théel resembles *Amperima* in the presence of tripartite spicules, and *Peniagone* in the structure of the calcareous ring. The absence of C-shaped spicules represents a difference from *Amperima,* to which *Achlyonice* is probably not closely related. The presence of tripartite spicules in both genera may be due to convergence.

(5) *Amperima* Pawson (=*Periamma* R. Perrier) is closely related to *Ellipinion* and *Scotoplanes* as indicated by the presence of C-shaped spicules in all species of the three genera. A less close

relationship is shown to *Kolga* and *Irpa,* both of which possess curved rods which are reminiscent of C-es. C-shaped spicules are otherwise absent in the Elasipoda.

The calcareous ring is similar in *Amperima, Ellipinion,* and *Scotoplanes,* as the pieces are isolated from each other and each one has four pairs of arms. This type of ring is here regarded as a derivative of the type found in *Elpidia* and *Irpa.*

The three genera differ in the arrangement of the dorsal papillae and in the type of spicule. *Amperima* and *Ellipinion* possess a velum, whereas in *Scotoplanes* the second and third pairs of papillae are placed on the posterior part of the dorsum. On the other hand, *Ellipinion* and *Scotoplanes* both possess rod-shaped spicules, whereas the spicules are tripartite in *Amperima.*

In the report on the hadal specimens (Hansen 1956) the genus *Ellipinion* was considered a synonym of *Scotoplanes.* The latter genus was defined according to R. Perrier (1902), who regarded the presence of rod-shaped spicules as being more significant than the different position of the dorsal papillae. In accordance with the generic distinctions presented here, the species *Scotoplanes galatheae* Hansen, 1956, is transferred to the genus *Ellipinion.*

(6) *Ellipinion* Hérouard is discussed under *Amperima.*

(7) *Scotoplanes* Théel comprises *S. globosa* and *S. clarki.* The genus is discussed under *Amperima.*

(8) *Kolga* Danielssen & Koren, with the single species *K. hyalina,* resembles *Irpa* in the shape of the tentacles, the external morphology of the gonads, and the presence of curved rods and irregularly ramified deposits. The curved rods indicate a relationship to *Amperima, Ellipinion,* and *Scotoplanes. Kolga* differs from all four genera by the structure of the calcareous ring which has some similarity to the *Peniagone* type.

(9) *Irpa* Danielssen & Koren comprises *I. abyssicola* and *I. ludwigi,* the latter being transferred from *Kolga.* The calcareous ring is similar to that of *Elpidia.* In other features the genus is closest to *Kolga* (q. v.).

(10) *Elpidia* Théel occupies an isolated position within the family. It has a spicule type which is unique in all holothurians, and has lost every trace of a velum. The calcareous ring is highly specialized and similar to that of *Irpa.*

Key to the genera of Elpidiidae

1. Deposits four-armed 2
1. Deposits not four-armed 4
2. Anterior brim present, composed of dorsal and ventrolateral papillae ..... *Psychrelpidia* (p. 131)
2. Anterior brim absent, or represented by a velum, which consists of dorsal papillae only 3
3. Papillae present throughout length of dorsal radii ..... *Rhipidothuria* (p. 131)
3. Papillae confined to anterior part of dorsal radii and usually forming a velum ..... *Peniagone* (p. 131)
4. Deposits rod-shaped, with two pairs of obliquely placed, horizontal arms and two vertical apophyses ..... *Elpidia* (p. 172)
4. Deposits not so 5
5. C-shaped deposits or irregularly curved rods with a middle enlargement present (except, possibly, in *Amperima furcata* and *Irpa ludwigi).* Tentacles 10 6
5. Neither C-shaped deposits nor irregularly curved rods with a middle enlargement. (Deposits entirely absent in *A. tui*). Tentacles 10–12 ..... *Achlyonice* (p. 155)
6. Deposits tripartite or rod-shaped, besides true C-es 7
6. Deposits irregularly rod-shaped or branched; curved rods with a middle enlargement present, but true C-es absent 9
7. Deposits tripartite ..... *Amperima* (p. 158)
7. Deposits rod-shaped 8
8. Dorsal papillae separated into one pair of large papillae, placed anteriorly, and

one large and one small pair, placed close together on the middle or posterior part of the body ..... *Scotoplanes* (p. 166)

8. Dorsal papillae placed close together anteriorly, usually forming a velum .... *Ellipinion* (p. 162)
9. Pieces of calcareous ring sturdy, firmly joined to each other, each with four pairs of arms, two pairs of which may possess irregular processes ..... *Irpa* (p. 171)
9. Pieces of calcareous ring delicate, meeting (at the most) at their periphery, each with five pairs of arms (a number of which may be subdivided) ..... *Kolga* (p. 170)

Genus ***Psychrelpidia*** Hérouard, 1923
Fig. 118

Hérouard 1923, pp. 75–76. – Type species: *Peniagone discrepans* Sluiter, 1901, by monotypy.

Diagnosis: Anterior brim present, composed of dorsal and ventrolateral papillae. Ventrolateral tubefeet numerous, slender, almost forming a brim. Deposits cross-shaped. Calcareous ring consisting of five isolated pieces, each probably with a varying number of arms.

Psychrelpidia discrepans (Sluiter, 1901)

Peniagone discrepans Sluiter, 1901a, pp. 27–28; Sluiter 1901b, pp. 75–76, pl. X: 3–4.

Record: Celebes Sea, 2035 m. One specimen.

Remarks: Sluiter pointed out that the species has features in common both with the Elpidiidae (the number of ten tentacles, the structure of the calcareous ring, and the absence of midventral tubefeet) and the Psychropotidae (the anterior brim, the numerous ventrolateral tubefeet, and the long and free dorsal papillae). Re-examination of the specimen (in ZMA) revealed two additional psychropotid features: The tentacles were partly retracted into their stalks (a similarity to *Benthodytes)* and the body was violet in colour. This colour is the usual one in the Psychropotidae, but rarely found in the Elpidiidae.

The specimen is 6 cm long.

Genus ***Rhipidothuria*** Hérouard, 1901
Fig. 118

Hérouard 1901, pp. 41–42. – Type species: *Rhipidothuria racowitzai* Hérouard, 1901, by monotypy.

Diagnosis: Papillae present throughout length of dorsal radii, the anterior two pairs placed close together. Deposits cross-shaped. (Structure of calcareous ring unknown).

Rhipidothuria racowitzai Hérouard, 1901

Hérouard 1901, pp. 41–42; Hérouard 1906, pp. 7–8, pl. I: 1–3.

Record: Antarctic, c. 450 m. Two specimens.

Genus ***Peniagone*** Théel, 1882
Figs. 119–120

Peniagone Théel, 1882, p. 42. – Type species, designated by Deichmann (1930): *Peniagone wyvillii* Théel, 1882.
Parelpidia Théel, 1882, p. 15.
Scotoanassa Théel, 1882, p. 55.
Elpidiogone R. Perrier, 1902, pp. 424–425.

Diagnosis: Dorsal papillae anteriorly placed, usually forming a velum. Deposits primary crosses, or cross-shaped. Calcareous ring consisting of five isolated pieces, each having a varying number of arms.

Remarks: The most primitive species of the genus are probably those having an ovoid body form, with tubefeet throughout the length of the ventral sole. Species with a similar body form are found in almost all the other genera of the family.

A specialized body form is found in the species formerly referred to *Parelpidia* and *Scotoanassa* – the former having a very elongated body and a reduced velum, the latter a broad and flattened body, a posteriorly directed oral tube, and the tubefeet confined to the hind edge of the body. The occurrence of intermediary forms made it inadvisable to retain the two genera.

Peniagone ecalcarea Sluiter, 1901, which lacks deposits and possesses an anterior brim composed of dorsal and ventrolateral papillae, has later

been transferred to the genus *Euriplastes* Koehler & Vaney, 1905 (family Pelagothuriidae).

The species of *Peniagone* are delicate creatures which are often extensively damaged during capture. The following species, based on poorly preserved specimens, are omitted from the present survey:

Peniagone horrifer Théel, 1882. Known from one Antarctic specimen. The external characters could not be made out with any certainty during re-examination. The longitudinal arrangement of the velum, supposed to be characteristic of the species, appeared to be caused by a distortion of the body.

Peniagone atrox Théel, 1882. One specimen taken south of Australia. The specimen was found on re-examination to be very defective, and the external characters of the species uncertain.

Peniagone vexillum R. Perrier, 1896. One specimen taken in the North Atlantic. The specimen was extensively damaged and only provisionally erected as a new species. Heding (1940), with some hesitation, referred to the same species an Antarctic specimen, also in poor condition.

Scotoanassa incerta Sluiter, 1901(a,b). Known from four Indonesian specimens; they were found to be so defective that neither the shape of the body nor the arrangement of the tubefeet could be made out.

Peniagone stabilis Koehler & Vaney, 1905. One specimen taken in the Bay of Bengal. The species was characterized by the posterior lobated border of fused tubefeet and the triangular velum, consisting of one large and two small papillae. This latter structure, however, is incompatible with that of a velum.

Peniagone obscura Koehler & Vaney, 1905. One specimen, taken at the same station as *P. stabilis*. The specimen was apparently too defective to allow an illustration, and little can be concluded from the description.

Peniagone piriei Vaney, 1908. Known from one Antarctic specimen. As the deposits had totally dissolved, the specimen is not even referable to genus.

Peniagone bispiculata H. L. Clark, 1920. Known from three eastern Pacific specimens. The description was not illustrated. The external features could not be made out during re-examination of the specimens (in USNM). The deposits, as noted by Clark, consist of slender primary crosses of two size groups, the majority with 0.10–0.12 mm long arms and a smaller number with 0.15–0.17 mm long arms. Clark failed to observe that the deposits possess a central apophysis in addition to the four apophyses on the arms. The deposits differ in shape from those of all other species of *Peniagone*. However, due to the uncertainty concerning the external features, the species is omitted from the present work.

Parelpidia anamesa H. L. Clark, 1920. Known from one specimen taken off Peru. The specimen was in a poor state of preservation. The number, size and arrangement of the tubefeet and papillae could not be made out.

Peniagone mus D'yakonov, 1952a, is known from three specimens taken southeast of Kamchatka. The specimen illustrated lacked tentacles, velum, and all the tubefeet, except one.

Key to the species of *Peniagone*

1. Papillae not fused into a velum (although their bases may be enclosed in a right and left elevation of the skin) 2
1. Papillae fused into a velum 7
2. Papillae 4–5 pairs, at least the anteriormost pair long and slender 3
2. Papillae 1–3 pairs, all rudimentary 5
3. Tubefeet 8–9 pairs. Deposits primary crosses with 4 apophyses ..... *papillata* (p. 145)
3. Tubefeet 10–12 pairs. Deposits primary crosses, sometimes with reduced stem; apophyses reduced in number on some or all of the deposits 4
4. Papillae separated into an anterior group of 3 pairs which on each side are fused at their bases, and 1 pair placed more posteriorly. All papillae long (although the first pair is longest) ..... *dubia* (p. 144)
4. Papillae consisting of 2 pairs of long and 2 pairs of reduced papillae, all closely placed, although completely separated ..... *incondita* (p. 145)
5. Tubefeet about 10 pairs, bordering the entire ventral sole ..... *incerta* (p. 143)

5. Tubefeet 8–9 pairs, bordering the posterior $^2/_3$ of the ventral sole 6
6. Body very elongated, *Synapta*-like. Arms of crosses about 0.12 mm long. *elongata* (p. 147)
6. Body short and broad. Arms of crosses about 0.60 mm long ..... *verrucosa* (p. 147)
7. Body flattened 8
7. Body ovoid or elongate 13
8. Velar papillae with a long and slender, free part ..... *purpurea* (p. 151)
8. Velar papillae to the greater part of their length enclosed in the velum 9
9. Tubefeet present both laterally and posteriorly 10
9. Tubefeet present only along hind edge of the body 12
10. Tubefeet consisting of 3 pairs of free, lateral tubefeet and 4 pairs which form two fan-shaped clusters at posterior end of body ..... *intermedia* (p. 152)
10. Tubefeet decreasing evenly in size in posterior direction, and not separated into a lateral and a posterior group 11
11. Deposits cross-shaped, with 5 apophyses ..... *foliacea* (p. 152)
11. Deposits nearly cross-shaped, with 4 apophyses ..... *expansa* (p. 152)
12. Tentacle discs with a pair of large, digitiform processes ..... *diaphana* (p. 153)
12. Tentacle discs devoid of large processes ..... *gracilis* (p. 155)
13. Body ovoid (less than three times as long as broad) 14
13. Body elongate (at least three times as long as broad) 22
14. Deposits with a well-developed stem 15
14. Deposits cross-shaped, or nearly so 19
15. Velum very large 16
15. Velum small 17
16. Tubefeet bordering almost the entire ventral sole, regularly decreasing in size posteriorly ..... *wyvillii* (p. 150)
16. Tubefeet bordering the posterior $^2/_3$ of the ventral sole, all of them large (with the possible exception of the one or two hindmost pairs) ..... *ferruginea* (p. 151)
17. Deposits with 4 apophyses ..... *porcella* (p. 134)
17. Deposits with 2–0 apophyses 18
18. Deposits with 2 apophyses. Rod-shaped deposits absent from body wall. *mossmani* (p. 134)
18. Deposits with 1–0 apophyses. Rod-shaped deposits present in body wall, interspersed among the primary crosses ..... *wiltoni* (p. 134)
19. Deposits with a central apophysis 20
19. Deposits lacking a central apophysis 21
20. Apophyses absent from arms of deposits ..... *humilis* (p. 138)
20. Apophyses present on arms of at least the dorsal deposits ..... *rigida* (p. 136)
21. Tubefeet 5 pairs, all of them large ..... *obsoleta* (p. 134)
21. Tubefeet 6–8 pairs, the posterior pairs reduced ..... *convexa* (p. 135)
22. Tubefeet bordering the entire ventral sole 23
22. Tubefeet bordering the posterior $^1/_3$–$^2/_3$ of the ventral sole 25
23. Posterior tubefeet separated by a median incision into a right and left group. Dorsal deposits usually almost cross-shaped and with one apophysis .. *willemoesi* (p. 144)
23. No posterior, median incision of body. Dorsal deposits usually with a distinct stem, and with 2–4 apophyses 24
24. Posterior tubefeet well developed and partly fused into a brim. Dorsal deposits with up to 0.3 mm long arms and up to 0.4 mm long apophyses ..... *affinis* (p. 142)
24. Posterior tubefeet small. Dorsal deposits usually with up to 0.15 mm long arms and 0.10 mm long apophyses ..... *azorica* (p. 138)
25. Tubefeet bordering the posterior $^1/_3$–$^1/_2$ of the ventral sole. Apophyses of dorsal deposits usually longer than the arms 26
25. Tubefeet bordering the posterior $^1/_2$–$^2/_3$ of the ventral sole. Apophyses of dorsal deposits shorter than the arms 27

26. Tentacles 10 ..... *vitrea* (p. 148)
26. Tentacles 8 ..... *islandica* (p. 150)
27. Body about five times as long as broad ..... *challengeri* (p. 146)
27. Body about three times as long as broad 28
28. Velum small ..... *vignoni* (p. 146)
28. Velum well developed 29
29. Velar papillae completely fused. Body colour dark violet ..... *lugubris* (p. 148)
29. Velar papillae with free distal parts. Body colour whitish ..... *japonica* (p. 147)

Peniagone porcella R. Perrier, 1896

Peniagone porcellus R. Perrier, 1896, p. 901; R. Perrier 1902, pp. 426–429, pls. XIII: 7–9, XIX: 13–23; Madsen 1953, pp. 155–156, fig. 4.

Diagnosis: Body ovoid. Tubefeet about 9 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Dorsal papillae 3 pairs, short, the 2 anterior pairs fused at their base to form a low velum. Deposits rather robust and spinous primary crosses with four apophyses.

Records: Off the Azores, 4060 m. Numerous specimens, taken by the *Talisman*. – Off the West Indies, 5033–5044 m. One specimen, taken by the Swedish Deep-Sea Expedition.

Relationships: *Peniagone porcella* appears to be most closely related to the Antarctic species *P. mossmani* and *P. wiltoni*. They differ by the number of apophyses on the deposits: *P. porcella* has four apophyses, *P. mossmani* two, and *P. wiltoni* one or none at all. *P. wiltoni* possesses, in addition, rod-shaped spicules interspersed among the crosses all over the body wall. In external appearance the three species are probably indistinguishable.

The fact that in *P. azorica* a reduced number of apophyses on the spicules may characterize local populations, or represent a geographic variation within the species, suggests that *P. mossmani* and *P. wiltoni* might together form a local or geographic form of *P. porcella*.

Peniagone mossmani Vaney, 1908

Vaney 1908, p. 411, pls. I: 10–11, II: 19, III: 32–33.

Known from one specimen, taken in the Antarctic at 4789 m, simultaneously with the specimen of *P. wiltoni*. Both species are discussed under *P. porcella*.

Peniagone wiltoni Vaney, 1908

Vaney 1908, pp. 413–414, pls. I: 6–7, III: 29–31.

Known from one specimen, taken in the Antarctic at 4789 m, simultaneously with the specimen of *P. mossmani*. Both species are discussed under *P. porcella*.

Peniagone obsoleta (Hérouard, 1899)
Fig. 56

Kolga obsoleta Hérouard, 1899, p. 170, fig. 1; Hérouard 1902, pp. 41–42, pls. VI: 11–15, VIII: 16, 18.
Peniagone nybelini Madsen, 1953, pp. 157–158, fig. 5.

Diagnosis: Body ovoid. Tubefeet 5 pairs, bordering the entire ventral sole, all of them large and placed at equal intervals. Velum small. Deposits almost cross-shaped, with rather horizontal, slender arms and four long, slender, pointed, usually somewhat outwardly curved apophyses placed near the centre of the cross.

Records: East of the Azores, 4360 m. Six specimens. – Mid-Atlantic near the equator, 5250–5300 m. One specimen *(P. nybelini)*.

Remarks: The proposed synonymy between *P. obsoleta* and *P. nybelini* is, in particular, based on the similarity shown by the deposits and by the size, number, and arrangement of the tubefeet.

Skin preparations made during re-examination of five of Hérouard's six specimens of *P. obsoleta* were compared to those made by Madsen from *P. nybelini*. While Madsen's illustration makes clear the variation of the deposits, the three deposits shown by Hérouard are not representative. In actual fact, the deposits of the two species differ in minor details only, e. g., the some-

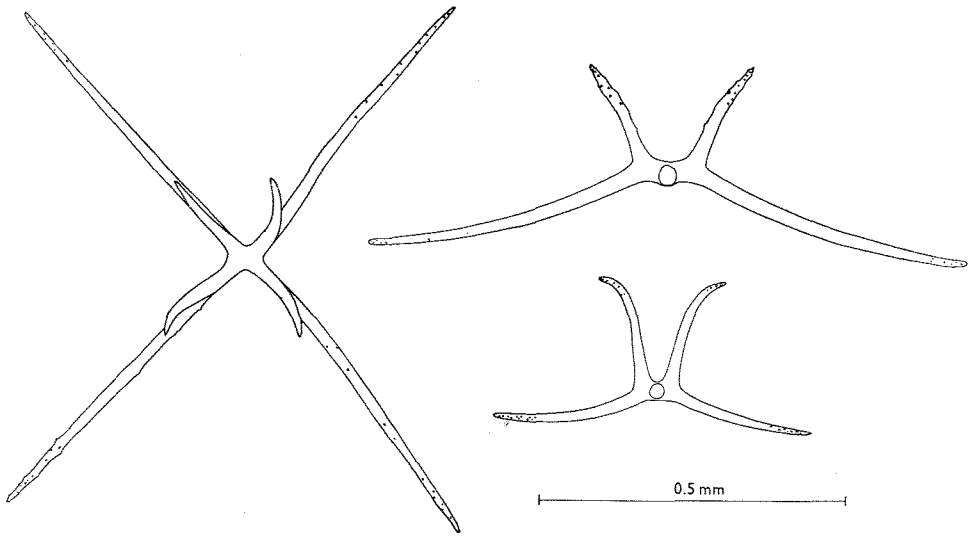


Fig. 56.
Peniagone obsoleta.
Monaco St. 753.
Dorsal deposits.

what enlarged arm ends in many of the *nybelini* deposits – details which represent hardly more than individual or local variations.

The presence of five pairs of large tubefeet, and apparently no small ones, is, within the genus *Peniagone,* unique to *P. obsoleta* and *P. nybelini.* (The presence of six tubefeet in the right side of the *nybelini* specimen forms no exception, as, according to Madsen, the extra tubefoot was formed through an abnormal duplication of a single one).

P. obsoleta is most closely related to *P. convexa* (q. v.).

Peniagone convexa n. sp.
Figs. 57–58, 95: 1, pl. X: 4–5

Diagnosis: Body ovoid. Tentacles with broad, soft discs with a thin, indented and pliable margin. Tubefeet 6–8 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the posterior 2–3 pairs rudimentary. Velum placed anteriorly, the body wall between the velum and the tentacle crown vertical. Deposits almost cross-shaped; their arms rather horizontally placed, with the ends curved slightly upwards; the four apophyses placed near the centre of the cross, their bases joined, and their distal parts pointed and usually curved outwards; arms and apophyses smooth, except at the tips.

Material:
St. 234, Madagascar–Mombasa (5°25'S, 47°09'E), 4820 m. – 1 specimen.
St. 282, Seychelles–Ceylon (5°32'N, 78°41'E), 4040 m. – 1 specimen.

Description:
St. 282. – The type specimen (Fig. 57) is 6 cm long and has a 2 cm broad ventral sole. Body strongly vaulted, reaching a height of 3.5 cm somewhat posterior to the velum. The posterior part of the body decreases abruptly in height – a feature which may, however, be due to contraction. The body wall anterior to the velum is vertical.

Tentacles 10 (Pl. X: 4). The stalks are short and thick; the discs are broad, soft, and slightly concave, with a thin, pliable and indented margin.

Tubefeet 7–8 pairs, bordering the entire ventral sole. The anterior 5 pairs are large, with Nos. 4

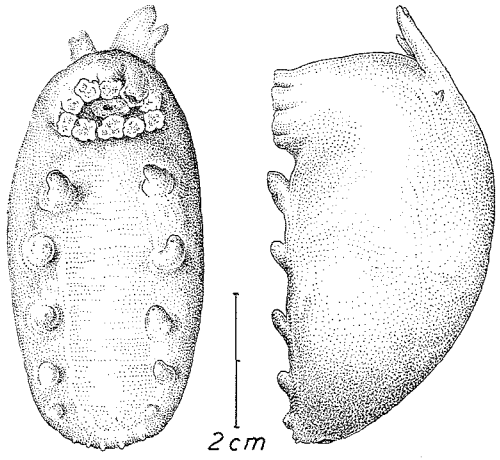


Fig. 57. *Peniagone convexa.* St. 282. Type specimen. PHW.

and 5 only slightly decreasing in size. There is an abrupt transition to the extremely reduced posterior 2–3 pairs. The ends of the tubefeet are rounded, usually with a minute groove, indicating a retracted sucking-disc.

Velum composed of two pairs of papillae, the two on the left considerably longer than those on the right – an indication that the size of the velum is of little importance as a species character. Behind the velum is a pair of minute, free papillae.

Skin white and thin, although rather tough.

Deposits similar to those of the specimen from St. 234, although somewhat corroded by the formalin.

St. 234. – The specimen is 6 cm long and rather defective. The dorsal skin is torn, and the intestines are absent.

Tentacles (Pl. X: 5) resembling those of the type specimen. (The two tentacles illustrated for the species are both within the variation at each station).

Tubefeet probably agreeing with those of the type, both in number and arrangement.

Velum completely separated into a right and left lobe, which are both contracted. Each lobe is composed of two fused papillae and is followed by a minute, free papilla.

Deposits (Fig. 58) almost cross-shaped. The arms are rather horizontally placed, with the ends curving slightly upwards. The four apophyses are placed near the centre of the cross. Their bases merge into each other, giving the deposit, when seen from above, the appearance of being superimposed by another and smaller cross. The apophyses are pointed and outwardly curved. The deposits are almost completely devoid of spines, except at the tips of the arms and the apophyses.

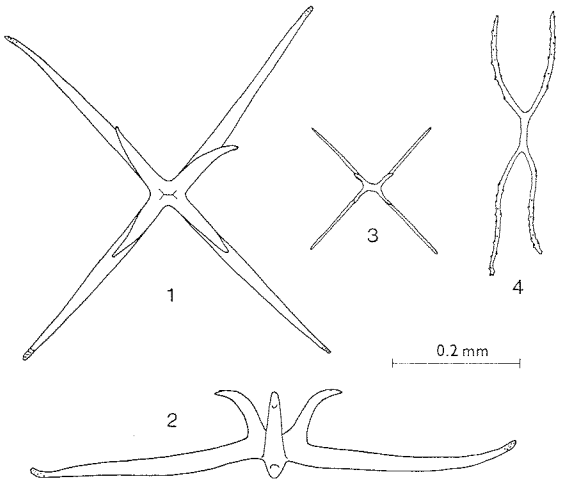


Fig. 58. *Peniagone convexa*. St. 234. Deposits. 1–3, dorsum; 4, gonad.

The deposits vary greatly in size (the deposits figured show their size variation). The dorsal deposits are usually larger than the ventral ones. There are very few rod-shaped deposits, even in the tentacles and tubefeet. Walls of gonads dense with irregular, slender primary crosses which lack apophyses.

Calcareous ring (Fig. 95: 1) belonging to the usual type in *Peniagone*. Two ring pieces examined each possessed 7 pairs of arms.

Polian vesicle single, 2 cm long, and placed in the left ventral interradius.

Relationships: The deposits indicate a close relationship to *P. obsoleta*. The two species differ primarily in the development of the tubefeet – *P. obsoleta* possessing only five pairs, which are all large and placed at equal intervals.

Peniagone rigida (Théel, 1882)
Figs. 59–60

Elpidia rigida Théel, 1882, pp. 20–21, pl. XXXII: 18–20.

Diagnosis: Body ovoid. Tubefeet 8–9 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the posteriormost 4–5 pairs rudimentary. Velum placed anteriorly, the body wall between the velum and the tentacle crown vertical. Deposits cross-shaped, the dorsal crosses with five apophyses, the ventral crosses with one.

Material:
St. 282, Seychelles–Ceylon (5°32'N, 78°41'E), 4040 m. – 1 specimen.

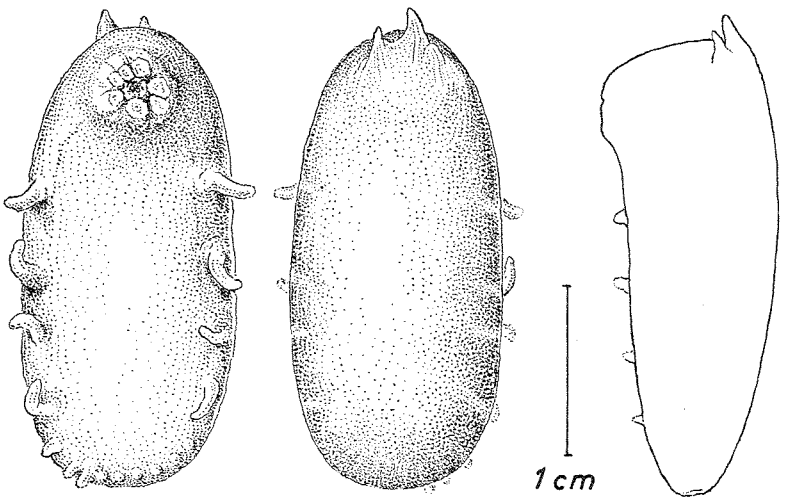
Description: The specimen (Fig. 59) is 28 mm long; ventral sole 10 mm broad.

Tentacles 10, with short stalks. Discs with papillae on the surface; no conspicuous marginal incisions are visible.

Tubefeet 8–9 pairs, the posterior 4–5 pairs rudimentary.

Velum placed anteriorly, the body wall between the velum and the tentacle crown vertical.

Fig. 59. *Peniagone rigida.* St. 282. PHW.



Skin white, thick, and rather soft. The outer, deposit-containing layer almost completely intact.

Deposits (Fig. 60) cross-shaped. The dorsal crosses (1) have very slender, slightly curved and slightly spinous arms which attain a length of 0.5 mm. The five high and slender apophyses are strongly spinous. The ventral crosses (2) are generally more robust. The arms are straight, spinous, often with blunt ends, and few attain a length of 0.3 mm. A strongly spinous central apophysis is present, but there are no apophyses on the arms.

A few curved rods surround the end-discs of the tubefeet, but no end-plates are present. The tentacle discs contain a few rods.

Remarks: The single previously known specimen, taken by the *Challenger* in the northwestern Pacific, was re-examined. Agreement with the *Galathea* specimen included the ovoid body form, the number and placing of the tubefeet, and the shape of the dorsal deposits (ventral deposits not examined).

The skin was, according to Théel, thin, brittle, and rough. However, on re-examination the skin appeared to be similar to that found in most species of *Peniagone,* i. e. rather soft under the outer deposit-containing layer.

Relationships: Most closely related to *P. humilis* (q. v.).

Distribution: Northwestern Pacific, 4204 m. Western Indian Ocean, 4040 m.

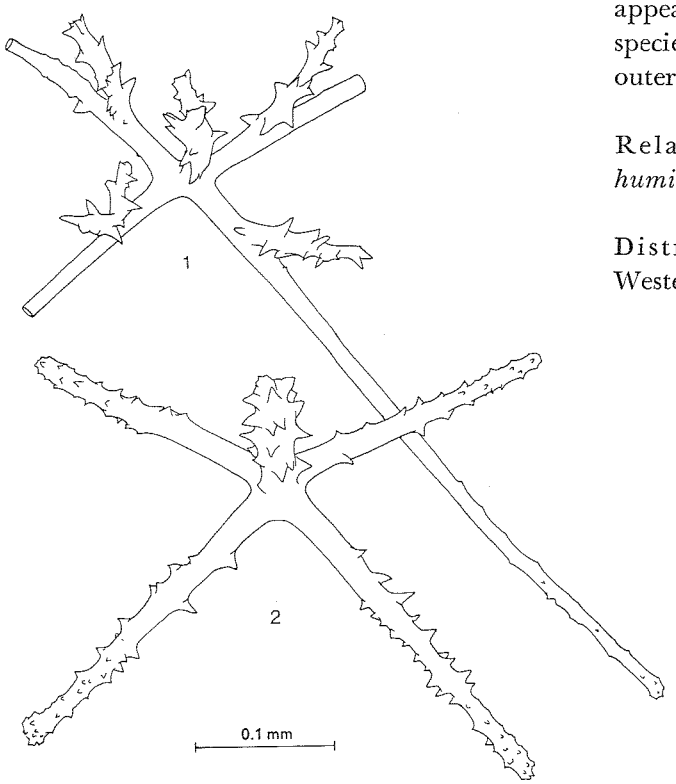


Fig. 60. *Peniagone rigida.* St. 282. Deposits. 1, dorsum; 2, ventrum.

Peniagone humilis n. sp.
Figs. 61–62

Diagnosis: Body ovoid. Ventral sole slightly increasing in breadth posteriorly. Tentacles with firm and vaulted discs with an almost smooth surface and an only feebly indented margin. Tubefeet 10 pairs, bordering the entire ventral sole, posteriorly of smaller size and partially enclosed in a low brim. Velum low, placed near the mouth, and composed of two pairs of completely fused papillae. Deposits cross-shaped, with a single, central apophysis; arms with upwardly curved ends.

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

Description: The specimen (Fig. 61) is about 20 mm long and 10 mm broad. The ventral skin is ruptured, and the body is somewhat distorted and contracted; the proportions of the body, as shown in the figure, should therefore be regarded with some reservation – although the species evidently belongs to the broad and strongly vaulted forms of the genus.

Ventral sole broadest posteriorly, its hind edge forming a large, semicircular curve.

Tentacles 10, short. Discs of a firm consistency, vaulted, with an almost smooth surface and an almost un-indented margin.

Tubefeet 10 pairs, bordering the entire ventral sole, and decreasing evenly in size in posterior direction. The anteriormost 4–5 pairs are separate, while the bases of the remaining tubefeet are enclosed in a low brim.

Velum low, but distinct, placed near the mouth. Its four papillae are almost equally large and

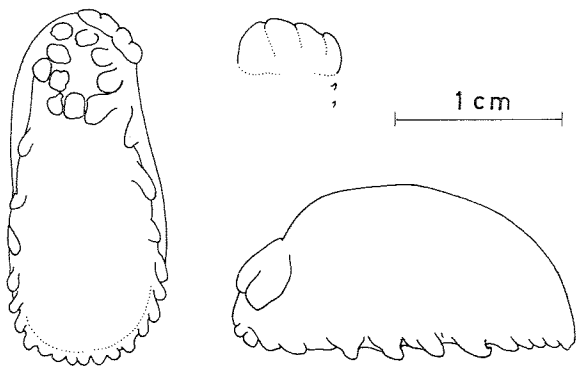


Fig. 61. *Peniagone humilis*. St. 663.

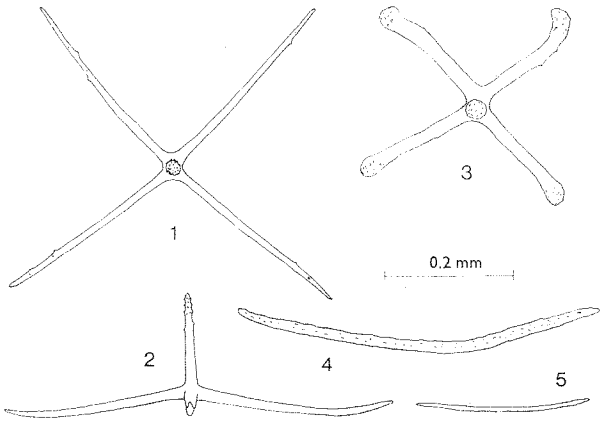


Fig. 62. *Peniagone humilis*. St. 663. Deposits. 1–2, dorsum; 3, ventrum; 4–5, tentacle.

completely fused. On the right side, two minute, free papillae are seen.

Skin whitish and soft.

Deposits (Fig. 62) cross-shaped with upwardly curved arms and a single, central apophysis. The deposits are smooth, except at the tips of the arms and apophyses. The ventral deposits are more robust than the dorsal ones. Rods present in tentacles and tubefeet. End-plate absent from tubefeet.

Relationships: In external features and deposits somewhat similar to *P. rigida,* but differs in the velum being positioned near the mouth, in the shape of the ventral sole, in the posterior tubefeet forming a low brim, and in the absence of apophyses on the arms of both the dorsal and ventral crosses.

Peniagone azorica von Marenzeller, 1893
Fig. 63, pl. X: 1–3

Peniagone azorica von Marenzeller, 1893a, pp. 12–13, pls. I: 4, II: 5; Hérouard 1902, pp. 42–43, pl. VI: 21–26; Hérouard 1923, pp. 87–88; Grieg 1921, p. 8, fig. 4; Heding 1942, p. 20.

Peniagone vedeli Hansen, 1956, pp. 42–44, figs. 12–13.

Peniagone willemoesi (Théel), Hansen 1967, pp. 495–498, fig. 12.

Diagnosis: Body elongate, somewhat flattened posteriorly. Tentacles with rather long stalks; discs with a papillate surface and a pair of retractile marginal lobes. Tubefeet 9–11 pairs, bordering the entire ventral sole, decreasing in size

posteriorly. Velum usually bipartite in the greater part of its length. Dorsal deposits extremely varying; the usual type with a well-developed stem, arms curving strongly downwards, and four high, slender apophyses; length of arms usually less than 0.15 mm; deposits with reduced stem and fewer apophyses, or deposits which are similar to the usual ventral type, occur as local or geographic variants. Ventral deposits nearly always with a well-developed stem, slightly curved arms, and four low apophyses.

Material:

St. 649, Kermadec Trench (35°16'S, 178°40'W), 8210–8300 m. – 160 specimens.
St. 650, Kermadec Trench (32°20'S, 176°54'W), 6620–6730 m. – 260 specimens.
St. 651, Kermadec Trench (32°10'S, 177°14'W), 6960–7000 m. – 6 specimens.
St. 653, Kermadec Trench (32°09'S, 176°35'W), 6180 m. – 1 specimen.
St. 654, Kermadec Trench (32°10'S, 175°54'W), 5850–5900 m. – 11 specimens.
St. 658, Kermadec Trench (35°51'S, 178°31'W), 6660–6770 m. – 600 specimens.
St. 661, Kermadec Trench (36°07'S, 178°32'W), 5230–5340 m. – 60 specimens.
St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 267 specimens.
St. 664, Kermadec Trench (36°34'S, 178°57'W), 4540 m. – 179 specimens.
St. 668, Kermadec Trench (36°23'S, 177°41'E), 2640 m. – 5 specimens.

Description: The specimens from the hadal part of the Kermadec Trench were previously (Hansen 1956) described as a new species, *Peniagone vedeli,* considered to be a close relative of the Atlantic species *P. azorica.* Examination of specimens from abyssal depths proved that the variation in the trench comprised the features of *P. azorica,* and that also the Antarctic species *P. willemoesi, P. incerta,* and *P. affinis* are possible synonyms. Hansen (1967), believing in the synonymy, regarded the Kermadec Trench specimens as belonging to *P. willemoesi.*

The following description deals, in particular, with the specimens taken at the five abyssal Kermadec stations.

Skin soft and mucous. The species belongs to the most watery members of the benthic Elasipoda, and almost no specimens are preserved intact. The thickness of the skin varies rather much from one specimen to another – a variation which cannot be explained simply by a different state of preservation, as specimens preserved in the same vial could differ greatly in this respect.

No correlation was present between the development of the mucous layer and the size of the specimens. The mucous specimens are apparently not juveniles.

Tentacles (Pl. X: 1–3) with rather long and slender stalks. Discs broad, covered with papillae, and with marginal indentations. In the fully extended state a deep aboral incision is present, separating two lobes which taper into a distal, finger-like part. In the contracted discs the lobes are broader or have completely disappeared. (The three tentacles illustrated are all from one specimen).

Tubefeet 9–11 pairs, bordering the entire ventral sole, and gradually decreasing in size posteriorly.

Velum usually bipartite in at least half its length. The specimen illustrated (Hansen 1956, fig. 12) had an only feebly bipartite velum.

A few specimens possess a pair of minute papillae in front of the velum.

Some specimens show an abrupt downward bend of the body part anterior to the velum, brought about by a strong contraction of the ventral, longitudinal muscles. This bend of the anterior part of the body has been regarded as characteristic of some other species of *Peniagone.* However, the fact that this feature does not necessarily represent the natural shape of the body is notable, although in some species (e. g. *P. diaphana* and *P. gracilis)* the bend is a constant feature.

Calcareous ring with about 10–12 pairs of irregularly shaped arms on each of the five pieces. In some specimens some pieces, or even the whole ring, seem to be absent.

Deposits (Fig. 63). Due to the mucous consistency of the skin, the outer, deposit-containing layer is completely worn off in most of the specimens.

Hansen (1956) emphasized the great variability of the deposits of the hadal specimens. The abyssal specimens from the trench added even further to this variation and also revealed a marked local variation of the deposits. In the following, the deposits are described separately for each station, arranged according to depth.

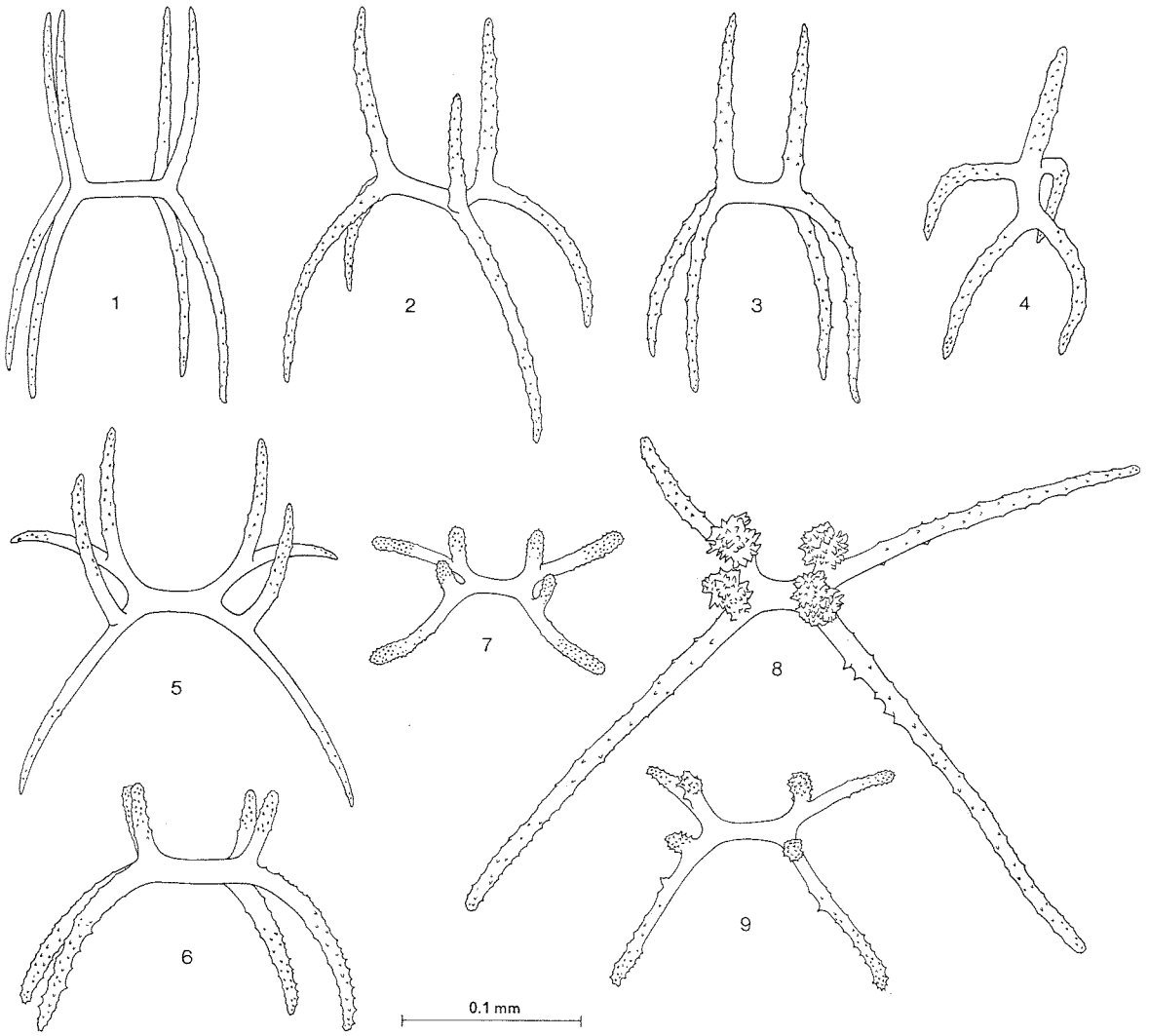


Fig. 63. *Peniagone azorica.* Deposits. 1–4, dorsum (St. 663); 5, dorsum (St. 668); 6, dorsum (St. 661); 7, dorsum (St. 649); 8, ventrum (St. 663); 9, ventrum (St. 668).

St. 668 (2640 m). The 11 fragments, which probably belonged to five specimens, were all examined by means of skin preparations. Three preparations could be determined as belonging to the dorsal side, and two to the ventral side; in the remaining the actual body position could not be determined.

The three pieces of dorsal skin possessed deposits with four high, curved apophyses. Most deposits were similar to the one shown as Fig. 63: 5; but some had longer arms and apophyses or arms which were placed almost vertically. The latter type was represented also at Sts. 661 and 663 (cf. Fig. 63: 1).

The two pieces of ventral skin had deposits with slightly curved arms and low apophyses (Fig. 63: 9). These deposits were similar to those of the hadal specimens.

Of the seven remaining pieces of skin, six possessed deposits similar to those found in the dorsal pieces, and one to those of the ventral pieces. Since none of the preparations had deposits intermediate in shape between these two distinct types, a clear separation between a dorsal and a ventral type apparently exists. A similar separation was found in specimens examined from the abyssal stations 661 and 663, whereas in the hadal specimens the dorsal deposits were similar to the ventral ones.

St. 663 (4410 m). Parts of the outer deposit-containing layer are preserved in only five of the numerous specimens from this station. The dorsal

deposits (Fig. 63: 1–4) are in all five specimens characteristically developed, with strongly curved arms and high apophyses. Usually, two apophyses are present, placed at the ends of the stem. A few deposits possess one, three or four apophyses. The size of the deposits varies a great deal: While most are of the size represented in the figure, many reach double that size.

Most of the ventral deposits are similar, both in size and appearance, to those from St. 668, although larger deposits prevailed in one preparation (Fig. 63: 8). In a few of the ventral deposits the apophyses were reduced to three or two; when two in number they were placed at the ends of the stem. Similarly, in deposits with four apophyses, the latter had a somewhat asymmetric position, one or two of them being placed near the ends of the stem.

St. 661 (5230–5340 m). Among the 60 specimens, 12 are preserved with parts of the outer deposit-containing layer. Dorsal deposits were present in two of them only. One specimen had dorsal deposits (Fig. 63: 6) with the strongly curved arms usually found in the abyssal specimens, but the apophyses were only of moderate height. Some of the dorsal deposits possessed only three or two apophyses.

The other specimen had only the dorsal deposits preserved. These were similar to the deposit from St. 663 shown in Fig. 63: 1.

The ventral deposits in all the specimens agreed with those from the other stations – having a well-developed stem and four, low apophyses.

No outer deposits were preserved in the specimens from Sts. 654 and 664.

Synonymy: *Peniagone azorica* has been reported from many stations in the northeastern Atlantic at depths of 2320–4020 m. Most of the known material was re-examined, and also a number of hitherto unrecorded specimens from two Monaco stations off the Azores, at smaller depths than previously recorded: St. 553, 1385 m: 1 specimen (in MNHN). St. 673, 2252 m: 34 specimens (30 in MOM, 2 in ZMUC, and 2 in MNHN).

The N. E. Atlantic specimens in external appearance were similar to the specimens from the Kermadec Trench. As in the latter, the mucous layer of the skin varied greatly in development. The velum was almost completely divided into a right and left section. Some specimens showed an abrupt, downward bend of the anterior part of the body, similar to that found in some of the Kermadec specimens.

The deposits were examined in 12 specimens, five from Monaco St. 673 (off the Azores), three from Monaco St. 2990 (Bay of Biscay), one from *Ingolf* St. 11 (west of Iceland), and three from *Ingolf* St. 41 (south of Iceland).

The dorsal deposits in all the preparations resembled the type found at *Galathea* St. 668 (Fig. 63: 5). Usually, however, the deposits attained a larger size, being often twice as large, but deposits of that size were also present in the Kermadec specimens.

The ventral deposits were in some of the examined specimens similar to the ventral deposits of the Kermadec specimens. In other Atlantic specimens the ventral deposits were indistinguishable from the dorsal ones of the same specimens, possessing curved arms and high apophyses. The occurrence of these two types of ventral deposits is apparently not geographically determined within the Atlantic, as both types occurred at the two Monaco stations and at *Ingolf* St. 41. Deposits with curved arms and high apophyses were not found in the ventrum of any of the Kermadec specimens.

Deposits with less than four apophyses were not found in the examined Atlantic specimens.

Variation: An extensive individual variation is shown by several features: The development of the mucous layer of the skin, the shape of the velum, the size and arrangement of the posterior tubefeet, and the deposits. In addition, the state of preservation and the degree of contraction may influence such characters as the shape of the tentacle discs, the size of the velum, and the degree of the downward bend of the anterior part of the body which depends on the amount of contraction in the ventral, longitudinal muscles.

The *dorsal deposits* show several interesting features in their variation. In addition to an often considerable individual variation, a local variation (and probably also a geographic variation) can be demonstrated with regard to the number and height of the apophyses, the curvature of the arms, and the degree of reduction of the stem.

The North Atlantic specimens all had dorsal deposits with a rather well-developed stem, four

high apophyses, and downwardly-curved arms. Similar deposits were present in the Kermadec specimens from *Galathea* St. 668.

The populations from the Kermadec Trench show a pronounced local variation in the dorsal deposits. In addition, there seems to be a consistent difference between the abyssal and the hadal specimens. All the examined abyssal specimens from the trench, like those from the Atlantic, had dorsal deposits with strongly curved arms and high, slender apophyses. But the hadal specimens had dorsal deposits with rather horizontally placed arms and low, spinous apophyses, agreeing with the usual ventral type in the species. Examination of 51 specimens from four hadal stations suggested that the similarity is not accidental. It may indicate that the hadal trench populations are in closer contact with each other than with the abyssal populations (p. 243).

The *ventral deposits* do not show a variation comparable to that of the dorsal ones, being nearly always provided with rather horizontally placed arms and four, low apophyses. However, in three Atlantic specimens the ventral deposits were found to be similar to the usual dorsal type, with strongly curved arms and high apophyses. These specimens were all taken simultaneously with specimens possessing normal, ventral deposits.

Relationships: *Peniagone azorica* is closely related to the three Antarctic species *P. incerta, P. affinis,* and *P. willemoesi.* The dorsal deposits of *P. incerta* and *P. affinis* are in their shape within the variation of *P. azorica* at St. 663. Those of *P. affinis* are larger than in the Kermadec specimens, but not appreciably larger than in Atlantic specimens of *P. azorica.* The dorsal deposits of *P. willemoesi* are almost cross-shaped, usually with one apophysis, and somewhat smaller than those of *P. azorica.*

The tubefeet in the three Antarctic species seem to decrease less in size posteriorly than in *P. azorica.*

The features distinguishing the four species may actually represent geographic or local variations of one species.

The ventral deposits are similar in the four species.

Distribution: Northeastern Atlantic, 1385–4020 m. Kermadec Trench, 2640–8210 (8300) m.

The occurrence of *Peniagone azorica* in the Romanche Trench (00°16'S, 18°35'W, depth 7100–7300 m) is indicated by a deep-sea photograph (Heezen *et al.* 1964, fig. 9). The specimen has five pairs of large and well spaced lateral tubefeet, three pairs of small and closely placed tubefeet along the hind end, and a velum which is cleft almost to the base. The authors report that, according to Dr. E. Deichmann, the species "appears to be closest to *Peniagone incerta* Théel". *P. incerta* in external appearance resembles *P. azorica,* but has a more feebly developed velum than *P. azorica* and the specimen photographed.

Deep-sea photographs from the PROA Expedition 1962 (Lemche *et al.* in press) suggest that *Peniagone azorica* occurs also in the New Britain Trench (depth 6790–7665 m) and the Solomon Trench (depth 7850–8625 m).

Peniagone affinis Théel, 1882
Fig. 64

Théel 1882, pp. 52–54, pls. VIII: 4–5, XXXIV: 12–13.

Diagnosis: Body elongate, somewhat flattened posteriorly. Tubefeet about 11 pairs, bordering the entire ventral sole, only slightly decreasing in size posteriorly; the anterior 5 pairs are placed with decreasing intervals, while the posterior 6 pairs are closely set and partly fused into a brim. Velum low, composed of two pairs of papillae of which the median pair is largest and free in about half the length of the papillae. Dorsal deposits with a short stem, strongly curved arms, and 2 or 3 (occasionally 1 or 4) high apophyses; length of arms up to 0.3 mm. Ventral deposits about half as large, with a well-developed stem, slightly curved arms, and 4 low apophyses.

Record: Off the Crozet Islands (southern Indian Ocean), 2924 m. Numerous specimens.

Remarks: Ten specimens (in BM) were re-examined, all by means of skin preparations.

In external appearance the specimens agree well with Théel's illustration, especially in the arrangement of the tubefeet, of which the posterior ones are well developed, closely placed, and partly fused into a brim. Velum feebly developed; only one had a velum of the size shown in Théel's drawing.

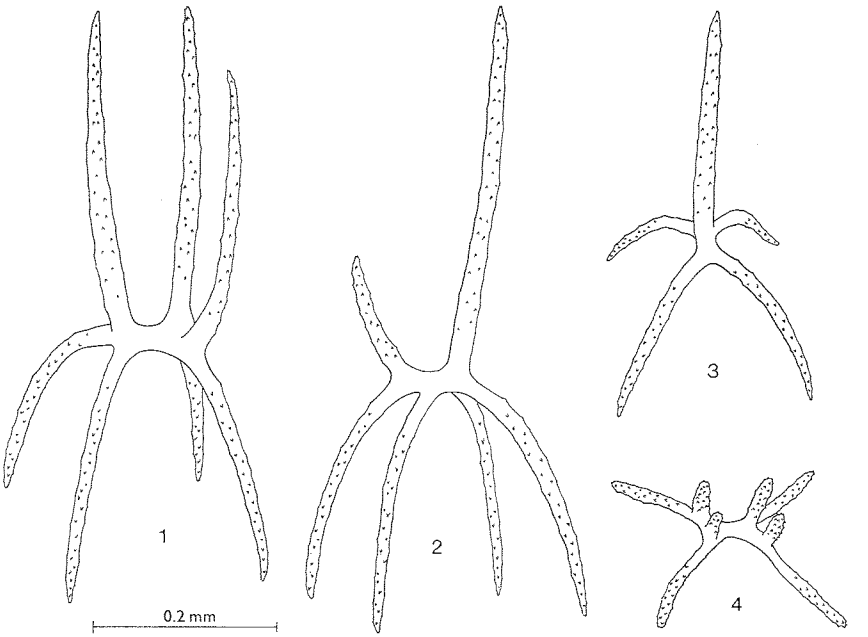


Fig. 64. *Peniagone affinis.* Deposits. *Challenger* St. 147. 1–3, dorsum; 4, ventrum.

Deposits (Fig. 64) dorsally with strongly curved arms and 2 or 3 (occasionally 1 or 4) apophyses; the arms are up to 0.3 mm long; the apophyses are up to 0.4 mm and often of unequal length in the same deposit. The stem is rather short or almost absent, especially in deposits with only one apophysis. The ventral deposits are only half as large as the dorsal ones; they have a well-developed stem, slightly curved arms, and four low apophyses.

As noted by Théel, the dorsal deposits are rather similar to those of *P. vitrea.* In external appearance the two species are very different, as *P. vitrea* has the tubefeet confined to the posterior third of the ventral sole.

P. affinis resembles *P. incerta* in external appearance and in shape of the deposits which, however, are twice as large as in *P. incerta.*

Peniagone incerta (Théel, 1882)
Fig. 65

Elpidia incerta Théel, 1882, pp. 26–27, pls. VIII: 1, XXXIII: 3–4.

Diagnosis: Body elongate, somewhat flattened posteriorly. Tubefeet about 10 pairs, bordering the entire ventral sole, slightly decreasing in size posteriorly; the posterior 5 or 6 pairs partly fused. Velum very small, or absent. Dorsal deposits with strongly curved arms, 2 (occasionally 3 or 4) apophyses and a well-developed stem. Ventral deposits with slightly curved arms, 4 low apophyses, and a well-developed stem.

Record: Antarctic Ocean, 2293 m. Four specimens.

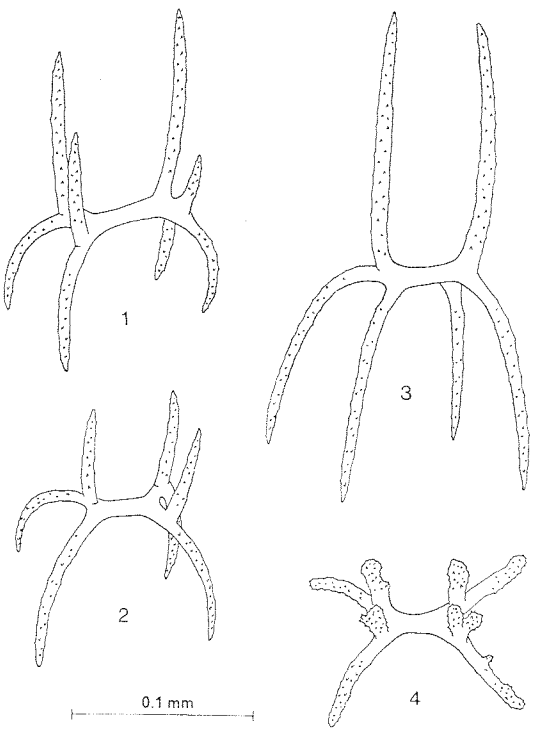


Fig. 65. *Peniagone incerta.* Deposits. *Challenger* St. 152. 1–3, dorsum; 4, ventrum.

Remarks: The four specimens known (two in BM and two in ZMA) were re-examined, all by means of skin preparations.

The species in external appearance resembles *P. affinis;* the posterior tubefeet are, as in the latter species, rather large and partially fused. Velum not present (or not preserved), its place being occupied by a pair of inconspicuous knobs.

Deposits (Fig. 65) dorsally with strongly curved arms and two high apophyses, placed at the ends of the stem. Occasionally, three or four apophyses are present. Arms as well as apophyses 0.10–0.15 mm long. The ventral deposits agree with those of *P. affinis* and *P. azorica,* having slightly curved arms and four low apophyses. Arm length c. 0.07 mm. One of the four specimens, however, had ventral deposits similar to the dorsal type.

The species is closest related to *P. affinis* and *P. azorica.*

Peniagone willemoesi (Théel, 1882)
Fig. 66

Elpidia willemoesi Théel, 1882, pp. 24–26, pls. VIII: 2–3, XXXIII: 10–12, XXXVII: 1.

non *Peniagone willemoesi* (Théel), Hansen 1967, pp. 495–498, fig. 12 (= *P. azorica).*

Diagnosis: Body elongate, posteriorly flattened. Tubefeet about 10 pairs, bordering the entire ventral sole, the hindmost pairs slightly smaller,

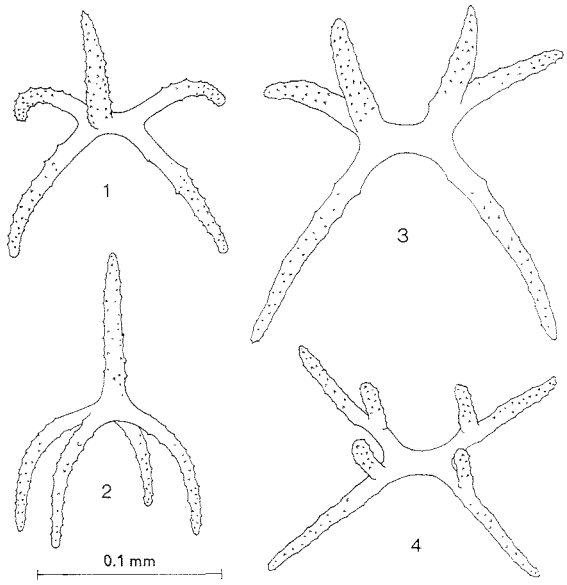


Fig. 66. *Peniagone willemoesi.* Deposits. *Challenger* St. 156 (the specimen in BM). 1–3, dorsum; 4, ventrum.

slightly fused, and separated by a median incision into a right and left group. Velum composed of two pairs of papillae. Dorsal deposits with strongly curved arms, an almost completely reduced stem, and 1 (occasionally 2–4) high apophysis. Ventral deposits with slightly curved arms, a well-developed stem, and 4 (sometimes 3) low apophyses which are often somewhat asymmetric in position.

Record: Antarctic Ocean, 3609 m. Four specimens.

Remarks: One specimen (in BM) and one lacking the tentacular crown and the velum (in ZMUC) were re-examined.

The specimen in BM was illustrated in the Challenger Report. The drawing shows two conspicuous features, viz. a velum consisting of three triangular lobes and a posterior median incision of the body, separating the posterior tubefeet into a right and left group. The re-examination showed that the median lobe of the velum was composed of two papillae – the velum consisting, as usual, of two pairs of papillae. The posterior median incision of the body was verified in the specimen in BM, but not in the more defective specimen in ZMUC.

Deposits (Fig. 66) dorsally with strongly curved arms, almost no stem, and practically all of them with only one, subcentral apophysis. However, deposits with 2–4 apophyses and a well-developed stem occur scatteredly among the other deposits. The arms are c. 0.10 mm long. The ventral deposits have slightly curved arms, a well-developed stem, and 4 (occasionally 3 or 5) low apophyses which are often somewhat asymmetric in position.

The species is closest related to *P. affinis, P. incerta,* and *P. azorica* (q. v.).

Peniagone dubia (D'yakonov & Savel'eva, 1958)

Elpidiogone dubia D'yakonov & Savel'eva, 1958 (in D'yakonov, Baranova & Savel'eva 1958, pp. 361–363, figs. 2–4).

Diagnosis: Body elongate. Tubefeet about 12 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Dorsal papillae 4 pairs, all long and slender, the first pair being longest;

anteriormost 3 pairs of papillae fused at their bases, while the last pair is separate and placed more posteriorly. Deposits primary crosses with a well-developed stem and 2 or 4 high apophyses.

Record: Southern part of the Okhotsk Sea, 2850 m. Six incomplete specimens.

Relationships: The long and almost entirely free papillae represent a similarity to *P. incondita* and *P. papillata,* while the separation of the papillae into an anterior group and a more posteriorly placed pair is unique to *P. dubia.* The deposits are different in the three species.

Peniagone incondita Agatep, 1967

Agatep 1967b, pp. 51–53, pl. II: 1–14.

Diagnosis: Body elongate. Tubefeet 10–11 pairs, bordering almost the entire ventral sole, decreasing in size posteriorly. Dorsal papillae 4 pairs, of which the anteriormost 2 pairs are long and slender; all papillae separate even at their base. Deposits, dorsally large crosses with reduced stem and 1 (occasionally 2) apophysis; ventrally primary crosses with 2 apophyses.

Records: Antarctic, 3537–5435 m. Four *Eltanin* stations with 115 specimens.

Relationships: The species is closest related to *P. papillata,* but differs in the number and position of the tubefeet, the entirely free papillae, the shape of the deposits, and the violet body colour.

Peniagone papillata n. sp.
Figs. 67–68

Diagnosis: Body elongate. Tubefeet 8–9 pairs, placed along the posterior $^2/_3$ of the ventral sole, decreasing in size posteriorly. Dorsal papillae 4–5 pairs, the 1–2 anteriormost pairs long, slender, and free in almost their whole length, the others rudimentary; the small papillae and the bases of the large papillae enclosed in a pair of low elevations which are either separate throughout, or slightly fused anteriorly – a true velum being absent. Deposits primary crosses with a well-developed stem and four low, spinous apophyses.

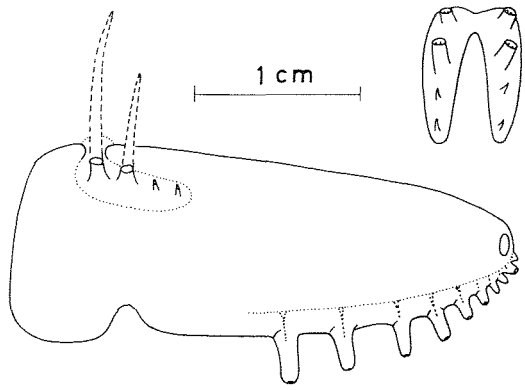


Fig. 67. *Peniagone papillata.* St. 716.

Material:
St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – 41 specimens.

Description: The specimens are all rather defective. They are 2–5 cm long, and the body form is similar to that of *P. azorica,* being elongated, and usually possessing a downwardly bent anterior part.

Tentacles 10. Only one tentacle preserved, the shape of which could not be determined.

Tubefeet 7–8 pairs, placed along the posterior two-thirds of the ventral sole. They decrease in size and distance from one another posteriorly, the posteriormost rudimentary and placed without intervals. Each tubefoot possesses a minute sucking-disc.

Dorsal papillae 4–5 pairs. In most specimens two pairs of conspicuous holes are present in the dorsal skin. These are scar-markings left by the two first pairs of dorsal papillae. In some specimens the basal parts of these papillae are preserved, but only one specimen has a complete papilla. It is 9 mm long (body length 30 mm) and very slender and pointed. This, apparently, represents the size and shape of the first two pairs of papillae – the scar-markings from the second pair of papillae usually being as large as those from the first pair. However, in some specimens the scar-markings from the second pair (and even from one of the papillae of the first pair) are small.

The small papillae and the bases of the large papillae are enclosed in a low, gelatinous pillow. The two pillows are either completely separate, or adjoin each other anteriorly.

Skin soft, mucous, and white-transparent.

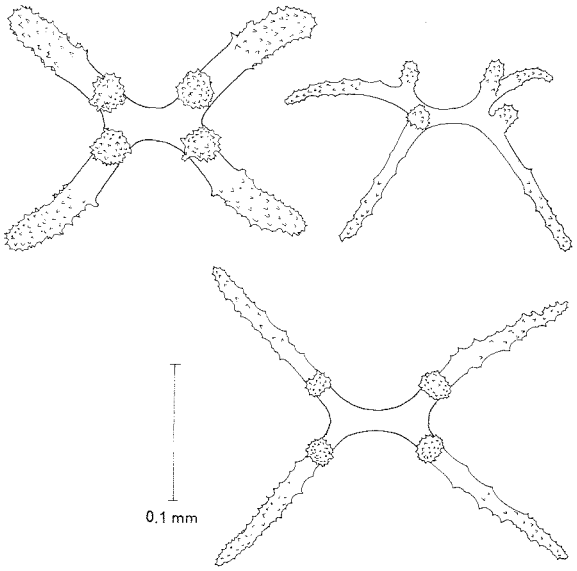


Fig. 68. *Peniagone papillata.* St. 716. Deposits.

Deposits (Fig. 68) examined in 16 specimens. They are rather uniformly developed – those illustrated representing the whole variation. No difference is found between the dorsal and ventral deposits. The small sucking-discs of the tubefeet are framed by rods, but no end-plates are present. The gonads contain slender primary crosses. No deposits were found in the wall of the intestine or in the muscles.

Calcareous ring consisting of five, isolated pieces, which have somewhat irregularly formed arms with flattened ends. The ring was examined in two specimens. The number of arms on the pieces varied from 7 to 9 on each side.

Polian vesicles two.

Type specimen: 3.5 cm long. The tentacles are all absent, but the tubefeet are better preserved than in any other specimen, all being preserved on the left side. The first two pairs of dorsal papillae are broken off near the base. In Fig. 67 the probable appearance of the papillae is shown by dotted lines, the reconstruction being based on the presence of one long, whiplash-like papilla in one of the other specimens.

Relationships: Most closely related to *Peniagone incondita* (q. v.).

Peniagone challengeri Théel, 1882

Théel 1882, pp. 49–50, pls. IX: 6–8, XXXIII: 16.

Diagnosis: Body very elongated, about 5 times as long as broad, somewhat flattened posteriorly. Tubefeet 8–9 pairs, approximately bordering the posterior half of the ventral sole, slightly decreasing in size posteriorly; posterior 3–4 pairs of tubefeet placed without intervals. Velum large, leaf-like, distally bipartite. Deposits with a well-developed stem and arms of varying length, with four, low apophyses; both arms and apophyses strongly spinous.

Record: South of Australia, 3276 m. Two specimens.

Remarks: The two specimens (both in BM) were re-examined. One was finely preserved, the other very defective.

The absence of tubefeet on the anterior part of the ventral sole was verified on the complete specimen, in which the skin was wholly intact on one side, between the tentacle crown and the anteriormost tubefoot. The posterior 3–4 pairs of tubefeet were separate and rather well developed. A median incision, separating the posterior tubefeet into a right and left group (as seen in Théel's illustration) could not be distinguished.

The velum is bipartite, with a broad, leaf-like basis – as illustrated by Théel. The velum probably varies to a lesser degree in preservation than usually in species of *Peniagone,* as it is covered with a tough skin.

The deposits (examined only ventrally) agreed perfectly with those described and illustrated by Théel.

Relationships: The species is possibly closest related to *P. azorica,* from which it differs by the elongated body form, the large and leaf-like velum, and the absence of tubefeet on the anterior part of the ventrum.

Peniagone vignoni Hérouard, 1901

Peniagone vignoni Hérouard, 1901, p. 42; Hérouard 1906, pp. 8–9, pls. I: 4–5, II: 13–23. *Peniagone theeli* Ekman, 1925, pp. 13–20, fig. 1.

Diagnosis: Body elongate, flattened posteriorly. Tubefeet 8–9 pairs, bordering the posterior half of the ventral sole, decreasing in size posteriorly. Velum very low, with almost free papillae. Deposits primary crosses with four low apophyses.

Records: *P. vignoni* (3 specimens) and *P. theeli* (10 specimens), both Antarctic. Depth 400 m (stated for *P. theeli* only).

Remarks: The proposed synonymy between *P. theeli* and *P. vignoni* is based on an examination of four specimens kept in ZMUC and hitherto unrecorded. The specimens were taken in the Ross Sea by the *Discovery* (St. 1658, 76°09'S, 168°40'E, 520 m).

P. theeli was regarded as being different from *P. vignoni* in the following respects: (1) *P. theeli* has a low velum, while *P. vignoni* has four small separate dorsal papillae. (2) A lateral brim is present above the tubefeet in *P. theeli,* absent in *P. vignoni.* (3) The tubefeet are more posteriorly placed in *P. theeli.* (4) Deposits are present in the body wall in *P. theeli,* but confined to the tentacles and tubefeet in *P. vignoni.*

The examined specimens have a feebly developed velum with almost free papillae. The rather flattened body shows in places a lateral edge which might well be due to a collapse of the body. The external, deposit-containing layer of the skin is almost entirely worn off, apparently due to a mucous consistency of the subcutaneous tissue. The deposits are best preserved in the tubefeet and tentacles in which the mucous, subcutaneous tissue is less well developed. In shape the deposits agree with those of both species. The tubefeet number 8–9 pairs. In their arrangement they bridge the difference between the two species.

The tentacles are well developed, with a long stalk and an enlarged disc, which in the extended state has two aboral lobes, similar to those found in *P. azorica.*

The species is closest related to *P. japonica* (q. v.).

Peniagone japonica Ohshima, 1915

Ohshima 1915, pp. 240–241, pl. IX: 10; Ohshima 1916–1919, with four figures.

Diagnosis: Body elongate, flattened posteriorly. Tubefeet about 8 pairs, bordering the posterior half of the ventral sole, decreasing in size posteriorly. Velum well developed, composed of two pairs of large and two pairs of small papillae, and gradually passing into a lateral brim which is present above the tubefeet throughout the length of the body. Deposits primary crosses with downwardly bent arms and four rather high apophyses.

Records: Off Japan, 1135–1669 m. 11 specimens.

Remarks: The species differs from *P. vignoni* by its larger velum which passes gradually into a marked lateral brim of the body, and by the shape of the primary crosses which have downwardly bent arms with rather high apophyses.

Peniagone elongata (Théel, 1879)

Parelpidia elongata Théel, 1879, p. 17, figs. 34–35; Théel 1882, pp. 15–16, pls. I: 3–4, XXXII: 16–17, XXXVII: 2.

Parelpidia cylindrica Théel, 1882, pp. 16–17, pl. I: 1–2.

Diagnosis: Body very elongated, about six times as long as broad. Tubefeet 8–9 pairs, bordering the posterior $^2/_3$ of the ventral sole, the posterior 3–4 pairs closely placed, but not reduced in size. Dorsal papillae 2–3 pairs, rudimentary, not forming a velum. Deposits cross-shaped, with strongly curved, c. 0.12 mm long arms, and a single, high, central apophysis.

Records: The two species here synonymized are known from one specimen each, taken at two adjacent *Challenger* stations off Chile: *P. elongata* at 4065 m, and *P. cylindrica* at 3947 m.

Remarks: The specimens (both in BM) were re-examined and found to be similar in all essential features.

P. elongata is closest related to *P. verrucosa* (q. v.).

Peniagone verrucosa (Théel, 1879)

Elpidia verrucosa Théel, 1879, p. 15, figs. 26–28; Théel 1882, pp. 19–20, pls. III: 1–2, XXXIV: 3–4, XXXIX: 2.

Diagnosis: Body ovoid. Tubefeet 9 pairs, bordering the posterior $^2/_3$ of the ventral sole, decreasing in size posteriorly. Dorsal papillae 2 pairs, rudimentary, not forming a velum. Deposits cross-shaped, with strongly curved c. 0.6 mm long arms, and a single, high, central apophysis. Interspersed among the normal type are crosses with a short stem bearing an apophysis at either end. Small primary crosses with four apophyses occur in tubefeet.

Record: Off Chile, 4065 m. One specimen, taken simultaneously with *P. elongata*.

Remarks: The specimen of *P. verrucosa* may be a strongly contracted *P. elongata*. The two species are retained as separate species because they also differ in the size of deposits and in the presence in *P. verrucosa* of primary crosses with two or four apophyses in addition to the normal type.

Peniagone lugubris Théel, 1882
Fig. 69

Théel 1882, pp. 44–45, pl. X: 1.

Diagnosis: Body elongate. Tubefeet bordering the posterior $^2/_3$ of the ventral sole, numbering 5 pairs (plus, possibly, 2–3 pairs of rudimentary tubefeet at the posterior tip of the body). The anteriormost 3 pairs of tubefeet separated by wide gaps. Velum very large, composed of two pairs of completely fused papillae. Deposits primary crosses with four apophyses.

Record: Mid-Atlantic, 4545 m. One specimen.

Remarks: The specimen (in BM) was re-examined and found to agree well with Théel's illustration. The skin was dark violet, tough and with a rather hard surface. The specimen might therefore have preserved its natural shape better than is usual in species of this genus. The posterior tip of the body was slightly torn; a few pairs of rudimentary tubefeet could have been present in this place, as in most species of the genus. One tentacle preserved, with a long stalk and an enlarged disc with a papillate surface.

The deposits (Fig. 69), not illustrated by Théel, were densely crowded both in the dorsal and ventral skin. They consisted of primary crosses with a well-developed stem and four low or moderately high apophyses; the arms were slightly curved. The dorsal crosses measured about 0.7 mm across (occasionally up to 1.0 mm), the ventral crosses 1.0–1.5 mm.

The five specimens which Madsen (1953) referred to this species are here re-determined to *P. ferruginea*.

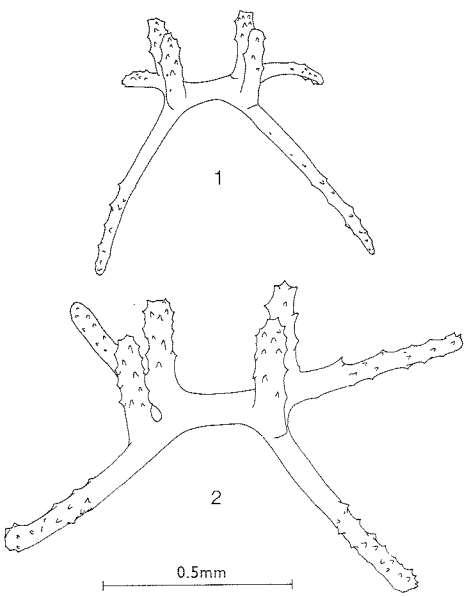


Fig. 69. *Peniagone lugubris*. Deposits from type specimen (*Challenger* St. 104). 1, dorsum; 2, ventrum.

Peniagone vitrea Théel, 1882
Fig. 70

Peniagone vitrea Théel, 1882, pp. 50–52, pls. VII: 7–9, XXXIV: 17–18, XLIV: 10; Clark 1920, p. 136; Ekman 1927, pp. 368–370, fig. 4; non Sluiter 1901b, p. 74.

Peniagone vitrea Théel var. *setosa* Ludwig, 1894, pp. 105–108.

Peniagone setosa Clark, 1920, p. 136.

Diagnosis: Body elongate, the part anterior to the broad velum being ventrally or posteriorly directed. Tubefeet 6–9 pairs, bordering the posterior third of the ventral sole, closely placed, slightly decreasing in size posteriorly. Deposits primary crosses with a short stem, strongly downwardly bent arms, and 1–4 spinous, pointed apophyses, which are usually longer than the arms.

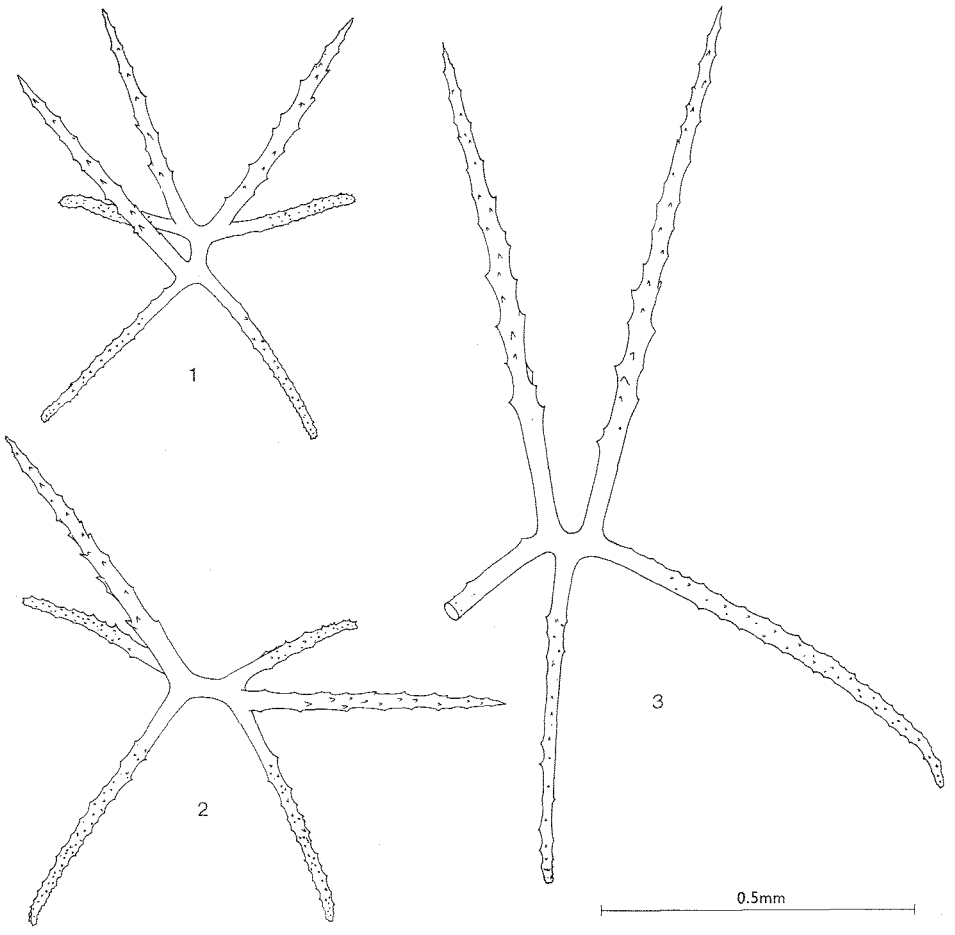


Fig. 70. *Peniagone vitrea*. Dorsal deposits. 1–2, *Challenger* St. 302 (the specimen in BM); 3, *Albatross* St. 3400 (var. *setosa*).

Material:

St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – 1 specimen.

Description: The specimen is c. 3 cm long and very defective. The deposits, however, are those typical of the species – primary crosses with a rather short stem, slender arms c. 0.4 mm in length, and two, occasionally three, high apophyses with distally directed spines.

Previous records: Off southern Chile, 2654 m. Several specimens of *P. vitrea* taken by the *Challenger* (Théel 1882). – Gulf of Panama, 1790–4337 m. 38 specimens of *P. vitrea* var. *setosa* (Ludwig 1894) and one of *P. setosa* (Clark 1920). – Central Pacific, 4507 m. One specimen of *P. vitrea* (Clark 1920). – Antarctic Ocean, 3423 m. One specimen of *P. vitrea* (Ekman 1927).

After an examination of his own Antarctic and the *Challenger* specimens, Ekman found that the features of *P. setosa* were included in the variation of *P. vitrea*.

The present re-examination of two of the *Challenger* specimens of *P. vitrea* (in BM), eight of Ludwigs' specimens of *P. vitrea* var. *setosa* (in USNM), and Clark's specimens of *P. vitrea* and *P. setosa* (in USNM), confirmed that all are one species, although differences in the deposits may represent a geographic variation.

The two *Challenger* specimens had dorsal deposits (Fig. 70: 1–2) with arm lengths of 0.2–0.4 and 0.3–0.6 mm, respectively. The latter had ventral deposits with arm lengths of 0.3–0.5 mm. In both specimens the deposits were larger than found by Théel (arm length "0.16 mm or sometimes more").

The nine specimens from the Gulf of Panama had deposits (3) with arm lengths of 0.4–0.7 mm (very few exceeding 0.6 mm).

The deposits of the Antarctic specimen, according to Ekman, measured up to 0.4 mm in arm length.

The deposits were remarkably similar in shape in the specimens from the three localities. The stem was short, and the apophyses very high (usually exceeding the arms in length), with pointed ends and distally directed spines. (Few apophyses were as short as those illustrated by Théel). The apophyses were usually two in number both in the specimens from off Chile and from the Gulf of Panama; deposits with three apophyses were not uncommon, while the number of four was very rare. Ekman did not state the number of apophyses in his Antarctic specimen; the deposit illustrated has four apophyses.

The deposits of the Central Pacific specimen of *P. vitrea* reported by Clark (1920) were found to resemble, both in shape and size, those illustrated by Théel for the *Challenger* specimens. The external morphology of the specimen could not be made out.

The tentacles have small discs. In the two re-examined *Challenger* specimens all the tentacles had the discs inwardly turned, agreeing with Théel's drawing. Two of the specimens re-examined from the Gulf of Panama (both from Ludwig's material) had similarly shaped tentacles, but one (from Clark's material) had only one tentacle like this, while the others had discs vertical to the axis of the stalk.

P. vitrea has been erroneously recorded from an Indonesian station of the *Siboga* (Sluiter 1901b). Re-examination of the single specimen taken (in ZMA) revealed that the deposits were tripartite. As C-shaped deposits were not present in the preparations, the specimen seems to belong to the genus *Achlyonice*.

Relationships: *Peniagone vitrea* agrees with *P. islandica* in the shape of the velum and the tentacles, and partly in the number and arrangement of the tubefeet.

The deposits of *P. islandica* are similar to those of the Antarctic specimen of *P. vitrea,* described by Ekman. The presence of eight tentacles, and possibly also the absence of the abrupt, downward bend of the anterior part of the body, separates *P. islandica* from *P. vitrea.* However, the degree of the bend may depend on the contraction of the ventral, longitudinal muscles – the two species possibly not differing in this respect.

Peniagone islandica Deichmann, 1930

Peniagone islandicus Deichmann, 1930, p. 137; Heding 1942, pp. 20–21, fig. 19.

Diagnosis: Body elongate. Tentacles 8. Tubefeet 9 pairs, bordering the posterior $^1/_3$–$^1/_2$ of the ventral sole, the anterior 5 pairs large and free (although closely set), whereas the posterior 4 pairs are minute and fused into a brim along the hindmost edge of the body. Velum broad. Deposits primary crosses with a short stem, strongly curved arms and four spinous, pointed apophyses, which are longer than the arms.

Record: Southwest of Iceland, 2137 m. Two specimens, taken by the *Ingolf.*

Remarks: Deichmann (1930) gave a diagnosis of the species which was later described in detail by Heding (1942).

Both specimens were re-examined and found to agree well with Heding's description. The tentacles were so well preserved that their number in both specimens could be stated to be eight with certainty. The tentacles resembled those of *P. vitrea,* as illustrated by Théel (1882, pl. XLIV: 10).

The species is most closely related to *P. vitrea* (q. v.).

Peniagone wyvillii Théel, 1882

Théel 1882, pp. 42–44, pls. X: 3–4, XXXVII: 6, XLIV: 5, 7; Grieg 1921, pp. 6–7, figs. 1–2, pl. III: 3–5.

Diagnosis: Body twice as long as broad. Tubefeet about 8 pairs, bordering almost the entire ventral sole, decreasing in size posteriorly. Velum very large, composed of two pairs of partially free papillae. Deposits, primary crosses with curved arms and four apophyses.

Records: The type specimen was taken in the Central Pacific at 4413 m. The five specimens reported by Grieg were taken in the North Atlantic at 2615–2865 m.

Remarks: The type specimen (in BM) was found on re-examination to be in a poor state of preservation and nothing could be added to

the description given by Théel. The deposits (not re-examined) were stated to be similar to those of *P. lugubris*.

Grieg (1921) determined his North Atlantic specimens to *P. wyvillii* because of their close similarity in external appearance to the type specimen, as illustrated by Théel. The deposits apparently differed by the absence of some or all of the apophyses. However, it seems doubtful whether the deposits illustrated by Grieg represent the fully developed deposits of the outer layer of the skin.

P. wyvillii is most closely related to *P. ferruginea,* from which it differs by the tubefeet, which are more spaced in position, occupy a larger part of the ventral sole, and diminish more regularly in size posteriorly. The light violet colour of the body and the shape of the deposits are more doubtful differences.

Peniagone ferruginea Grieg, 1921

Peniagone ferruginea Grieg, 1921, pp. 7–8, fig. 3, pl. I: 4–6.
Peniagone lugubris Théel, Madsen 1953, pp. 153–155, figs. 2–3.

Diagnosis: Body two and a half times as long as broad. Tubefeet about 7 pairs, bordering the posterior $^1/_2$–$^2/_3$ of the ventral sole, closely placed and almost equally large, apart from the one or two posteriormost pairs which may be rudimentary. Velum very large, composed of two pairs of partially free papillae. Deposits, primary crosses with four, usually high apophyses.

Records: The type specimen was taken off the Canary Islands at 2800–3000 m. The five specimens reported by Madsen were taken in the mid-Atlantic at 5600–5610 m.

Remarks: Madsen referred his specimens to *P. lugubris* which, according to Théel, had exclusively large-sized tubefeet. The type specimen of *P. ferruginea* possessed in addition to the large tubefeet a rudimentary hindmost pair.

Re-examination of a 3.0 cm long specimen (in ZMUC) from Madsen's material revealed, in addition to the six pairs of large tubefeet, a rudimentary posterior one on the left side (the right side was not sufficiently well preserved to permit the demonstration of a right rudimentary tubefoot). The specimen illustrated by Madsen (1953, fig. 2) had seven pairs of equally large tubefeet, with no space for a rudimentary pair. Apparently, the presence of a rudimentary posterior pair of tubefeet is not a constant feature in the species.

The similarity between Madsen's specimens and the type specimen of *P. ferruginea* also applied to the deposits, and to the dark colour of the body. (The type specimen was "greyish rusty-brown", with the tentacles and the oral disc dark violet. Madsen's specimens were when alive reddish-violet, in alcohol blackish-violet).

Re-examination of the type specimen of *P. lugubris* (q. v.) showed difference from *P. ferruginea* both in external features and (less distinct) in the deposits.

P. ferruginea seems to be most closely related to *P. wyvillii* (q. v.).

Peniagone purpurea (Théel, 1882)

Elpidia purpurea Théel, 1882, pp. 21–23, pls. VII: 4–6, XXXIII: 13–14, XLIV: 6.
Elpidia ambigua Théel, 1882, pp. 27–28, pl. XXXIII: 6.
Peniagone lacinora Agatep, 1967b, pp. 53–55, pl. III: 1–9.

Diagnosis: Body flattened. Tentacles with bilobed discs. Tubefeet 7–9 pairs, the first two pairs being separate and ventral in position, while the remaining 5–7 pairs are closely placed and partly fused. Velum consisting of two pairs of very long and slender papillae, which are fused only at their bases. Edge of velum proceeding along the body side as a brim above the tubefeet. Deposits, primary crosses with a well-developed stem and four long apophyses.

Records: The three species synonymized were all taken in the Antarctic Ocean, at 2934–4789 m.

Remarks: Théel regarded *Elpidia ambigua* as a close relative of *E. purpurea,* differing only by its lighter violet colour, the more densely crowded deposits, and by the presence of a few wheel-shaped deposits. None of these differences can be attributed a taxonomic significance. Re-examination of one specimen of each species (both in BM) confirmed that they agree in all essential features, including the shape of the velum (although in the *ambigua* specimen only one of the papillae was preserved in its full length).

Agatep stated that *P. lacinora* differs from the two above-mentioned species in the size and position of the first two pairs of tubefeet. In *P. purpurea* and *P. ambigua* all the tubefeet were small and closely placed along the border of the ventral sole. In *P. lacinora* the tubefeet of the first two pairs were large, separated from each other and from the remaining tubefeet, and placed beneath the lateral edge of the body. This apparently conspicuous difference is probably due to a different state of preservation. Contraction of the body in the specimens of *P. purpurea* and *P. ambigua* might explain the fact that the first two pairs of tubefeet were small and placed more closely to the remaining tubefeet, and that a body brim was absent above them.

P. lacinora agrees with *P. purpurea* and *P. ambigua* in the violet colour of the body, the peculiarly shaped velum, the thin and soft skin, the merging of the bases of the posterior tubefeet to form a brim, the shape of the deposits, and the bi-lobed tentacle discs.

Deep-sea photographs (Lemche *et al.* in press) reveal the common occurrence of *P. purpurea* (or a closely related, undescribed species) at a depth of 8030 m in the Palau Trench.

Relationships: The species is most closely related to *P. foliacea* and *P. expansa.* It differs from both in the long free velar papillae, the violet body colour, and the deposits being primary crosses. *P. foliacea* and *P. expansa* have cross-shaped deposits without stem.

Peniagone foliacea (Hérouard, 1912)

Kolga foliacea Hérouard, 1912, pp. 5–6, figs. 3–4.
Peniagone foliacea (Hérouard), Hérouard 1923, pp. 86–87, pls. I: 31, IX: 1–2.

Diagnosis: Body flattened. Tubefeet 7 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Velum very large, as broad as the body, forwardly directed, its lateral edges continuing into a brim along the anterior half of the body. Deposits almost cross-shaped, with four apophyses placed near the centre of the cross, their bases joined.

Record: Between the Azores and Portugal, 4275 m. One specimen.

Remarks: In external features the species is most similar to *P. expansa,* although it has a much smaller velum. The deposits resemble those of *P. obsoleta* and *P. convexa,* in particular in the position and shape of the apophyses.

Peniagone expansa Koehler & Vaney, 1905

Koehler & Vaney 1905, pp. 68–69, pls. IV: 10, XII: 27–28.

Diagnosis: Body flattened. Tubefeet about 8 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Velum large, as broad as the body, forwardly directed. Deposits cross-shaped with five apophyses.

Record: Bay of Bengal, 3194 m. One specimen.

Remarks: In external features the species is reminiscent of *P. foliacea.* The deposits (both ventral and dorsal) resemble the dorsal deposits of *P. rigida.*

Peniagone intermedia Ludwig, 1894

Ludwig 1894, pp. 108–110, pl. XII: 1–6.

Diagnosis: Body flattened. Mouth posteriorly directed. Tubefeet, 3 free lateral pairs and 4 pairs which are fused into two fan-shaped clusters at the posterior end of the body. Velum large, as broad as the body, forwardly directed, its lateral edges continuing into a brim along the anterior half of the body. Deposits spinous primary crosses with four apophyses.

Records: The type specimen was taken at *Albatross* St. 3400 at 2406 m between the Galapagos Islands and South America. The other specimens from Ludwig's material, as well as those recorded by Clark (1920), were too poorly preserved to allow a correct identification.

Relationships: Probably most closely related to *P. diaphana* and *P. gracilis,* both of which were formerly referred to *Scotoanassa.* The similarities include the flattened body, the velum which forms the anterior margin of the body, the hindmost tubefeet being fused into a brim, the posteriorly directed mouth, and the deposits, which possess a well-developed stem. However, the pres-

ence of three pairs of free, lateral tubefeet clearly distinguishes *P. intermedia* from both species.

A large velum which forms the anterior margin of the body is found also in *P. purpurea, P. foliacea,* and *P. expansa.* From these species *P. intermedia* primarily differs by the clear separation between the free lateral and the fused posterior tubefeet.

Peniagone diaphana (Théel, 1882)
Fig. 71, pl. X: 7–8

Scotoanassa diaphana Théel, 1882, pp. 55–56, pls. IX: 3–5, XXXV: 18, XLIV: 9.

Scotoanassa translucida Hérouard, 1899, pp. 71–72, fig. 3; Hérouard 1902, pp. 43–45, pls. III: 4–6, VI: 17–20; Hérouard 1923, pp. 88–90, pls. III: 7–8, IV: 4; Madsen 1953, pp. 158–159, fig. 6.

Diagnosis: Body flattened. Mouth placed on a posteriorly directed, retractile tube. Tentacles with two conspicuous, digitiform processes on the discs, the latter obliquely placed to the axis of the stalk; discs covered with conspicuous, slightly ramified papillae. Tubefeet 4–5 pairs, enclosed in a brim bordering the hind edge of the body. Velum broad, forwardly directed, forming the anterior continuation of the dorsal surface; the four papillae composing the velum project only slightly from the anterior edge. Deposits with a well-developed stem and four apophyses.

Material:

St. 52, San Tomé–Cameroon (1°42'N, 7°51'E), 2550 m. – One complete and two fragmentary specimens.

St. 63, off Gabon (2°00'N, 9°14'E), 1520 m. – 1 specimen.

St. 574, Tasman Sea (39°45'S, 159°39'E), 4670 m. – 2 specimens and 6 isolated tentacles from a larger specimen.

Description:

St. 52. – The complete specimen is 7.5 cm long and 3.5 cm broad. The anterior edge of the flattened body, although identical with the velum, does not appear to be composed of papillae in external view. The posterior brim is composed of four pairs of fused tubefeet, the tips of which project slightly from the edge of the brim. The anterior and posterior brims continue directly into the lateral edge of the body, but a true lateral brim is not present. Mouth placed 2.5 cm from anterior edge of body at the end of a posteriorly directed tube, which is, however, almost completely retracted.

Tentacles not preserved.

Skin whitish, with a faint reddish-purple tinge. The outer layer hard and rough, caused by the crowding of the deposits, and easily separated from the soft connective tissue.

Deposits (Fig. 71: 1) slenderly built primary crosses with long arms and a well-developed stem. Dorsal and ventral deposits similar.

The two fragmentary specimens possess deposits similar to those of the complete specimen.

Calcareous ring of the usual type in the genus. The five isolated pieces each possesses at least seven pairs of slender, often distally branched arms.

St. 63. – The specimen is 2.2 cm long and 0.7 cm broad. Although in a poor state of preservation it shows the external features characteristic of the species. The velum consists of two pairs of papillae and forms the anterior margin of the body. Three pairs of tubefeet on the posterior margin of the body. The body is flattened, with the edge of the velum proceeding into the lateral edge of the body. The mouth is placed on a ventrally directed tube. (Tentacles not preserved).

The outer, deposit-containing layer of the skin is completely lost on the dorsum, and partly on the ventrum. The ventral crosses (Fig. 71: 4–5) show large variation: Anteriorly with short and pointed arms (5), posteriorly much larger crosses with high apophyses (4).

St. 574. – Both specimens are 10.5 cm long and 5.5 cm broad. The anterior edge of the body is somewhat defective, and the papillae composing the velum are not visible in external view. The posterior brim in both specimens consists of four pairs of papillae and a single unpaired, median papilla. The posterior brim continues directly into the lateral edge of the body, although it is clearly distinguishable from it. Mouth placed at the end of a posteriorly directed tube.

Tentacles. Only one tentacle is preserved. However, at the same station six isolated, much larger tentacles were taken (Pl. X: 7–8), being similar in shape to the small one. The tentacle discs, including the two processes, are covered with conspic-

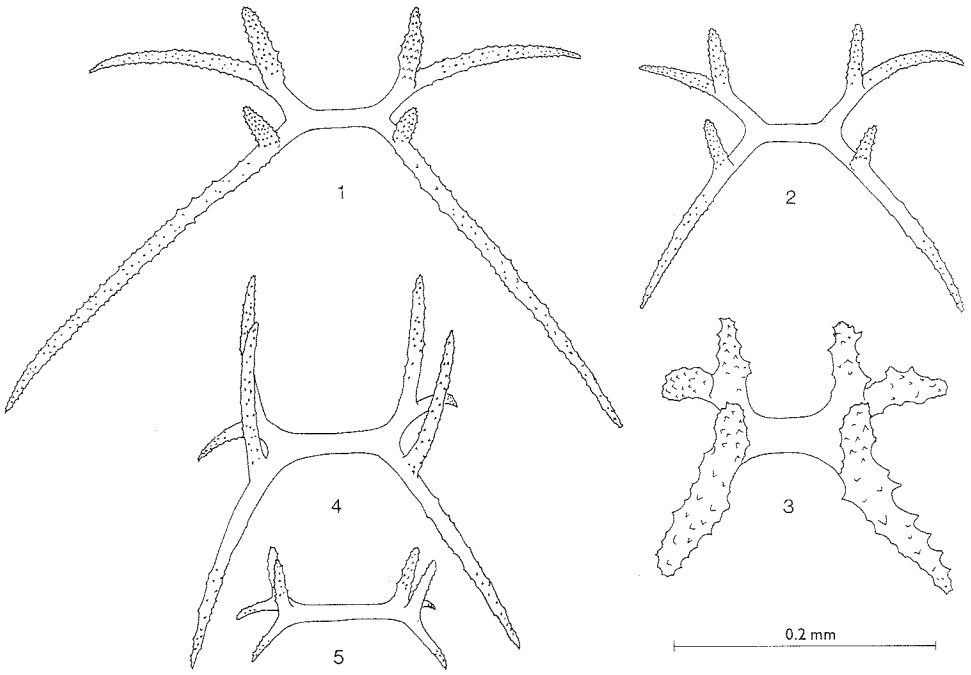


Fig. 71. *Peniagone diaphana.* Deposits. 1, St. 52, ventrum; 2, St. 574, dorsum; 3, St. 574, ventrum; 4–5, St. 63, posterior and anterior part of ventrum.

uous, slightly ramified papillae. The size (10–14 mm) compared with that of the small tentacle (5 mm) suggests that they belonged to a very large specimen of *P. diaphana.*

Skin whitish, and similar in structure to that of the Atlantic specimens.

Deposits similar in the two specimens and dorsally (2) resembling those of the Atlantic specimens (1), but with shorter and slightly more curved arms. Ventral deposits (3) very sturdy, only few approaching the dorsal ones in slenderness.

Calcareous ring absent (one specimen examined). Hérouard (1902) similarly noted the absence of a ring in some Atlantic specimens examined. Apparently, the ring is resorbed with advancing age.

Synonymy and variation: *Scotoanassa translucida* Hérouard was believed to differ from *S. diaphana* by the somewhat differently shaped posterior brim and the more robust deposits. However, the posterior brim in the *Galathea* specimens from the Tasman Sea (taken comparatively near the type locality of *P. diaphana* in the Great Australian Bight) is similar to that of the Atlantic species *S. translucida,* as illustrated by Hérouard.

The differences reported between the deposits of the two species cannot be regarded as taxonomically significant, in view of the subsequently acquired knowledge of the variation in this character. The ventral deposits of the *Galathea* specimens from the Tasman Sea are remarkably different from those of the type specimens of both *P. diaphana* and *P. translucida,* but resemble those of the Atlantic specimens described by Madsen. Apparently, the differences found represent local rather than geographic variations.

S. diaphana and *S. translucida* agree in a number of features, including the shape of the body, the mouth being placed at the end of a posteriorly directed tube, the shape of the velum, the inclusion of 4–5 pairs of tubefeet in the posterior brim, and the presence of a pair of digitiform processes on the tentacle discs.

Relationships: Closely related to *P. gracilis* (q. v.) and more distantly to *P. intermedia.*

Biology: The Atlantic material reported by Hérouard (1923) included specimens from four pelagic stations. They were considered to be larval or to have just completed their larval stage. Two of them were described – one 5 mm long, almost spherical, and supposed to have only five

tentacles, the other 10 mm long and having 10 tentacles (the shape of the body was not mentioned).

During re-examination of Hérouard's specimens, the external characters of the two larval specimens could no longer be ascertained. However, in addition to the larval specimens, a 3 cm long specimen, having the normal appearance of the species, was found to originate from the pelagic Station 3001, proving that the ability to lead a pelagic life is not confined to the larval stage. The depths (actually, the wire lengths) of the four pelagic stations were stated to be 0–4200, 0–4500, 0–4800, and 0–4900 m.

Distribution: Atlantic, 2550–5600 m. Great Australian Bight, Tasman Sea, 4670–4732 m.

Peniagone gracilis (Ludwig, 1894)

Scotoanassa gracilis Ludwig, 1894, pp. 111–113, pl. XII: 7–8.

Diagnostic features: The species differs from *P. diaphana* by the shape of the primary crosses which have strongly curved arms with very high apophyses, and possibly also by the absence of the two large, digitiform processes on the tentacle discs.

Record: Off the Galapagos Islands, 2475 m. Four specimens.

Relationships: Re-examination of the *Albatross* material in USNM revealed only some fragments which gave no additional information to the original description.

The alleged absence of the pair of digitiform processes on the tentacle discs remains to be verified on well-preserved specimens. In *P. diaphana* the processes, when placed close together, are easily overlooked.

The deposits fall outside the known variation in *P. diaphana*. On the other hand, the differences are not greater than can be found as local or geographic variations within a single species.

Ludwig supposed that *P. gracilis* differed from *P. diaphana* also by the tubefeet being placed below the brim (and not on the edge of it), and by the prolongation of the brim into a posteriorly directed, median prong. But the specimens were so defective that the exact shape of the body could not be determined with certainty.

Peniagone spp.

Specimens representing several species are left undescribed.

Sts. 231 and 232. Fragments of four specimens.

St. 466. Eight specimens which have lost their deposits.

St. 495. Fragments of a dark brown specimen, probably belonging to a new species.

St. 626. Four juvenile specimens, ovoid in shape and 9–10 mm long. Tubefeet in one specimen numbering 6–7 pairs, placed around the posterior half of the ventral sole. However, tubefeet might have been present also along the anterior half of the ventral sole. Spicules slender primary crosses with four high apophyses.

St. 658. One dark violet specimen resembling *P. purpurea;* deposits lacking, possibly dissolved.

Genus ***Achlyonice*** Théel, 1879
Fig. 121

Théel 1879, p. 13. – Type species: *Achlyonice ecalcarea* Théel, 1879, by monotypy.

Diagnosis: Tentacles 10–12. Deposits tripartite, rod-shaped, or absent. Calcareous ring consisting of five isolated pieces, each having a varying number of arms.

Remarks: *Scotoplanes gilpinbrowni* Pawson, 1965a, known from one incomplete specimen taken at 1782 m depth north of New Zealand, should probably be transferred to the genus *Achlyonice*. C-shaped spicules were absent, the deposits consisting exclusively of slender rods with spinous ends, resembling those found in *A. monactinica*. The two species also agree in the number (11 pairs) and arrangement of the tubefeet. However, since neither tentacles nor velum were preserved, the specimen cannot be identified with certainty.

Key to the species of *Achlyonice*

1. Deposits absent. Dorsal papillae not forming a velum ..... *tui* (p. 158)
1. Deposits present. Dorsal papillae forming a velum 2
2. Body ovoid. Tubefeet with large sucking-discs, all closely placed, not notably decreasing in size posteriorly. Deposits regularly tripartite, usually with an apophysis on each arm; in addition, rod-shaped deposits occur ..... *ecalcarea* (p. 156)
2. Body elongate. Tubefeet with minute sucking-discs, spaced in position anteriorly, closely placed and reduced in size posteriorly. Deposits rod-shaped, sometimes with a side-branch, but never regularly tripartite ..... *monactinica* (p. 157)

Achlyonice ecalcarea Théel, 1879
Figs. 72–73, 93: 1, pl. X: 9

Achlyonice ecalcarea Théel, 1879, p. 13, fig. 8. Non Clark 1913, p. 230.
Achlyonice paradoxa Théel, 1882, pp. 57–59, pls. V: 1–2, XXXIX: 3, 7, XLI: 5.
Achlyonice lactea Théel, 1882, pp. 59–60, pl. XXXII: 21–23.

Diagnosis: Body ovoid. Tentacles 12. Ventral sole increasing in breadth posteriorly. Tubefeet 10–14 pairs, with large sucking-discs, all closely placed, bordering the entire ventral sole, not notably decreasing in size posteriorly. Velum composed of three pairs of almost completely fused papillae. Deposits tripartite, usually with a spinous, bipartite apophysis on each arm; in addition, rod-shaped deposits are present.

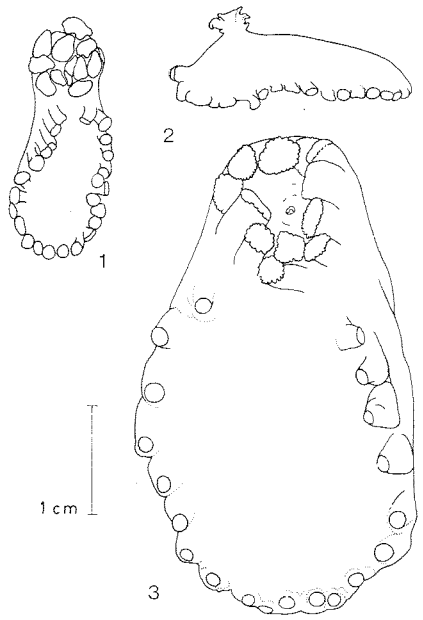


Fig. 72. *Achlyonice ecalcarea*. 1–2, *Galathea* St. 663; 3, Java-South Africa Exp. St. 78.

Material:
Galathea St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 1 specimen.
Dr. Th. Mortensen's Java–South Africa Exp. St. 78, St. Helena (8 miles W. by N. of Sugarloaf), 2400–2780 m. – 1 specimen.

Description:
1. – Specimen from the Kermadec Trench (Fig. 72: 1–2). Length 21 mm. Ventral sole 6 mm broad anteriorly, increasing in breadth posteriorly to 9 mm.

Tentacles 12, similar in shape to those of the specimen from St. Helena, although less well preserved.

Tubefeet 12–13 pairs, bordering the entire ventral sole. The tubefeet are all closely placed and almost equal in size. The sucking-discs are very large on all the tubefeet, their diameter almost equal to that of the tubefeet.

Velum composed of three pairs of almost completely fused papillae.

Skin white and soft, although rather firm.

Deposits (Fig. 73) tripartite, nearly all with a spinous, often bifurcate, apophysis on each arm. Similar apophyses are present on many of the rod-shaped deposits. Dorsal and ventral deposits similar. Wheels (Fig. 93: 1) occur scatteredly in the dorsal and ventral skin.

The tentacles possess numerous sturdy rods and irregular deposits, all of them lacking apophyses. The discs of the tubefeet are bordered by sturdy, smooth, curved rods, but end-plates are absent.

2. – Specimen from off St. Helena (Fig. 72: 3). Length 44 mm. Ventral sole reaching a breadth of 23 mm.

Tentacles 12, the discs (Pl. X: 9) with a papillate surface and indented marginal processes; the fully extended discs show a deep incision on the aboral margin, separating two particularly large processes.

Tubefeet 10 pairs, the hindmost ones slightly smaller than the others. They are somewhat conical in shape, mutually converging at their base, and are all provided with a large sucking-disc.

Velum similar in shape to that of the *Galathea* specimen.

Deposits similar to those of the *Galathea* specimen; the similarity even includes the presence of scattered wheels.

Synonymy: *A. ecalcarea,* taken in two specimens by the *Challenger* at 4204 m in the northwestern Pacific, was erected in the preliminary report on the *Challenger* holothurians. Théel at that time found no deposits in the specimens. On later examination of the specimens he discovered traces of dissolved tripartite deposits, and, therefore, in the final report changed the name to *A. paradoxa*. This change of name, as noted by Clark (1913), is not valid.

Both specimens (one in BM, the other in ZMA) were re-examined. They agreed in external features with the two specimens described above. The rather small size of the discs of the tubefeet in the specimen illustrated by Théel (in BM) was found to be due to contraction; a few fully extended discs were equal in diameter to the tubefeet.

A. lactea was taken in four specimens by the *Challenger* at 2928 m west of the Crozet Islands (southern Indian Ocean). Two specimens (both in BM) were re-examined and found to agree with the specimens described above in the shape of the ventral sole, the arrangement and shape of the tubefeet, the shape of the tentacles, and the type of deposits. Wheels were present in both specimens.

The specimens described by Clark (1913) from Baja California (depth 1598 m) were referred to *A. ecalcarea* because they lacked deposits, despite the fact that the absence of deposits in the *Challenger* specimens of *A. ecalcarea* was due to dissolution. Re-examination of one of Clark's specimens (in MCZ) threw doubt on his determination. It has 12 pairs of tubefeet which border only the posterior two-thirds of the ventral sole, and only the posteriormost tubefeet are placed without intervals. Eleven tentacles could be counted in the specimen (but 12 tentacles might have been present). The superficial layer of the skin is worn off, which may explain the absence of deposits.

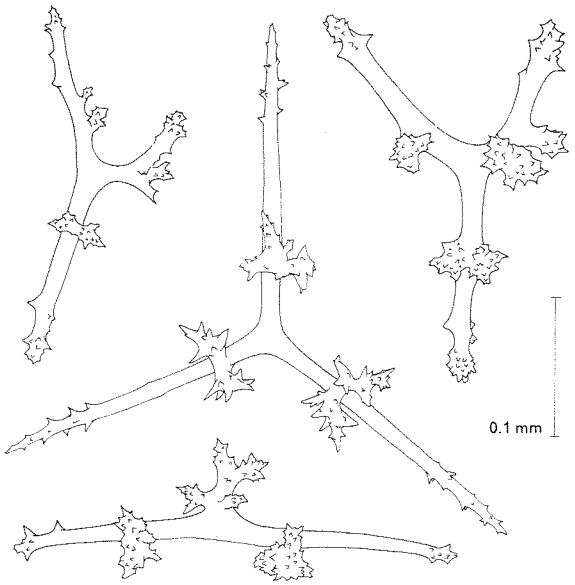


Fig. 73. *Achlyonice ecalcarea.* Deposits. *Galathea* St. 663.

Distribution: Probably cosmopolitan. Depth 2780–4924 m.

Achlyonice monactinica Ohshima, 1915

Ohshima 1915, pp. 241–242, pl. IX: 11; Ohshima 1916–1919, with four figures.

Diagnosis: Body ovoid to elongate. Tentacles 12, connected with one another by a membranaceous fold of skin, which leaves only the four posteriormost tentacles free. Tubefeet 10–13 pairs, with minute sucking-discs, bordering almost the entire ventral sole, decreasing in size and placed with decreasing intervals posteriorly. Velum low but with long free, filiform parts of papillae. Deposits rod-shaped, occasionally with a side-branch but not regularly tripartite.

Records: Off Japan, 1645–1669 m. 17 specimens.

Remarks: The species is characterized primarily by the rod-shaped deposits, the membranaceous fold of skin which encloses the stalks of the ten-

tacles, and the long free, filiform parts of the velar papillae. Although only the second pair of velar papillae was seen to project into a long filiform part, the first pair has probably the same structure.

Achlyonice tui (Pawson, 1965)

Amperima tui Pawson, 1965a, pp. 216–217, pl. IV: 1–3.

Diagnosis: Body ovoid to elongate. Tentacles 10–12. Tubefeet 12 pairs, bordering the posterior $^2/_3$ of the ventral sole, all rather closely placed; the posterior 6 pairs inconspicuous. Dorsal papillae consisting of two pairs of closely placed but separate papillae arranged in a transverse row, and two small pairs behind the row. Deposits absent.

Record: North of New Zealand, 1170 m. 16 specimens.

Remarks: Because of the complete lack of calcareous deposits the reference to *Achlyonice* is uncertain. It is motivated by the number of tentacles which in no other elpidiid genus is known to exceed 10.

Genus *Amperima* Pawson, 1965
Fig. 121

Periamma R. Perrier, 1896, p. 901.
Amperima Pawson, 1965a, pp. 215–216. – Type species: *Periamma roseum* Perrier, 1896.

Diagnosis: Dorsal papillae anteriorly placed, usually forming a velum. Deposits consisting of tripartite spicules and C-es. Calcareous ring consisting of five isolated pieces, each with four pairs of arms.

Remarks: The species of *Amperima* are more easily defined than those of the related genus *Ellipinion,* primarily because of the more clearly differentiated deposits. Materials of all previously known species, except *A. velacula,* has been examined.

Key to the species of *Amperima*

1. Posterior tubefeet large, forming two fan-shaped clusters ..... *insignis* (p. 162)
1. Posterior tubefeet small, not forming two fan-shaped clusters 2
2. Tubefeet absent from anterior part of ventral sole ..... *robusta* (p. 161)
2. Tubefeet bordering the entire ventral sole 3
3. Deposits, all regularly tripartite. An apophysis present on each arm 4
3. Deposits, tripartite interspersed with irregularly rod-shaped, quadripartite, and pentapartite. Apophyses absent, or placed without regularity 5
4. Apophyses undivided ..... *rosea* (p. 158)
4. Apophyses bifurcate ..... *furcata* (p. 159)
5. Large tripartite deposits with a smooth proximal arm part. Smaller deposits robust and strongly spinous ..... *velacula* (p. 161)
5. Deposits, all of the same type, although greatly varying in size; arms slender and spinous throughout their length ..... *naresi* (p. 159)

Amperima rosea (Perrier, 1896)
Fig. 74, 93: 2

Periamma roseum R. Perrier, 1896, p. 901; R. Perrier 1902, pp. 419–423, pls. XIII: 10–12, XX: 1–11; Hérouard 1923, pp. 91–94.

Diagnosis: Body ovoid. Tubefeet 9–10 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the hindmost pairs rudimentary. Velum well developed, composed of two pairs of papillae. Deposits regularly tripartite, with an undivided, spinous apophysis on each arm.

Records: Between the Azores and Portugal, 4060–5005 m. Numerous specimens.

Remarks: Five of Perrier's specimens and three of Hérouard's were re-examined by means of skin preparations. The deposits (Fig. 74) all

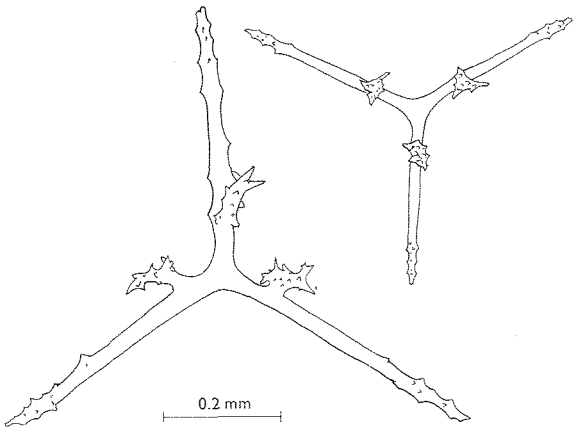


Fig. 74. *Amperima rosea.* Deposits. *Talisman* St. 137.

possessed a single, undivided apophysis on each arm. Wheels (Fig. 93: 2) were found in three of Perrier's and two of Hérouard's specimens. C-es few in number (absent in some of the preparations).

Amperima furcata (Hérouard, 1899)
Fig. 75

Kolga furcata Hérouard, 1899, p. 171, fig. 2; Hérouard 1902, pp. 40–41, pls. III: 7, VI: 4–10, VIII: 17.

Periamma furcata (Hérouard), Hérouard 1923, p. 91.

Diagnostic features: In external features probably similar to *A. rosea,* but the deposits have bipartite apophyses.

Records: Vicinity of the Azores and in the Bay of Biscay, 1846–2320 m. (Number of specimens not stated).

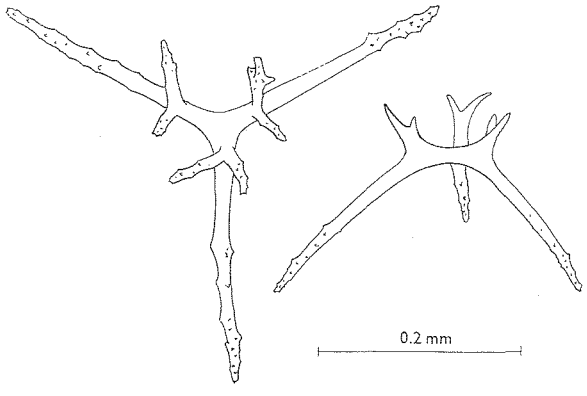


Fig. 75. *Amperima furcata.* Deposits. Monaco St. 698.

Remarks: Two specimens from Monaco St. 698 were re-examined. Their external features could no longer be made out, but the deposits (Fig. 75) were finely preserved. They were regularly tripartite and all possessed a bifurcate apophysis on each arm, this feature being apparently a reliable species character. C-shaped deposits were not found, nor was their presence mentioned by Hérouard. This suggests that the species actually belongs to the genus *Achlyonice.* On the other hand, C-shaped spicules may be very rare in the species of *Amperima* (cf. *A. rosea*). A correct identification to genus requires an examination of the calcareous ring.

Amperima naresi (Théel, 1882)
Fig. 76, pl. X: 6

Peniagone naresi Théel, 1882, pp. 47–49, pls. IX: 1–2, XXXIII: 15.

Periamma naresi (Théel), Hansen 1956, pp. 38–40, figs. 7–9; Belyaev & Vinogradova 1961, p. 129.

Periamma tetramerum H. L. Clark, 1920, p. 134, pl. II: 4; D'yakonov, Baranova & Savel'eva 1958, pp. 363–365, figs. 5–7.

Amperima naresi (Théel), Agatep 1967a, pp. 57–61, figs. 2–3.

Diagnosis: Body ovoid. Tubefeet 8–10 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the hindmost pairs rudimentary. Velum well developed, composed of two pairs of papillae. Deposits slenderly built, of varying and often irregular shape, being tri-, quadri-, pentapartite, and rod-shaped; arms irregularly spinous; apophyses, if present, placed without regularity.

Material:
St. 466, Sunda Trench (10°21'S, 110°12'E), 7160 m. – 114 specimens.

Description: The specimens were described previously (Hansen 1956), and only a few supplementary remarks are made here.

Tentacles 10. Discs (Pl. X: 6) with rather few, large, retractile papillae on the surface, and an indented margin. Some of the discs possess a pair of small aboral lobes.

Deposits (Fig. 76) examined in 25 specimens, including five previously examined. Dorsal and ventral deposits similar. In the previous report

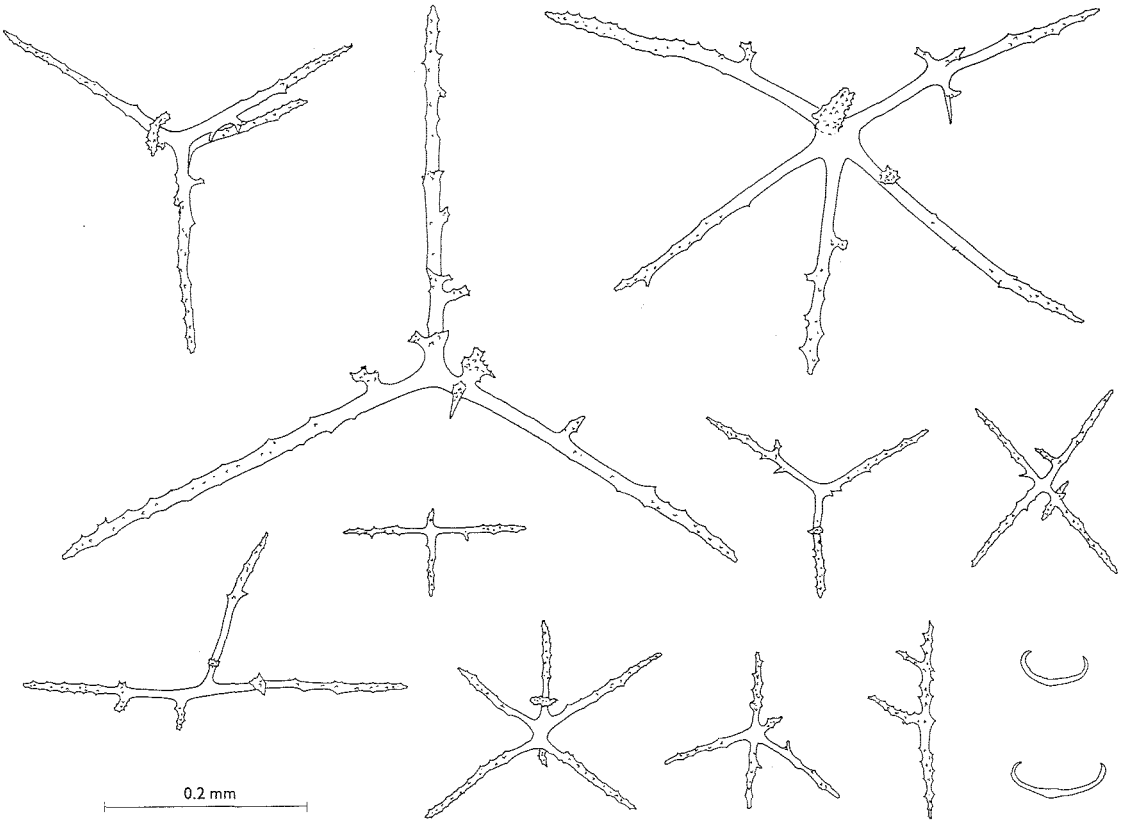


Fig. 76. *Amperima naresi.* Deposits. St. 466.

it was stated that the tripartite deposits, as reported by Théel, could be divided into two size groups; most of the deposits had arm lengths of about 0.11 mm, whereas a smaller number had arms twice as long. The examination of additional specimens showed that these size groups cannot always be distinguished. Deposits of intermediate size were often found; the size of the deposits sometimes varied considerably from one specimen to another. In some preparations nearly all had arms longer than 0.2 mm, a few even attaining a length of 0.8 mm.

Interspersed among the tripartite deposits are found rods (usually with side-branches), and quadri- and pentapartite deposits. (In two preparations the quadripartite deposits were as numerous as the tripartite ones). A few wheels were present in some of the preparations. The wheels were similar both in shape and size to those of *A. rosea* (Fig. 93: 2).

End-plates absent from tubefeet.

Calcareous ring absent in five specimens examined.

Synonymy: The type specimen, taken by the *Challenger* between Australia and the Antarctic, was re-examined. The presence of a very large velum, as seen on Théel's figure, could be verified – indeed, the velum was larger than that found in any of the *Galathea* specimens. However, agreement with the *Galathea* specimens in other features, including the characteristically shaped deposits, makes it improbable that the *Challenger* and *Galathea* specimens are different species.

The numerous Antarctic specimens taken by the *Eltanin* (Agatep 1967a) agreed with the *Galathea* specimens both in external features (including the greatly varying velum) and deposits.

Periamma tetramerum Clark, known from six specimens taken at 5835 m off Peru, was distinguished from *A. naresi* by the predominance of quadripartite deposits. As these are rather common also in the *Galathea* specimens, there seems no reason to keep the two species apart.

D'yakonov, Baranova & Savel'eva (1958) reported six specimens of *Periamma tetramerum* from 2850 m depth in the southern Okhotsk Sea. The

specimens were held to agree perfectly with Clark's description, which was confirmed by the figures of the deposits.

Relationships: Appears to be most closely related to *A. velacula* (q. v.).

Distribution: Antarctic and Indo-Pacific, 2010–7130 m.

Amperima velacula Agatep, 1967

Agatep 1967a, pp. 61–68, figs. 4–6.

Diagnosis: Body ovoid. Tubefeet 9–10 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the hindmost pairs rudimentary. Velum small. Deposits consisting of scattered large tripartite spicules with a smooth proximal arm part, and smaller, very robust and spinous spicules which are tripartite, quadripartite, or irregularly shaped.

Records: Seven Antarctic stations of the *Eltanin*. Depth 2837–4850 m, except one station at the South Shetland Islands with a depth of only 131 m.

Remarks: The irregular shape of the deposits indicates a relationship with *A. naresi,* but the large tripartite deposits differ by the smooth proximal part of the arms and the smaller deposits by their great robustness and spinousness. Wheels occurred scatteredly in the ventral skin of most of the specimens. They had a tripartite centre, and were apparently similar in shape to those of *A. rosea* and *A. naresi*. Agatep did not mention whether wheels were also present in his specimens of *A. naresi*.

In external appearance the species is probably indistinguishable from *A. naresi*. The velum is not smaller than in many specimens of this species.

Amperima robusta (Théel, 1882)
Figs. 77–78

Scotoplanes robusta Théel, 1882, pp. 35–36, pls. VI, XXXIV: 6–7, XXXVII: 9.
Amperima robustum (Théel), Agatep 1967a, pp. 56–57.

Diagnosis: Body elongate. Tubefeet about 11 pairs, bordering the posterior $^2/_3$ of the ventral sole, decreasing in size posteriorly. Velum well developed, composed of two pairs of papillae. Deposits tripartite, dorsally with three apophyses and distal arm spines; ventrally smaller, more robust, and without apophyses.

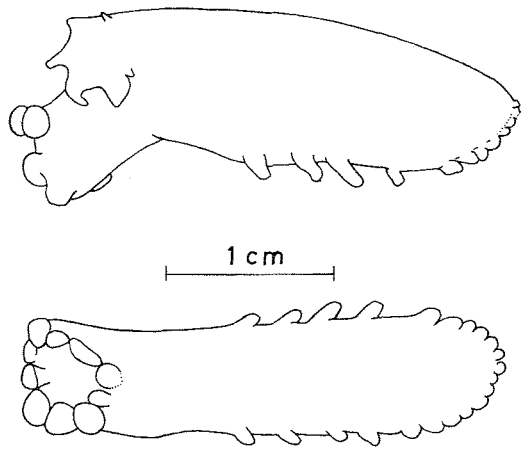


Fig. 77. *Amperima robusta*. St. 668.

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

Description: The specimen (Fig. 77) is 30 mm long and 8 mm broad.

Tentacles 10; obliquely forwardly directed; discs convex with a smooth surface and a smooth, non-lobated margin.

Tubefeet 11 pairs, bordering the posterior two-thirds of the ventral sole. Anteriormost 4–5 pairs rather long, with rounded ends, and separated by gaps equal to the width of a tubefoot. Remaining tubefeet closely placed and decreasing in size posteriorly.

Velum consisting of two pairs of fused papillae, followed by a pair of small, free papillae.

Deposits (Fig. 78) tripartite, with conspicuous spines confined to the distal part of the arms. The dorsal deposits have on each arm a small apophysis (sometimes represented by a few spines only). The ventral deposits are smaller, more robust, often less regularly shaped, and the arms are destitute of apophyses. Rods are found occasionally. C-shaped deposits present both in dorsal and ventral skin.

Remarks: Previously recorded from the Antarctic at 2010–4240 m, one specimen being taken by the *Challenger* and 51 by the *Eltanin*. The well-preserved *Challenger* specimen (in BM) was re-

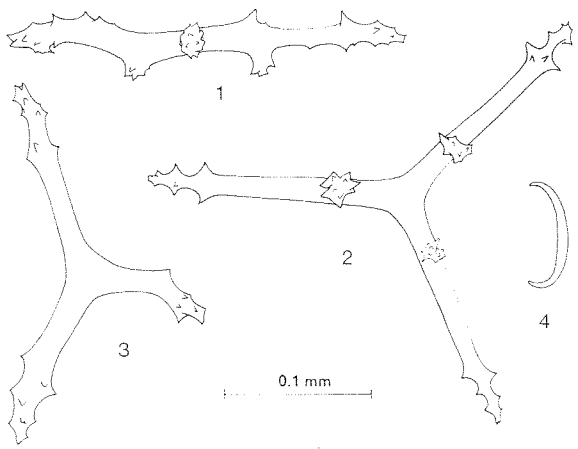


Fig. 78. *Amperima robusta.* Deposits. St. 668. 1–2, dorsum; 3, ventrum; 4, C-shaped spicule.

examined. The absence of tubefeet on the anterior part of the ventral sole was verified. Théel mentioned two processes on the outer margin of the tentacle discs; they were found to be scarcely visible. The tripartite deposit figured by Théel is similar to the dorsal deposits in the *Galathea* specimen. (Deposits were not re-examined).

Relationships: Differs from the other species of the genus by the absence of tubefeet on the anterior part of the ventral sole, and by its small and robust ventral spicules which are destitute of apophyses.

Distribution: Antarctic, 2010–4240 m. Kermadec Trench, 2640 m.

Amperima insignis (Théel, 1882)

Scotoplanes insignis Théel, 1882, pp. 36–38, pls. VII: 1–3, XXXIII: 7.

Diagnosis: Body flattened posteriorly. Tubefeet 11 pairs, 6 pairs of which are free and border the lateral edge of the ventral sole, while the posterior 5 pairs are fused into two conspicuous, fan-shaped clusters. Dorsal papillae 3 pairs, small, not fused into a velum. Deposits tripartite, spinous, and devoid of apophyses.

Record: Antarctic, 3594 m. One specimen.

Remarks: The specimen (in BM) was re-examined. As Théel remarked, the body is so strongly contracted that its natural shape cannot be deduced with any certainty. However, the species is well characterized by the posterior tubefeet being fused into a pair of fan-shaped clusters. The dorsal papillae are small and do not form a velum. Théel reported three dorsal papillae, followed by a pair of minute papillae, but on re-examination two pairs of larger and one pair of smaller papillae were found; hence, the papillae corresponded, both in number and arrangement, to those of a normal velum.

The deposits, according to Théel, very much resemble those of *A. robusta.*

Genus ***Ellipinion*** Hérouard, 1923

Fig. 122

Hérouard 1923, p. 82. – Type species: *Scotoplanes delagei* Hérouard, 1896.

Diagnosis: Dorsal papillae anteriorly placed, usually forming a velum. Deposits consisting of rods and C-es. Calcareous ring consisting of five isolated pieces, each with four pairs of arms. (In *E. kumai* an additional, unpaired arm is present on each piece).

Remarks: The species of *Ellipinion* are difficult to evaluate taxonomically as they are rather uniform in external appearance and their deposits are only feebly differentiated. The two species erected here are based on questionable taxonomic characters. Additional material may prove that they are identical with species previously known.

The species *Scotoplanes albida* Théel, 1882, which, according to definition, should be transferred to *Ellipinion,* is omitted from the present survey as it is based on one, insufficiently preserved specimen. The specimen was not illustrated, and a re-examination did not reveal anything of importance regarding its external appearance.

Key to the species of *Ellipinion*

1. Tubefeet 5 pairs, all large. Tentacle crown straight forwardly directed *galatheae* (p. 165)
1. Tubefeet 7–12 pairs. Tentacle crown ventrally or obliquely forwardly directed . 2
2. Skin with vesicular warts 3
2. Skin smooth 4

3. Tentacle discs possessing two large, rounded lobes ..... *molle* (p. 165)
3. Tentacle discs devoid of large lobes ..... *papillosum* (p. 165)
4. Tubefeet 7–10 pairs, the anteriormost pairs spaced in position 5
4. Tubefeet 11–12 pairs, all closely placed 6
5. Deposits confined to tips of papillae. Velum not very high and slender .. *kumai* (p. 166)
5. Deposits present all over the body wall. Velum very high and slender, composed of two pairs of equally long and almost completely fused papillae ....*facetum* (p. 166)
6. Tubefeet rather slender, and placed with small intervals. Ventral sole broadest posteriorly ..... *delagei* (p. 163)
6. Tubefeet broad, adjoining each other. Ventral sole broadest anteriorly 7
7. Tentacle crown very large, obliquely forwardly directed. Velum placed above the third tubefeet pair ..... *bucephalum* (p. 163)
7. Tentacle crown of usual size, ventrally turned. Velum anterior to the first tubefeet pair ..... *solidum* (p. 164)

Ellipinion delagei (Hérouard, 1896)

Scotoplanes delagei Hérouard, 1896, pp. 167–168, fig. 3; Hérouard 1902, pp. 39–40, pls. VI: 1–3, VIII: 8–9.
Ellipinion delagei (Hérouard), Hérouard 1923, pp. 90–91.

Diagnosis: Ventral sole increasing in breadth posteriorly. Tubefeet 11–12 pairs, bordering the entire ventral sole, the first pair close to the tentacle crown; all rather closely placed and, with the exception of the somewhat reduced posteriormost two pairs, all of the same size. Velum small, composed of three pairs of almost equally large and partially free papillae.

Records: North Atlantic, 1165–2478 m. Several specimens.

Remarks: The specimens (in MOM) were reexamined, and two (both from Monaco St. 553) were found to be in a fine state of preservation. The characteristic shape of the ventral sole was verified, while the shape of the velum could no longer be made out. The C-shaped deposits, according to Hérouard, possessed an outwardly directed spine rising from the middle enlargement of the C, which thus becomes tripartite. Similar variations from the C-es are found also in other species of the genus, but not as a dominant type.

E. delagei is closest related to *E. bucephalum* and *E. solidum* but differs from both in the C-es being transformed into tripartite spicules, in the shape of the ventral sole, and in the less closely placed tubefeet. Besides, it differs from *E. bucephalum* by the smaller size of the tentacle crown.

Ellipinion bucephalum n. sp.

Figs. 79–80

Diagnosis: Tentacle crown large and obliquely forwardly directed. Tubefeet 11–12 pairs, bordering the entire ventral sole, the first pair close to the tentacle crown; the tubefeet are broad and even the anteriormost ones are closely placed. Velum placed above the third tubefeet pair, composed of two pairs of stout and one pair of small papillae, all fused almost in their whole length.

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

Description: The specimen (Fig. 79) is 2.4 cm long and 0.9 cm broad.

Tentacle crown very large, and obliquely forwardly directed.

Tentacles 10, with short stalks; discs broad, vaulted, with a smooth margin and an almost smooth surface.

Tubefeet 11–12 pairs, bordering the entire ventral sole, posteriormost 2 pairs probably reduced (hind edge of body defective). The tubefeet are

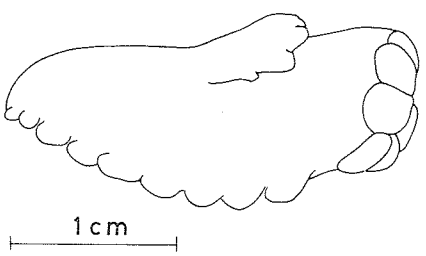


Fig. 79. *Ellipinion bucephalum*. St. 663.

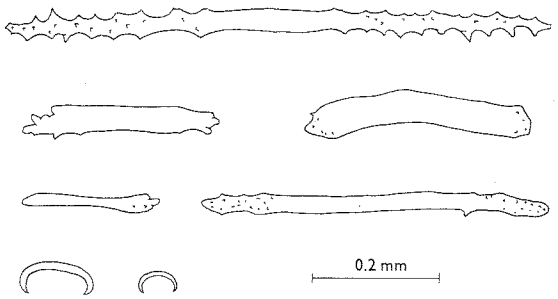


Fig. 80. *Ellipinion bucephalum.* Deposits. St. 663.

broad and even the anteriormost ones adjoin each other at their bases. Sucking-discs well developed.

Velum composed of three pairs of almost completely fused papillae.

Skin whitish and rather firm.

Deposits (Fig. 80) consisting of scattered rods of varying shape and size, and a superficial layer of crowded C-es. Tentacles and tubefeet with short rods. End-plates absent from tubefeet.

Relationships: *E. bucephalum* resembles *E. solidum* in number, size, and arrangement of the tubefeet, but differs by the large size of the tentacle crown and by the more posterior position of the velum.

Ellipinion solidum n. sp.
Figs. 81–82

Diagnosis: Tubefeet about 12 pairs, bordering the entire ventral sole, all of them closely placed. Velum anterior to first tubefeet pair, composed of two pairs of stout and one pair of small papillae, all fused almost in their whole length.

Material:

St. 231, Madagascar–Mombasa (8°52'S, 49°25'E), 5020 m. – 1 specimen.

St. 232, Madagascar–Mombasa (9°03'S, 49°22'E), 4930 m. – 1 specimen.

Description:

1. – The type specimen (Fig. 81), from St. 232, is 5.5 cm long, 2.5 cm high, and 2.3 cm broad.

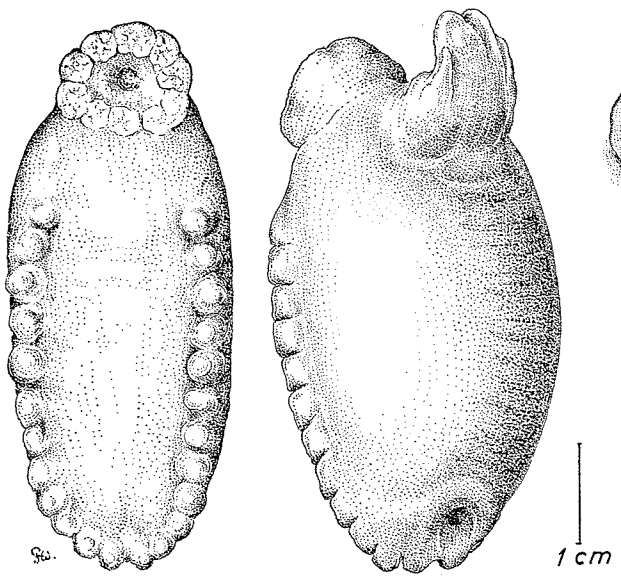
Tentacles 10, discs not preserved.

Tubefeet 12 pairs, bordering the entire ventral sole. They decrease somewhat in size posteriorly, although less than in other species of the genus (not counting *E. galatheae,* with its five pairs of almost equally large tubefeet). The sucking-discs are conspicuous, although somewhat retracted. No gaps present between the tubefeet, not even between the anteriormost ones.

Velum consisting of two pairs of stout and one pair of small papillae, all of them fused throughout almost their whole length; the velum is rather firm and probably less changeable in shape than in most other velum-bearing species.

Skin whitish and rather firm.

Deposits (Fig. 82) almost entirely absent, consisting of extremely scattered C-es in body wall and tubefeet, the latter in addition with a few rods, but no end-plate. No deposits were found in the gonads or in the intestinal wall.



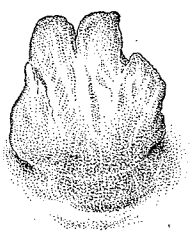


Fig. 81. *Ellipinion solium.* St. 232. Type specimen (lacking tentacle discs). PHW.

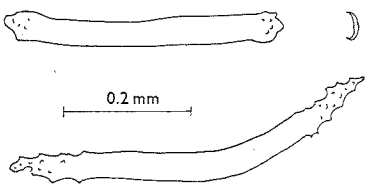


Fig. 82. *Ellipinion solidum.* St. 232. Deposits from a tubefoot.

2. – The specimen from St. 231 is somewhat torn, but nevertheless, some additional information can be gained. It is 6.5 cm long, and the ventral sole is 2.5 cm broad.

Tentacles (only two are preserved) with short stalks and slightly vaulted discs covered with small papillae; margin slightly indented.

Tubefeet lacking at the posterior end of the body. The preserved tubefeet (5 left and 9 right) are well developed and unretracted, cylindrical and with broad sucking-discs. The anteriormost tubefeet are about 4 mm long and 2 mm broad. The tubefeet were probably similar, both in arrangement and number, to those of the type specimen.

Velum defective, but apparently similar in shape to that of the type.

Deposits absent in a preparation from the body wall. Rods present in tentacles and tubefeet; a few C-es present in the tubefeet; end-plate absent.

Calcareous ring absent.

Relationships: Closest related to *E. bucephalum* (q. v.).

Ellipinion galatheae (Hansen, 1956)
Pl. X: 10

Scotoplanes galatheae Hansen, 1956, pp. 41–42, figs. 10–11.

Diagnosis: Body flattened. Tentacle crown large and forwardly directed. Tentacle discs with about 10 conical, retractile marginal knobs. Tubefeet 5 pairs, bordering almost the entire ventral sole, all of them large, although the hindmost pair is somewhat smaller.

Material:
St. 435. Philippine Trench (10°20'N, 126°41'E), 9820–10.000 m. – 1 specimen.

Remarks: The specimen, 17 mm long, was described previously (Hansen 1956) and referred to *Scotoplanes* because of its rod-shaped deposits. However, in accordance with the generic definitions adopted in the present work, the species should be referred to *Ellipinion*.

The species occupies an isolated position within the genus, being characterized by the large and forwardly directed tentacle crown, and by the presence of only five pairs of tubefeet. The tubefeet of the fifth pair are closely placed, leaving no room for reduced posterior tubefeet.

The tentacles (Pl. X: 10) are characteristic in shape, the enlarged discs having about ten conical, retractile knobs on the margin.

Velum, or velar papillae, not preserved.

Ellipinion molle (Théel, 1879)

Elpidia mollis Théel, 1879, p. 14, figs. 29–30.
Scotoplanes mollis (Théel), Théel 1882, pp. 31–32, pls. II: 1–2, XXXIII: 17, XLIV: 2.
Ellipinion mollis (Théel), Hérouard 1923, p. 82.

Diagnosis: Body ovoid. Skin covered with vesicular warts. Tentacle discs with two large, rounded marginal lobes. Tubefeet 7 pairs, bordering the entire ventral sole, decreasing in size posteriorly, the hindmost pairs rudimentary. Velum almost completely bipartite, each side consisting of two fused papillae of which the first is very large. Post-velar papillae absent.

Record: South of Australia, 4732 m. One specimen.

Remarks: Re-examination of the specimen (in BM) confirmed the presence of vesicular warts on the skin (called "papillae" by Théel), the characteristic shape of the velum, and the presence of a pair of rounded lobes on all the tentacle discs. But contrary to the six pairs of almost equally large tubefeet shown in Théel's figure, seven pairs of tubefeet were, in actual fact, present; as usual in the genus they decreased in size posteriorly, the hindmost pair being very small.

The species is closest related to *E. papillosum* (q. v.).

Ellipinion papillosum (Théel, 1879)

Elpidia papillosa Théel, 1879, pp. 16–17, fig. 31–33.
Scotoplanes papillosa (Théel), Théel 1882, pp. 32–33, pls. II: 5–6, XXXVII: 12; D'yakonov, Baranova & Savel'eva 1958, p. 361, fig. 1.
Ellipinion papillosa (Théel), Hérouard 1923, p. 82.
Scotoplanes angelicus Agatep, 1967b, pp. 59–61, pl. VI: 1–21.

Diagnosis: Similar to *E. molle,* differing by the absence of marginal lobes on the tentacle discs, and by the presence of a pair of free, post-velar papillae.

Records: The type specimen was taken by the *Challenger* at 4823 m in the South Atlantic. D'yakonov, Baranova & Savel'eva (1958) reported the species from 700 m in the southern part of the Okhotsk Sea. *Scotoplanes angelicus,* here considered a synonym of *E. papillosum,* was taken in three specimens at 4731 m in the Antarctic part of the South East Pacific Basin.

Remarks: Re-examination of the type specimen (in BM) revealed agreement with *E. molle* in the presence of vesicular warts on the skin, in body shape, and in number and distribution of the tubefeet. The small size of the tubefeet, as seen in Théel's figure, was found to be due to contraction. The velum was somewhat defective and apparently contracted; possibly, it was not different from that of *E. molle.*

Two rather doubtful features remain to distinguish *E.papillosum* from *E. molle,* viz. the presence of a pair of post-velar papillae and the absence of a pair of marginal lobes on the tentacle discs. (In *Scotoplanes globosa* such lobes were clearly visible in specimens preserved in formalin but difficult or even impossible to distinguish in alcohol-preserved specimens).

Scotoplanes angelicus agrees in both the above-mentioned features with *E. papillosum.* The presence in *S. angelicus* of a large number of irregular C-es is hardly taxonomically significant.

Ellipinion kumai (Mitsukuri, 1912)

Periamma kumai Mitsukuri, 1912, pp. 213–214, fig. 39, pl. VI: 56–58.

Diagnosis: Body ovoid. Tubefeet 8–10 pairs, bordering the entire ventral sole, decreasing in size posteriorly. Velum well developed, composed of two pairs of papillae. Deposits confined to ambulacral appendages.

Records: Sagami Sea (Japan), c. 500 m.

Remarks: Mitsukuri referred the species to *Periamma (= Amperima)* because tripartite deposits were present in the gonadal wall. These deposits, however, are different from the tripartite deposits of *Amperima,* and appear to be rods with an occasional side-branch.

Ellipinion facetum (Agatep, 1967)

Scotoplanes facetus Agatep, 1967b, pp. 57–59, pl. V: 1–14.

Diagnosis: Body somewhat elongate, 2.5 times as long as broad. Velum high and slender, composed of two pairs of equally long and almost completely fused papillae. Tubefeet 10 pairs, bordering the entire ventral sole, decreasing in size posteriorly.

Record: The Antarctic part of the South East Pacific Basin, 4789 m. One specimen.

Remarks: Differs from the other species of the genus by the peculiarly shaped velum.

Ellipinion sp.

Three fragmentary specimens resembling *E. molle* and *E. papillosum* were taken at St. 661.

Genus ***Scotoplanes*** Théel, 1882
Fig. 123

Scotoplanes Théel, 1882, p. 29 (partim). – Type species: *Scotoplanes globosa* Théel, 1882.

Diagnosis: Dorsal papillae separated into one pair of large anterior papillae, and one large and one small pair placed close together on the middle or posterior part of the body. Tentacle discs with a few, large papillae on the surface and a knobbed margin divided into a pair of large, aboral, retractile lobes. Deposits consisting of rods and C-es. Calcareous ring consisting of five isolated pieces, each with four pairs of arms.

Key to the species of *Scotoplanes*

1. Skin smooth. Dorsal papillae rather sturdy ..... *globosa* (p. 167)
1. Skin covered with vesicular warts. Dorsal papillae in the extended state slender and pointed ..... *clarki* (p. 169)

Scotoplanes globosa (Théel, 1879)
Fig. 83, 95: 4, pl. IX: 9

Elpidia globosa Théel, 1879, pp. 14–15, figs. 17–19.
Scotoplanes globosa (Théel), Théel 1882, pp. 29–31, pls. IV, V: 3, XXXIV: 8–9, XXXVI: 5–6, XLIV: 12; Vaney 1908, pp. 409–410, pl. III: 25–28; Hansen 1956, pp. 40–41; D'yakonov, Baranova & Savel'eva 1958, p. 360; Agatep 1967b, pp. 55–57, pl. IV: 1–13.
Elpidia murrayi Théel, 1879, p. 16, figs. 23–25.
Scotoplanes murrayi (Théel), Théel 1882, p. 34, pls. III: 3–4, XXXIV: 2, XLIV: 4; Savel'eva 1966, p. 295, pl. LXIV: 7.
Scotoplanes theeli Ohshima, 1915, pp. 242–243; Ohshima 1916–1919, with three figures.

Diagnosis: Skin smooth. Dorsal papillae rather sturdy.

Material:
St. 32, Monrovia–Takoradi (4°05'N, 2°13'W), 2100 m. – 37 specimens.
St. 650, Kermadec Trench (32°20'S, 176°54'W), 6620–6730 m. – 31 specimens.
St. 653, Kermadec Trench (32°09'S, 176°35'W), 6180 m. – 1 specimen.
St. 654, Kermadec Trench (32°10'S, 175°54'W), 5850–5900 m. – 16 specimens.
St. 658, Kermadec Trench (35°51'S, 178°31'W), 6660–6770 m. – 17 specimens.
St. 663, Kermadec Trench (36°31'S, 178°38'W), 4410 m. – 5 specimens.
St. 665, Kermadec Trench (36°38'S, 178°21'E), 2470 m. – 1 specimen.
St. 668, Kermadec Trench (36°23'S, 177°41'E), 2640 m. – 66 specimens.

Description: The hadal material of *Scotoplanes globosa* was described previously (Hansen 1956). The following description deals especially with the variation in the taxonomic characters, as revealed by the examination of the abyssal specimens.

Length 4–9 cm at St. 32, and 2–9 cm in the Kermadec Trench.

Tentacles 10 (Pl. IX: 9). Discs with few and large papillae on the surface and conspicuous knobs on the margin. In many specimens (especially those preserved in formalin) the discs are seen to possess a pair of lobes on the margin. The discs are similar in shape in the West African and the Kermadec specimens.

Tubefeet 5–7 pairs. In the Kermadec Trench a correlation is suggested between number of tubefeet and depth (Table 17). The number of tubefeet is independent of the size of the specimens.

Table 17. *Scotoplanes globosa*. Number of tubefeet pairs in 110 specimens from the *Galathea*.

Number of tubefeet pairs		5	6	7
St. 32	2100 m	–	15	6
– 668	2640 m	1	15	25
– 663	4410 m	–	1	2
– 654	5850–5900 m	5	–	–
– 650	6620–6730 m	12	14	–
– 658	6660–6770 m	2	12	–

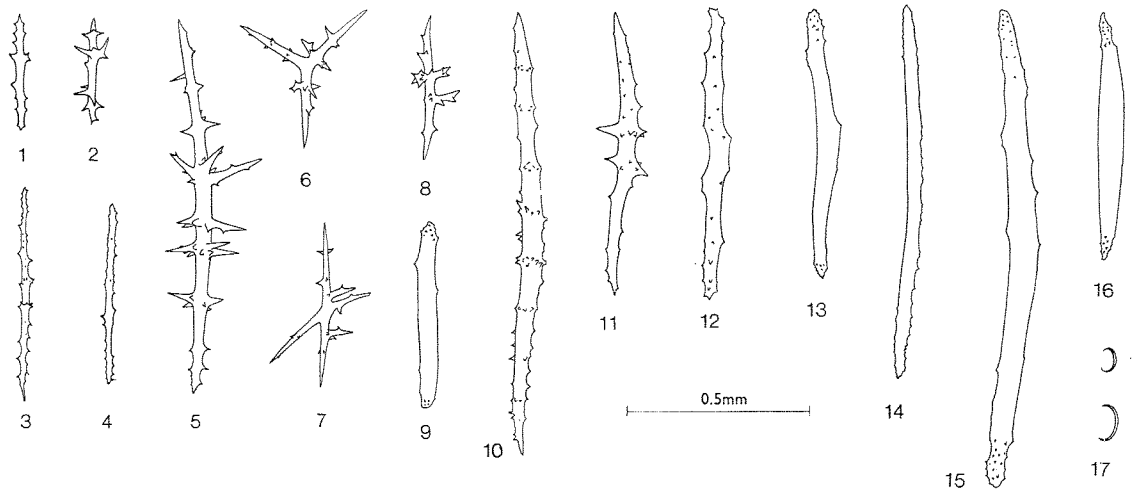


Fig. 83. *Scotoplanes globosa*. Deposits. 1–4, St. 32; 5–8, St. 650; 9–12, St. 663; 13–15, St. 668; 16, St. 665; 17, C-shaped spicules.

Papillae. The second pair of papillae may be placed anteriorly to the middle of the body, or as little as one-fourth body length from the posterior end. This variation is present even among specimens from the same station. No correlation was found between the arrangement of the papillae and the size of the specimens. In all specimens a rudimentary third pair of papillae is present immediately behind the second pair.

Deposits (Fig. 83) examined in all the specimens.

The West African specimens (St. 32) have small and slender rods; the four rods shown in Fig. 83: 1–4 represent their variation both in size and shape.

The Kermadec specimens have rods of two, rather distinct types. In the specimens from the deepest stations (Sts. 654, 653, 650, and 658; depth 5850–6770 m) the rods are strongly spinous (Fig. 83: 5–8), whereas the specimens from the two shallow stations (Sts. 665 and 668; depth 2470–2640 m) have smooth or feebly spinous rods (13–16). The deposits (9–12) of the specimens from St. 663 (depth 4410 m) are most similar to those from the shallow stations, although they are slightly more spinous and thus to some degree form a transition to the hadal type.

No correlation is present between the shape and size of the rods and the size of the specimens.

The C-shaped deposits vary somewhat in size and sturdiness, but there is no correlation between the locality of the specimens and the type of the C-es.

Calcareous ring (Fig. 95: 4) examined both in West African and Kermadec specimens. As also described by Théel, the segments are reduced and possess four pairs of arms, thus belonging to the usual type in *Amperima, Ellipinion,* and *Scotoplanes.*

Remarks: Agatep (1967b) reported the species from 23 Antarctic stations of the *Eltanin* (depth 598–5289 m). The specimens were 1.7–10 cm long, had 6–8 pairs of tubefeet, and deposits consisting of C-es and spinous rods. In the specimens from two stations many of the rods had two pairs of obliquely placed arms, thus having a peculiar similarity to those of *Elpidia* (p. 184).

Deep-sea photographs provided by the PROA Expedition (Lemche *et al.* in press) reveal the occurrence of *Scotoplanes* (probably *S. globosa)* in the New Britain Trench (depth 6780–7710 m) and the New Hebrides Trench (depth 6740–6760 m).

Herds of *Scotoplanes (S. globosa* or *S. clarki)* were observed and photographed in the San Diego Trough (depth 1060–1243 m) from the U.S. Navy bathyscaphe *Trieste I* (Barham *et al.* 1967). The observations revealed an affinity of *Scotoplanes* to accumulated sediments (pp. 196). Based on the same photographs Hansen (1972) suggested a peculiar mechanism for walking, apparently common to three families of the Elasipoda (pp. 205–206).

Synonymy: *S. theeli* Ohshima was previously (Hansen 1956) proposed as a synonym of *S. globosa.*

S. murrayi Théel, known from a single specimen taken at 2303 m in the Antarctic Ocean, is likewise here considered a synonym of *S. globosa.* Théel did not specify the differences between the two species, but it appears that the presence of only five pairs of tubefeet, compared to seven pairs in *S. globosa,* and the brittle and glassy skin were regarded as the distinguishing features of *S. murrayi.* However, the number of tubefeet falls within the variation of the *Galathea* specimens of *S. globosa.* The different consistency of the skin was seen on re-examination of the type specimen to be caused by the densely crowded deposits.

On the other hand, the four specimens from the eastern Pacific which Clark (1920) referred to *S. murrayi* are not identical with *S. globosa.* These specimens are here referred to *S. clarki* n. sp.

Baranova (1957) and Savel'eva (1966) mentioned *S. murrayi* from abyssal depths in the Bering Sea. The specimen illustrated by Savel'eva has a smooth skin, indicating that the species is *S. globosa.*

Variation: The parallel variation found in the shape of the deposits and the number of tubefeet suggests a taxonomic difference between the specimens from the abyssal (2470–4410 m) and hadal (5850–6770 m) stations in the Kermadec Trench. Contact between populations is apparently more pronounced in a horizontal than in a vertical direction. It is not possible to decide from the material whether there is an abrupt or a gradual transition in taxonomic characters between the hadal and abyssal populations. However, the fact that specimens from the deepest abyssal station have deposits somewhat reminiscent of those from the hadal stations suggests that the transition is gradual.

The deposits of the hadal specimens are rather similar to those of the abyssal specimens described by Théel from the Antarctic Ocean and off Valparaiso.

Distribution: *S. globosa* has an almost cosmopolitan distribution. However, it is remarkable that it has never been recorded from the North Atlantic. The closely related species, *S. clarki*, seems to replace *S. globosa* in a region along the Pacific coast of Central America and northern South America (p. 246).

Although a dominant species in some of the Pacific trenches, it has on several occasions been recorded from remarkably shallow water. Ohshima (1915) recorded it (as *S. theeli*) from 545 and 970 m northeast of Hokkaido (temp. 2.2° and 1.6°C, respectively). The penetration to shallow depths may here as well as in the Antartic Ocean (598 m) be conditioned by low temperature. The specimens recorded from a depth of 1060–1243 m in the San Diego Trough also lived at a rather low temperature (c. 3°C). The fact, however, that the species is here associated with an abundant supply of sediments indicates that the ascent of the species to shallow water does not depend on the temperature alone.

Scotoplanes clarki n. sp.
Figs. 84–85

Scotoplanes murrayi Théel, Clark 1920, pp. 133–134, pl. III: 6.
Scotoplanes sp., Hansen 1967, p. 490, fig. 6.

Diagnosis: Skin covered with vesicular warts. Dorsal papillae in the extended state slender and pointed.

Material:
St. 716, Acapulco–Panama (9°23'N, 89°32'W), 3570 m. – About 100 specimens (including type specimen).

Description: The specimens are 2.5–7.0 cm long. Type specimen (Fig. 84) 6 cm long.

Skin greyish and covered with vesicular warts, which are especially well developed on the dorsal surface. The warts resemble those in *Ellipinion molle*.

Tentacles 10; discs with few and large papillae on the surface and conspicuous, retractile knobs on the margin. A pair of large, marginal lobes is seen on some of the discs. The shape of the discs is probably identical in the two species of *Scotoplanes*.

Tubefeet 5–6 pairs. The sixth pair, when present, is always reduced, whereas the fifth pair may vary in size from being the same length as the anterior tubefeet to half as long. The ends of the tubefeet are rounded and have no sucking-discs. Usually, the tubefeet are slightly smaller than in *S. globosa*.

Papillae similar in number, size distribution, and arrangement to those of *S. globosa*, including the presence of a rudimentary third pair. The large papillae are apparently very contractile, as indicated by a number of transverse lines on many of them. In the fully extended state the papillae are slender and pointed. In most specimens they measure about one-third of the body length; a few of the smaller specimens possess papillae which are the same length as the body.

Deposits (Fig. 85) examined in 15 specimens. They all have rather smooth and spindle-shaped rods, resembling those in specimens of *S. globosa* from Sts. 665 and 668. In the preparations from

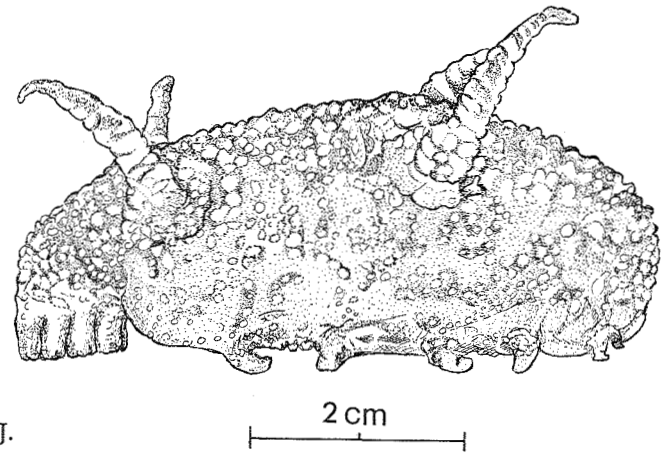


Fig. 84. *Scotoplanes clarki*. St. 716. Type specimen. LJ.

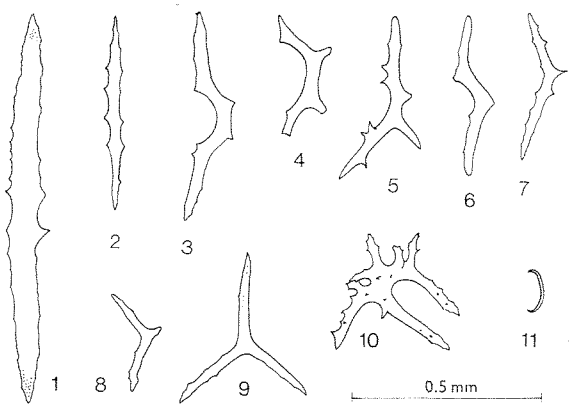


Fig. 85. *Scotoplanes clarki.* Deposits. St. 716. 1–8, rods from dorsum and ventrum; 9, tripartite spicule; 10, irregular spicule from papilla; 11, C-shaped spicule.

two of the specimens a number of irregularly shaped rods are present, some of which seem to derive from primary crosses (Fig. 85: 3–4) – a similarity to two of the rods illustrated by Théel (1882, pl. XXXIV: 2) for *S. globosa*. In some preparations a few tripartite deposits are present.

Numerous rods present in tentacles, tubefeet, and papillae. End plates absent from tubefeet.

C-shaped spicules numerous in the skin, mesenteries, and gonads.

Calcareous ring (examined in one specimen), rudimentary, each piece with four pairs of arms.

Remarks: To *S. clarki* are referred four specimens taken by the *Albatross* at two stations off Peru (4809 and 5107 m), and by Clark referred to *S. murrayi* Théel. While the type specimen of *S. murrayi* appeared on re-examination to be identical with *S. globosa,* Clark's specimens showed the warty skin and the strongly contractile papillae distinguishing the present species. The re-examination comprised a specimen from either station (St. 4651, in MCZ; St. 4672, in USNM).

Distribution: Gulf of Panama and off the coast of Peru, 3570– 5107 m.

Genus ***Kolga*** Danielssen & Koren, 1879
Fig. 123

Danielssen & Koren 1879, p. 99; Danielssen & Koren 1882, p. 17. – Type species: *Kolga hyalina* Danielssen & Koren, 1879, by monotypy.

Diagnosis: Dorsal papillae anteriorly placed, forming a velum. Tentacle discs with 5–7 marginal lobes, each divided into about 3 lobules. Deposits spinous rods and irregularly shaped C-es. Calcareous ring consisting of five delicate pieces, which are isolated or adjoin each other loosely; each piece with five pairs of arms, a number of which may be secondarily subdivided.

Kolga hyalina Danielssen & Koren, 1879
Figs. 86, 95: 2–3, pls. IX: 8, XII: 11

Kolga hyalina Danielssen & Koren, 1879, pp. 83–106, pls. I–II; Danielssen & Koren 1882, pp. 3–20, pls. I–III; Mikhajlovskij 1902, p. 463; Mortensen 1932, pp. 43–44, fig. 5; Heding 1942, p. 19, fig. 18; Gorbunov 1946, p. 47; Koltun 1964, pp. 13–78; Baranova 1964, p. 368; Agatep 1967c, p. 140.

Elpidia nana Théel, 1879, pp. 15–16, figs. 20–22.

Kolga nana (Théel), Théel 1882, pp. 39–42, pls. II: 3–4, XXXIII: 1–2, XXXIV: 5, XXXVI: 25, XLII: 5, 8.

Diagnosis: Body ovoid. Tubefeet 7–9 pairs, bordering the entire ventral sole, decreasing in size and placed with decreasing intervals posteriorly. Velum very contractile, consisting of one large median pair and one or two smaller lateral pairs. Deposits spinous rods, often bent at an angle, and small, irregularly C-shaped spicules with an enlargement in the middle; irregular perforated plates occasionally present in oral disc.

Re-examination: The numerous specimens from the *Godthaab* and the *Ingolf* were found to agree with the thorough description given by Danielssen & Koren, although a greater variation was observed in the shape of the tentacles and the calcareous ring.

The *tentacles* (Pl. IX: 8) show a marked variation in shape, although they typically possess five marginal lobes, each divided into three lobules. This type of tentacle is otherwise found only in the genus *Irpa*.

The *deposits* (Fig. 86) consist of numerous minute, irregularly C-shaped spicules with an enlargement in the middle, and large, robust and spinous rods which are often bent at an angle. The rods are numerous in the ambulacral appendages, but very scattered in the rest of the skin.

The small reticulated plates, which according to Danielssen & Koren and Théel occur in the oral disc, were not found in the examined specimens.

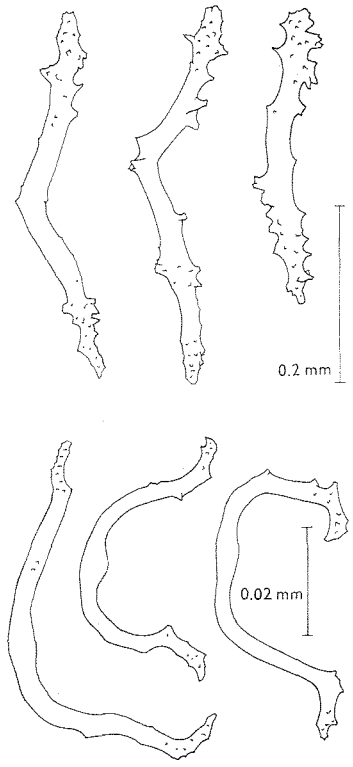


Fig. 86. *Kolga hyalina.* Deposits from ventrum. *Ingolf* St. 113.

The *calcareous ring* (Fig. 95: 2–3) was examined in four specimens from *Ingolf* St. 113 and in one from *Godthaab* St. 54 (pp. 187–188).

Remarks: Agatep (1967c) reported 57 specimens of *K. hyalina* from the Canadian Basin of the Arctic Ocean (depth 2850 m). The tentacles were said to possess four knobs, each divided into two smaller processes. The tubefeet number was stated to be 14 pairs (probably a lapse for 7 pairs).

Agatep in the same paper mentioned that *K. hyalina* was found at two Antarctic stations of the *Eltanin* (depths 4473 and 4850 m).

Synonymy: *Kolga nana* (Théel) was taken by the *Challenger* in several specimens off Nova Scotia at 2282 m and in one specimen in the Antarctic Ocean at 2305 m. Although Théel suspected that the specimens belonged to *K. hyalina,* he preferred to describe them as a new species for lack of specimens for comparison.

Re-examination of the *Challenger* specimens (in BM) showed that the Nova Scotia specimens are within the variation shown by *K. hyalina.* The Antarctic specimen was too damaged to allow a determination.

Distribution: Arctic Basin, North-West Atlantic, and Antarctic. Depth 1510–4850 m.

Genus ***Irpa*** Danielssen & Koren, 1878
Fig. 123

Danielssen & Koren 1878, p. 264; Danielssen & Koren 1882, p. 28. – Type species: *Irpa abyssicola* Danielssen & Koren, 1878, by monotypy.

Diagnosis: Dorsal papillae 3–5 pairs, anteriorly placed, not forming a velum. Tentacle discs with 5–7 marginal lobes, each divided into about 3 lobules. Deposits spinous rods and irregularly shaped C-es. Calcareous ring strong and continuous, each piece with four pairs of arms.

Remarks: In addition to the type species, *I. abyssicola,* the species *Kolga ludwigi* is here regarded as belonging to *Irpa* because of the structure of the calcareous ring (p. 130).

Key to the species of *Irpa*

1. Body elongate. Tubefeet 12 pairs, bordering the entire ventral sole. Dorsal papillae 5 pairs ..... *abyssicola* (p. 171)
1. Body ovoid. Tubefeet 6 pairs, bordering the posterior half of the ventral sole. Dorsal papillae 3 pairs ..... *ludwigi* (p. 172)

Irpa abyssicola Danielssen & Koren, 1878

Danielssen & Koren 1878, pp. 257–266, pl. IV; Danielssen & Koren 1882, pp. 21–28, pl. IV.

Diagnosis: Body elongate. Tubefeet 12 pairs, bordering the entire ventral sole. Dorsal papillae 5 pairs. Deposits, spinous rods in the tubefeet, and irregularly C-shaped spicules, usually with an enlargement in the middle, in the body wall.

Record: Norwegian Sea, 1977 m. One specimen.

Relationships: See *I. ludwigi.*

Irpa ludwigi (von Marenzeller, 1893)

Kolga ludwigi von Marenzeller, 1893b, pp. 20–23, pls. III: 7, IV: 8.
Periamma ludwigi (von Marenzeller), Hérouard 1923, p. 83.

Diagnosis: Body ovoid. Tubefeet 6 pairs, bordering the posterior half of the ventral sole. Dorsal papillae 3 pairs. Deposits, simple or slightly branched rods in ambulacral appendages, and scattered wheels in the body wall.

Records: Mediterranean south of Sicily, 755–1292 m.

Relationships: *I. ludwigi* and *I. abyssicola* differ in shape of body, number and distribution of tubefeet, and absence in *I. ludwigi* of irregular C-shaped spicules. The absence of the latter is probably not important, in view of the extremely reduced state of the deposits in this species. The presence of wheel-shaped deposits in the body wall of *I. ludwigi* is shared with a number of species of Elpidiidae (pp. 185–186).

Genus ***Elpidia*** Théel, 1876
Figs. 124–125

Elpidia Théel, 1876, pp. 1–7; Théel 1877, pp. 1–30, pls. I–V. – Type species: *Elpidia glacialis* Théel, 1876, by monotypy.
Tutela R. Perrier, 1896, p. 901.

Diagnosis: Tentacle discs with long and slender, retractile processes. Tubefeet 4(–5) pairs, large, well spaced, and equal in size. Papillae separate, present throughout the length of the dorsal radii, or distributed into an anterior and posterior group. Deposits rod-shaped with two pairs of obliquely placed, horizontal arms and two vertical, pointed apophyses. Calcareous ring strong and continuous, each piece with four pairs of arms.

Taxonomy: The genus *Elpidia* occupies an isolated position within the Elpidiidae (p. 130). The relationship is closest with the genus *Irpa,* as indicated by the identical structure of the calcareous ring (p. 189).

Hansen (1956), in a previous report on the *Galathea* specimens, regarded the genus as monotypic with the species *E. glacialis,* divided into five geographic subspecies.

Belyaev (1971) revised the genus on the basis of the rich and varied collections of Russian expeditions. He divided the genus into 16 named species and an additional five, provisionally termed "species 1–5". The five subspecies erected by Hansen (1956) were all raised to the rank of species.

In Belyaev's revision, the species *E. hanseni* is divided into two geographic subspecies, but otherwise the subspecies concept is not applied.

In the present survey, forms which overlap in taxonomic characters are regarded as geographic subspecies and not as distinct species.

The segregation of *Elpidia glacialis* and *E. hanseni* into endemic trench subspecies, and the existence in the Kurile-Kamchatka Trench of four closely related species of the genus, provide information on the evolutionary processes in the hadal fauna (p. 242).

As pointed out by Belyaev (1971), the species fall into two groups, which differ in the robustness of the deposits.

(1) *E. theeli, E. minutissima, E. chilensis,* and *E. adenensis* have slender deposits (diameter of axis less than 0.04 mm, and usually less than 0.03 mm). All the species are abyssal.

(2) *E. glacialis, E. longicirrata, E. birsteini, E. hanseni,* and *E. atakama* have robust deposits (diameter of axis 0.04–0.25 mm). Deposits of extreme robustness are characteristic of the two deepest living species, *E. birsteini* and *E. hanseni* (p. 241). All the hadal forms belong to this group, which is represented at smaller depths in polar seas only.

The mutual relationship of the two species groups, as well as the geographic and bathymetric place of origin of the genus, can only be conjectured. Belyaev (1971) regarded the species group with slender deposits as the most primitive and suggested that the genus originated at abyssal depths in the southern parts of the Pacific and Indian Oceans.

Most species descriptions given below are very short. Detailed descriptions are found in Belyaev's recent thorough and well-illustrated revision.

Ecology: The genus *Elpidia,* and *E. glacialis* in particular, differs strikingly from all other holo-

thurians in geographic as well as bathymetric distribution. It penetrates to the bottom of the deepest trenches, while in the Arctic it occurs at shallower depths than any other member of the Elasipoda. The background for the peculiar distribution of *Elpidia* is to be sought for among ecological features which are common to the different localities of the genus.

A preference for, or a tolerance to, extremely low temperatures may partly explain its occurrence in the Arctic Basin. However, it does not explain the occurrence of the genus at hadal depths in the trenches, where the temperature is not lower than in the abyssal zone.

The nutritive conditions seem to be much more important than the temperature in determining the distribution of *Elpidia*. Belyaev (1971) emphasized that, with the exception of the Arctic, the species of *Elpidia* are restricted to highly productive regions, in particular those close to the coast. Belyaev explained the special preference for the hadal depths of the trenches by the abundant sedimentation due to which the nutritive conditions are better than in the surrounding abyssal regions. The highest density of population was found in the Kurile-Kamchatka Trench which is situated in one of the most productive regions of the ocean. The Mariana and Tonga Trenches, which are more oceanic and have a poorer supply of nutrient matter, do not seem to be inhabited by *Elpidia*.

The species of *Elpidia* most often exhibit a high density of population. This is especially pronounced in the trenches, but also the Arctic and Antarctic localities are usually rich in number of individuals. A rather abundant occurrence of *Elpidia* off the coast of North-West Africa is indicated by the fact that it was taken by all three research vessels *(Travailleur, Talisman, Valdivia)* which investigated the region.

The different *Elpidia* localities may have in common that the food supply, although abundant, is irregular or limited to a short period of the year.

The bottom deposits of the trenches, to a considerable degree, consist of material brought down by turbidity currents and mud slides. These processes, which may lead to sudden large supplies of organic matter, seem to have a great influence on the composition of the hadal animal communities (p. 240).

The region off the coast of North-West Africa is remarkable in having the richest upwelling in the North Atlantic. LaFond (1966) suggested that large amounts of organic matter may accumulate on the continental slope in such regions, swept off the shelf through turbulence and turbidity currents. The accumulation and mass burial of organic matter, according to LaFond, creates conditions resembling those prevailing in trenches and isolated basins.

The Antarctic Ocean has a high organic production due to a persistent upwelling at the highest latitudes. The high concentrations of nitrate and phosphate combined with the short duration of the illuminated period result in a "phytoplankton outburst of incredible richness" for a period of three or four months (Raymont 1963). This may lead to periodic accumulations of organic matter on the bottom, and thus to ecological conditions resembling those found in the trenches and on the lower continental slope off North-West Africa.

The distribution of *Elpidia glacialis* in the Arctic region may similarly depend on a periodicity in the supply of food to the bottom, correlated with the short duration of the illuminated period.

The ascent of *Elpidia glacialis* to a depth of only 70 m in the western Kara Sea may be due to ecological conditions which are favourable not only to this species, as many other deep-sea species ascend to shallow depths in this sea. The western Kara Sea is remarkable for the great dominance of echinoderms, which account for four-fifths of the biomass. Zenkevich (1963) suggested that the ascent of deep-sea species is made possible partly by the temperature which, below a depth of 50 m, is negative throughout the year, and partly by the darkness due to the low transparency of the water and the ice cover which lasts almost all the year round.

However, the long-lasting ice cover also limits the phytoplankton production and the supply of food to the bottom to a short period of the year – a similarity to other localities of *Elpidia*.

Despite the fact that the species of *Elpidia* seem to be adapted to the exploitation of large supplies of sediment or organic matter, they are apparently not indiscriminate mud swallowers. A selectivity in food uptake is suggested by the long, digitiform processes on the tentacle discs and by the relatively small volume of the intestine (p. 196).

Key to the species of *Elpidia*

1. Deposits slender (diam. of axis less than 0.04 mm) 2
1. Deposits robust (diam. of axis at least 0.04 mm) 5
2. Deposits up to 0.80 mm long. Apophyses 20–50 % the length of the deposits ... 3
2. Deposits up to 1.25 mm long. Apophyses 7–15 % the length of the deposits ... 4
3. Dorsal papillae 3 pairs ..... *minutissima* (p. 175)
3. Dorsal papillae 5–7 pairs ..... *theeli* (p. 174)
4. Deposits slightly serrate. Dorsal papillae 2 pairs ..... *chilensis* (p. 175)
4. Deposits smooth. Dorsal papillae 4 pairs ..... *adenensis* (p. 175)
5. Deposits ventrally extremely robust, including ellipsoid bodies without arms .... *hanseni* (p. 181)
5. Deposits less robust, never ellipsoid in shape 6
6. Dorsal papillae 3 pairs, at least the first pair long and filiform 7
6. Dorsal papillae 3–8 pairs, rudimentary or well developed, but never filiform .. 8
7. Dorsal papillae, all long and filiform ..... *longicirrata* (p. 181)
7. Dorsal papillae of first pair long and filiform, the others rudimentary *birsteini* (p. 181)
8. Apophyses 20–50 % the length of the deposits ..... *atakama* (p. 181)
8. Apophyses 0–10 % the length of the deposits ..... *glacialis* (p. 175)

Elpidia theeli Hansen, 1956
Figs. 87, 88, 93: 3

Elpidia glacialis theeli Hansen, 1956, pp. 34–38, fig. 6; Hansen 1967, p. 491, figs. 7, 8: 3.
Elpidia theeli Hansen, Belyaev 1971, pp. 350–351, fig. 14B.
Elpidia antarctica Belyaev, 1971, pp. 352–353, fig. 16.

Diagnosis: Body length up to 33 mm. Dorsal papillae 5–7 pairs, up to 12 mm long (rudimentary in small specimens). Deposits up to 0.60 mm long; diam. of axis c. 0.02 mm. Apophyses 20–50 % the length of the deposits.

Records: Tasman Sea, 4510 m. 14 specimens. – Antarctic, 650–700 m. Two specimens.

Remarks: The 14 specimens from *Galathea* St. 602 in the Tasman Sea were originally (Hansen 1956) described as a subspecies of *E. glacialis*. However, as the deposits are (with no overlapping) much smaller than those of the other subspecies of *E. glacialis*, I agree with Belyaev (1971) that it should be raised to the rank of a species. In fact, the deposits are the smallest in the genus.

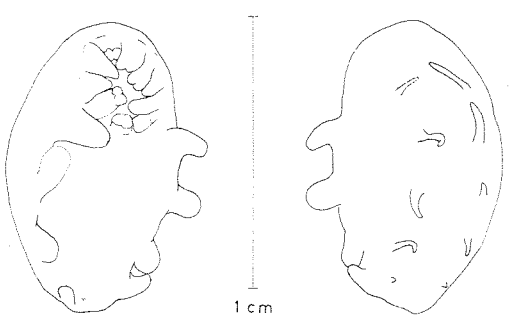


Fig. 87. *Elpidia theeli*. St. 602.

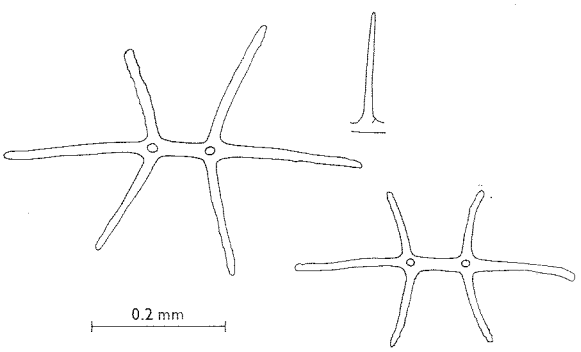


Fig. 88. *Elpidia theeli*. Deposits. St. 602.

The *Galathea* specimens are 7–12 mm long. The dorsal papillae in the largest specimen (Fig. 87) are 0.3–1.6 mm long. In the smaller specimens, all the papillae are rudimentary. In the preliminary report (Hansen 1956) it was incorrectly stated that the subspecies has rudimentary papillae.

The fact that the papillae increase in length (also proportionately) with the body size points to *E. antarctica* as a synonym of *E. theeli*. *E. antarctica* is known from two specimens, 22 and 33 mm long. The small specimen had 4 left and 6 right pa-

pillae, 1.3–3.7 mm long. The large specimen had 5 pairs of 9–12 mm long papillae. The deposits agreed in size and slenderness, as well as in height of apophyses, with those of *E. theeli*.

Elpidia minutissima Belyaev, 1971

Belyaev 1971, pp. 342–344, figs. 8–9.

Diagnosis: Body length up to 13 mm. Dorsal papillae 3 pairs, 0.5–1.0 mm long. Deposits up to 0.80 mm long; diam. of axis c. 0.02 mm. Apophyses 25–35 % the length of the deposits.

Records: Aleutian Trench, 5740 m. 359 specimens. – Bering Sea, 4382 m. One specimen.

Elpidia chilensis Belyaev, 1971

Belyaev 1971, pp. 344–345, fig. 10.

Diagnosis: Dorsal papillae 2 pairs, on the anterior half of the body, 8–9 mm long (in specimens 18–22 mm long). Deposits up to 1.25 mm long, slightly serrate; diam. of axis 0.02–0.03 mm. Apophyses 10–14 % the length of the deposits.

Records: Peru-Chile Trench, 2710–4600 m. Three specimens.

Elpidia adenensis Belyaev, 1971

Belyaev 1971, pp. 351–352, fig. 15.

Diagnosis: Dorsal papillae 4 pairs, decreasing in length posteriorly from 2.0 to 0.4 mm (in a specimen 11 mm long). Deposits up to 1.25 mm long, smooth (but otherwise resembling those of *E. chilensis*); diam. of axis c. 0.02 mm. Apophyses 7–15 % the length of the deposits.

Record: Gulf of Aden, 3070 m. One specimen.

Elpidia **sp. 2** Belyaev, 1971

Belyaev 1971, p. 357.

The name refers to the specimens reported from off Morocco (2210–2480 m) by Perrier (1896, 1902) and Heding (1940). Perrier, in his first paper, described the specimens as *Tutela echinata* n. g., n. sp., and stated that they had three pairs of papillae, some of which were almost invisible. This information was overlooked by Hansen (1956, 1967), who referred the specimens to the subspecies *E. g. glacialis*, because of Heding's information that the arrangement of the papillae of the *Valdivia* specimen agreed with that of Arctic specimens. (The specimen is now so damaged that the arrangement of the papillae cannot be made out).

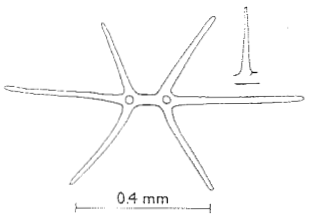


Fig. 89. *Elpidia* sp. 2 Belyaev, 1971. *Valdivia* St. 33.

The deposits of the *Valdivia* specimen (Fig. 89) are slender (diam. of axis c. 0.02 mm), up to 1.0 mm long dorsally, and 0.6 mm long ventrally. Apophyses 10–25 % the length of the deposits.

Elpidia glacialis Théel, 1876

Figs. 90, 91, 92, 95: 5, pls. X: 11–13, XII: 10

Théel 1876, pp. 1–7; Théel 1877, pp. 1–30, pls. I–V.

Diagnosis: Body length up to 62 mm. Dorsal papillae 3–8 pairs, rudimentary or well developed, but never long and filiform. Deposits varying from 1.20–1.75 mm in maximum length; diam. of axis 0.04–0.20 mm. Apophyses 0–10 % the length of the deposits.

Remarks: *E. glacialis* is found at abyssal and bathyal depths in Arctic and Antarctic seas, and at hadal depths in a number of trenches. The species is divided into six geographic subspecies, all of which were regarded as distinct species by Belyaev (1971).

Lemche *et al.* (in press) provided photographic evidence of the occurrence of *Elpidia* in the Palau Trench (8026–8046 m). The specimens had rudimentary papillae (actually invisible in the photographs) and may represent yet another Pacific trench subspecies of *E. glacialis*.

Key to the subspecies of Elpidia glacialis

1. Dorsal papillae well developed, arranged in an anterior and posterior group .... *glacialis* (p. 176)
1. Dorsal papillae well developed or rudimentary, following each other in a regular sequence 2
2. Dorsal papillae 3(–4) pairs, well developed 3
2. Dorsal papillae 4–8 pairs, rudimentary 4
3. Dorsal papillae up to 12 mm long (specimens up to 42 mm long). Deposits up to 1.55 mm long; diam. of axis c. 0.04–0.05 mm ..... *sundensis* (p. 178)
3. Dorsal papillae up to 3 mm long (specimens up to 33 mm long). Deposits up to 1.75 mm long; diam. of axis c. 0.08–0.09 mm ..... *uschakovi* (p. 180)
4. Dorsal papillae 6–8 pairs ..... *solomonensis* (p. 180)
4. Dorsal papillae 4–6 pairs 5
5. Deposits up to 1.75 mm long; diam. of axis 0.09–0.20 mm ..... *kurilensis* (p. 180)
5. Deposits up to 1.30 mm long; diam. of axis c. 0.05–0.06 mm .... *kermadecensis* (p. 180)

Elpidia glacialis glacialis Théel, 1876
Figs. 90: 1–3, 91

Elpidia glacialis Théel, 1876, pp. 1–7; Théel 1877, pp. 1–30, pls. I–V; Mortensen 1932, pp. 41–43, pl. I: 4–5; Heding 1942, pp. 16–19, figs. 16–17; Belyaev 1971, 332–333, fig. 1 (complete list of references).

Elpidia glacialis glacialis Théel, Hansen 1956, pp. 34–38; Hansen 1967, p. 491, figs. 7, 8: 1.

Elpidia sp. 1 Belyaev, 1971, pp. 356–357.

Diagnosis: Body length up to 62 mm. Dorsal papillae well developed, arranged in an anterior and posterior group, usually with 2–3 and 1 pair, respectively. Deposits up to 1.20 mm long; diam. of axis c. 0.04–0.05 mm.

Distribution: *E. g. glacialis* is found at bathyal and abyssal depths in the Arctic Ocean and the Baffin Bay. In two localities it has been found at depths less than 300 m: The Kara Sea (east coast of Novaja Zemlja): 70–230 m (Théel 1877,

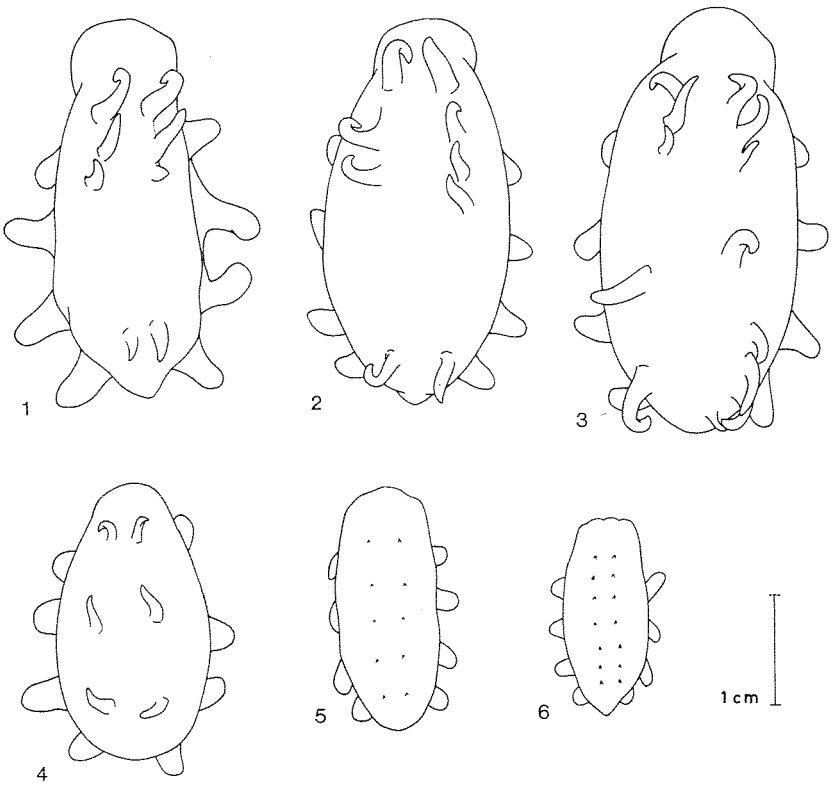


Fig. 90. *Elpidia glacialis*. 1–3, *E. g. glacialis (Godthaab* St. 54); 4, *E. g. sundensis (Galathea* St. 466); 5, *E. g. kermadecensis (Galathea* St. 649); 6, *E. g. solomonensis (Galathea* St. 521).

Zenkevich 1963), and Jørgen Brønlund Fjord (Peary Land): 190–200 m (Andersen 1971).

The absence of shallow records from other regions is not only due to lack of investigation. In three regions investigated also at sublittoral depths the upper records of the species are remarkably deep: Baffin Bay (Mortensen 1932), 610 m. Off the Novosiberian Islands (Gorbunov 1946), 520 m. Off Spitsbergen (Mikhajlovskij 1902), 2203 m. Similarly, investigations in the sublittoral zone of the Chukotsk Sea (D'yakonov 1952b), off Point Barrow, Alaska (MacGinitie 1955), and in the Bering Sea (Ivanov 1964) failed to reveal its presence. Probably, the extensive areas with depths less than 200 m on both sides of the Bering Strait are uninhabited by *Elpidia*. The Arctic populations of *E. glacialis* thus appear to be separated from the Pacific populations by a distance of at least 1500 kilometres.

Variation:

(1) Papillae and tubefeet. Information in literature suggests that there is some geographic or local variation in the number of papillae within the Arctic region. Specimens with 3 anterior and 1 posterior pair predominated at 1412–2386 m northeast of Iceland (Heding 1942); at 311–362 m between Franz Joseph Land and Novaja Zemlja (Mikhajlovskij 1904); at 70–230 m in the Kara Sea; and at the deepest *Godthaab* station, 1880 m, in the Baffin Bay. Specimens with 2 anterior and 1 posterior pair predominated at 2203–2992 m west of Spitsbergen (Mikhajlovskij 1902) and at 3175 m in the Canadian Basin (Agatep 1967c).

The 150 specimens from the five shallowest *Godthaab* stations in the Baffin Bay (610–850 m) had the highest number of papillae known from the Arctic region: 85 % of the specimens had 4 or more pairs of anterior papillae, and 40 % had 2 or more pairs of posterior papillae.

The papillae in the specimens from the shallow Baffin Bay stations were often placed in irregular sequence along the radii, sometimes with papillae between the anterior and posterior group. A similar irregularity was found in many of the Kara Sea specimens.

The shallow Baffin Bay specimens were also remarkable by the fact that 95 % had 5 pairs of tubefeet.

The 86 specimens from the deep *Godthaab* station (1880 m) agreed in number of papillae (3 and 1 pairs) with those of most other Arctic populations, and only two of the specimens had 5 pairs of tubefeet. A number of 5 pairs has not otherwise been recorded within the genus.

The difference in number of papillae and tubefeet between the shallow and deep Baffin Bay populations was observed by Heding (1942) who, however, counted the papillae for only three of the five shallow stations. A high number of papillae and tubefeet is, however, also found in the specimens from the two remaining shallow sta-

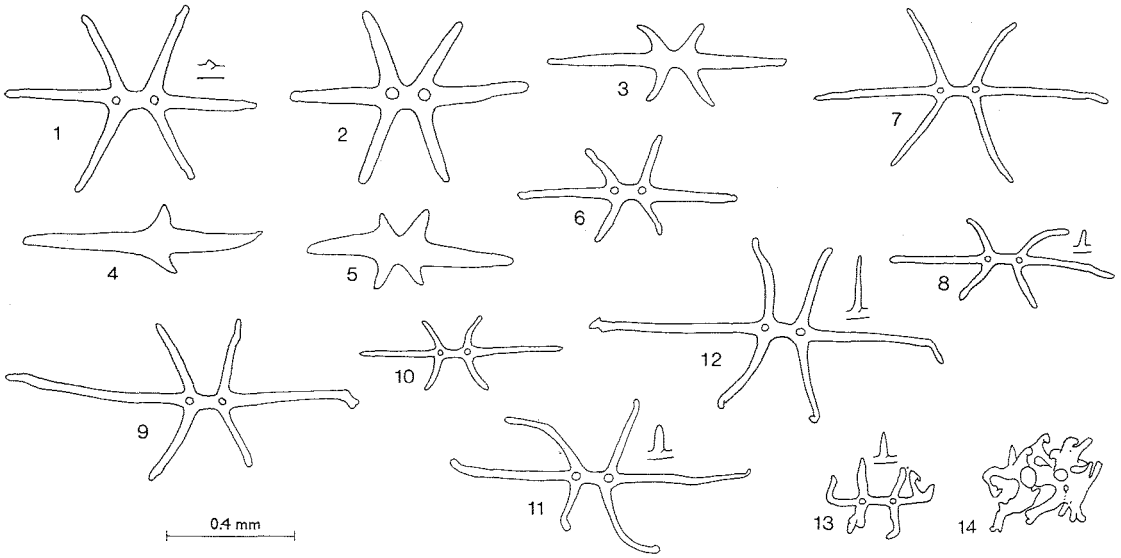


Fig. 91. *Elpidia glacialis glacialis*. Deposits. 1–5, *Ingolf* St. 113, ventrum; 6–8, *Ingolf* St. 120, ventrum; 9–10, *Godthaab* St. 144, ventrum; 11, *Godthaab* St. 119, ventrum; 12–14 *Godthaab* St. 54, dorsum.

tions. The five stations are situated on both sides of the Baffin Bay.

(2) Deposits. The deposits were compared in 60 specimens (ten from each station) from three *Ingolf* stations between Iceland and Jan Mayen (St. 113, 2465 m; St. 117, 1889 m; St. 120, 1666 m) and three *Godthaab* stations from the Baffin Bay (St. 54, 1880 m; St. 119, 610 m; St. 144, 733 m).

The specimens from *Ingolf* St. 113 differed from those of the other five stations by their robust deposits (Fig. 91: 1–5) which usually lack the apophyses. Some of the specimens showed reduction of the arms. Length of deposits up to 0.8 mm (occasionally 0.9 mm). Diam. of axis up to 0.07 mm. The dorsal deposits were less robust than the ventral ones (all deposits illustrated are ventral), but nevertheless they were distinctly more robust than those of the specimens from the other stations.

The deposits were more slender (diam. of axis 0.04 mm) in the specimens from the two other *Ingolf* stations (6–8) and the three *Godthaab* stations (9–12). They were up to 1.0 mm long in the *Ingolf* specimens and 1.2 mm in the *Godthaab* specimens. There was no difference in appearance and size between the deposits of the deep and the shallow *Godthaab* specimens. In one *Godthaab* specimen all the deposits were completely deformed (Fig. 91: 13–14).

Relationship of the Baffin Bay population: Heding (1942), comparing the *Godthaab* and *Ingolf* specimens, concluded that "the specimens from Baffin Bay may be regarded as survivors now developing into an endemic species". This apparently induced Belyaev (1971) to refer the Baffin Bay specimens to a separate species (*Elpidia* sp. 1).

However, the view is contradicted by the fact that the differences between the deposits of the Baffin Bay specimens and those of the specimens from *Ingolf* Sts. 117 and 120 are very small compared to the differences between the deposits from the two latter stations and the closely situated *Ingolf* St. 113. Further, the specimens from the deep Baffin Bay station agree in number and arrangement of the papillae with the usual Arctic form. The differences found in the latter feature are between the specimens from the shallow and deep Baffin Bay stations, and not between those from the Baffin Bay as a whole and the Arctic Ocean.

Moreover, it seems doubtful whether the deep-sea fauna of the Baffin Bay is effectively isolated from the main Arctic deep-sea fauna. Bailey (1956) presented evidence that the deep water (1250–2100 m) of the Baffin Bay originates in the Arctic Ocean. At depths greater than 250 m the Arctic Ocean water is heavier than any waters found in the Baffin Bay. As the sill depth in the Smith Sound Channel (connecting the Baffin Bay with the Arctic Ocean) is about 200 m, "it may be expected that a flow of heavy Arctic water may take place at relatively frequent intervals".

The straits connecting the Baffin Bay with the Arctic Ocean were investigated at a depth down to 90 m by the *Fram* (Grieg 1907). *Elpidia glacialis* was, however, not among the 26 species of echinoderms taken.

Elpidia glacialis sundensis Hansen, 1956

Figs. 90: 4, 92: 1–5

Elpidia glacialis sundensis Hansen, 1956, pp. 34–38, figs. 1, 5; Hansen 1967, p. 491, figs. 7, 8: 2.
Elpidia glacialis Théel, Théel 1882, pp. 18–19; Agatep 1967b, p. 61, pl. 7: 1–5.
Elpidia sundensis Hansen, Belyaev 1971, pp. 355–356, fig. 18.
Elpidia javanica Belyaev, 1971, pp. 354–355, fig. 17.
Elpidia sp. 5 Belyaev, 1971, pp. 358–359.

Diagnosis: Body length up to 42 mm. Dorsal papillae 3 pairs, up to 12 mm long. Deposits up to 1.55 mm long, slightly serrate; diam. of axis c. 0.04–0.05 mm.

Records: Sunda Trench, 6433–7160 m. C. 3000 specimens. – Antarctic, 1153–4840 m. 115 specimens.

Remarks: Hansen (1956) referred to the subspecies *E. g. sundensis* not only the specimens from the Sunda Trench but also the single Antarctic specimen taken by the *Challenger*. The Antarctic specimens of the *Eltanin* (Agatep 1967b) are here referred to the same subspecies because all the intact specimens had three pairs of well-developed papillae. Agatep erroneously stated that the specimens "belong to *Elpidia glacialis glacialis*, based on Hansen's (1956) 5 geographical subspecies".

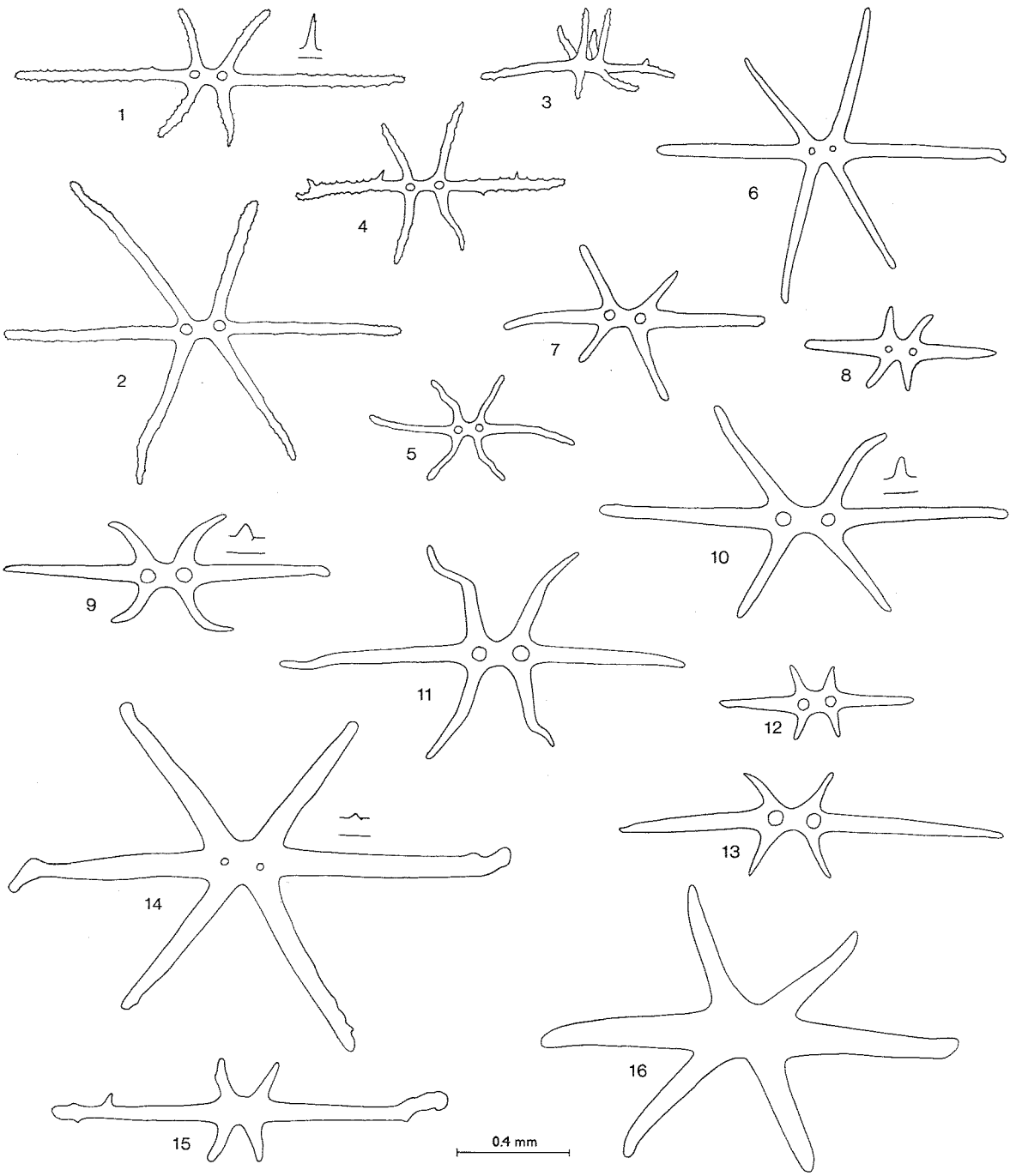


Fig. 92. *Elpidia glacialis.* The hadal subspecies. Deposits. 1–5, *E. g. sundensis* (1–3, St. 466, ventrum; 4, St. 465, ventrum; 5, St. 465, dorsum); 6–8, *E. g. kermadecensis* (6, St. 650, ventrum; 7–8, St. 649, ventrum); 9–13, *E. g. solomonensis* (9–10, St. 521, ventrum; 11 and 13, St. 517, dorsum; 12, St. 517, ventrum); 14–16, *E. g. kurilensis, Ryofu Maru* St. E 2, Japan Trench (14, dorsum; 15–16, ventrum).

Belyaev (1971) regarded the species *E. sundensis* as endemic to the Sunda Trench. The above-mentioned Antarctic specimens, as well as two Antarctic specimens taken by the *Ob,* were provisionally referred to as *Elpidia* sp. 5, a name which was even suspected to cover more than one species.

The relationships of the Antarctic specimens are uncertain due to insufficient knowledge of the variation of the deposits. The present refer-

ring of the specimens to *E. g. sundensis* is based on the similarity in external features only.

The *Galathea* specimens from the Sunda Trench (Fig. 90: 4) are up to 42 mm long. Breadth of body 55–71 % of length.

Dorsal papillae 3 pairs, varying in length from 2 mm (in a 23 mm long specimen) to 7 mm (in a 28 mm long specimen). Belyaev found a variation in length of 6–12 mm.

Deposits in the Sunda Trench specimens rather slender and almost all serrate (Fig. 92: 1–5). They were up to 1.55 mm long in Belyaev's specimens. In the *Galathea* specimens they reach only 1.25 mm. Apophyses usually less than 10 % the length of the deposits.

Elpidia javanica Belyaev, 1971, is known from five specimens in the Sunda Trench (6820–6850 m). The species was held to differ from all other species of *Elpidia* by the absence of dorsal papillae. The deposits show a very specific similarity to those of *E. sundensis*. This suggests that *E. javanica* was erected on specimens of *E. sundensis* which had lost the papillae (the papillae may be so small that they leave little trace when torn off) or that the ventral side was mistaken for the dorsal side (cf. Belyaev 1971, fig. 17: 9).

Elpidia glacialis uschakovi Belyaev, 1971

Elpidia uschakovi Belyaev, 1971, pp. 346–348, fig. 12.

Elpidia glacialis uschakovi Belyaev, Lemche *et al.* (in press), photographic evidence.

Diagnosis: Body length up to 33 mm. Dorsal papillae 3(–4) pairs, up to 3 mm long. Deposits up to 1.75 mm long, slightly serrate; diam. of axis c. 0.08–0.09 mm.

Records: New Hebrides Trench, 6680–6830 m. Nine specimens.

Remarks: *E. g. uschakovi,* according to Belyaev, differs from *E. g. sundensis* by the more slender body form (breadth about 40 % of length), the smaller size of the papillae, and by the greater thickness of the calcareous rods of the tentacles (0.08–0.10 mm, against 0.05 mm in *E. g. sundensis).* The latter feature is connected with the greater robustness of all the deposits.

E. g. uschakovi, in the size (and partly in the number) of the papillae, is intermediate between *E. g. sundensis* on one hand, and *E. g. kermadecensis, E. g. solomonensis,* and *E. g. kurilensis* on the other. In the elongate body form it resembles the three latter. In the length (and partly in the robustness) of the deposits it agress with *E. g. kurilensis.*

Elpidia glacialis kermadecensis Hansen, 1956

Figs. 90: 5, 92: 6–8

Elpidia glacialis kermadecensis Hansen, 1956, pp. 34–38, figs. 2–3; Hansen 1967, p. 491, figs. 7, 8: 4.

Elpidia kermadecensis Hansen, Belyaev 1971, pp. 349–350, fig. 14A.

Diagnosis: Body length up to 30 mm. Dorsal papillae 4–6 pairs, rudimentary (rarely approaching 1.0 mm in length). Deposits up to 1.30 mm long; diam. of axis c. 0.05–0.06 mm.

Records: Kermadec Trench, 6620–8300 m. C. 1800 specimens.

Elpidia glacialis solomonensis Hansen, 1956

Figs. 90: 6, 92: 9–13

Elpidia glacialis solomonensis Hansen, 1956, pp. 34–38, figs. 2, 4; Hansen 1967, p. 491, figs. 7, 8: 5; Lemche *et al.* (in press), photographic evidence.

Elpidia solomonensis Hansen, Belyaev 1971, pp. 348–349, fig. 13.

Diagnosis: Body length up to 27 mm. Dorsal papillae 6–8 pairs, rudimentary. Deposits up to 1.50 mm long; diam. of axis c. 0.06–0.07 mm. Axis tapered; arms outwardly curved and tapered.

Records: New Britain Trench, 6780–9043 m. 115 specimens.

Elpidia glacialis kurilensis Baranova et Belyaev, 1971

Fig. 92: 14–16

Elpidia kurilensis Baranova et Belyaev, 1971, in Belyaev 1971, pp. 333–336, figs. 2–3.

Diagnosis: Body length up to 53 mm. Dorsal papillae 4–5 pairs, rudimentary. Deposits up to 1.75 mm long; diam. of axis 0.09–0.15 mm in dorsal, 0.09–0.20 mm in ventral deposits. Apophyses rudimentary or absent.

Records: Aleutian, Kurile-Kamchatka, and Japan Trenches, 6156–8100 m. 214 specimens.

Material:
Fourth cruise of the Japanese Expedition of Deep Seas (JEDS–4) St. E 2, eastern slope of the Japan Trench (38°00'N, 144°05'E – 37°57'N, 143°57'E), 6700–7340 m. – 2 specimens.

Description: The specimens are 25 and 35 mm long. They have four pairs of tubefeet and ten tentacles with completely retracted disc processes. The large specimen, and probably also the small one, has four equidistant pairs of rudimentary and completely retracted dorsal papillae. The skin is hard, due to the crowded deposits (Fig. 92: 14–16). Most of the deposits are about 1.0 mm long, some up to 1.5 mm. Diameter of axis 0.09–0.15 mm in dorsal, 0.09–0.20 mm in ventral deposits. (Belyaev (1971) stated the maximum length of the deposits to be 1.75 mm, and the diameter of the axis to be 0.09–0.15 mm). The apophyses are reduced – in most of the ventral deposits absent.

The deposits of *E. g. kurilensis* are the largest and most robust in the species. In robustness, the deposits of the here described specimens approach those of *E. birsteini.*

Remarks: The specimens, taken by the *Ryofu Maru,* were kindly placed at my disposal by Dr. Masuoki Horikoshi. A brief account of the expedition was given by Suyehiro *et al.* (1962), but without description of the animals.

Elpidia longicirrata Belyaev, 1971

Belyaev 1971, pp. 338–339, fig 5.

Diagnosis: Body length up to 55 mm. Dorsal papillae 3 pairs, all long and filiform. Deposits up to 1.75 mm long; diam. of axis 0.07–0.09 mm. Apophyses absent.

Records: Kurile-Kamchatka Trench, 8035–8345 m. Five specimens.

Elpidia birsteini Belyaev, 1971

Belyaev 1971, pp. 336–338, fig. 4.

Diagnosis: Body length up to 47 mm. Dorsal papillae 3 pairs, the first pair long and filiform, the others rudimentary. Deposits up to 1.55 mm long; diam. of axis 0.07–0.10 mm in dorsal, 0.10–0.20 mm in ventral deposits. Apophyses absent.

Records: Kurile-Kamchatka Trench, 8060–9345 m. 1423 specimens. – Idzu-Bonin Trench, 8530–8540 m. One specimen.

Elpidia hanseni Belyaev, 1971

Belyaev 1971, pp. 339–342, figs. 6–7.

Diagnosis: Dorsal papillae 2(–3) pairs. Ventral deposits extremely robust, the largest ones ellipsoid and without arms; diam. of axis 0.10–0.25 mm. Apophyses of ventral deposits reduced or absent.

Elpidia hanseni hanseni Belyaev, 1971

Elpidia hanseni Belyaev, 1971, pp. 339–342, fig. 6.

Diagnosis: Body length up to 31 mm. Dorsal papillae 2 pairs, from less than 1.0 to 4.5 mm long, and occasionally a third pair, less than 1.5 mm long. Deposits up to 1.10 mm long, the dorsal ones with axis 0.07–0.18 mm in diam. Axis and arms tapered, arms often outwardly curved (the slenderer deposits resembling those of *E. glacialis solomonensis).*

Records: Kurile-Kamchatka Trench, 8610–9530 m. C. 34000 specimens.

Elpidia hanseni idzubonensis Belyaev, 1971

Elpidia hanseni idzubonensis Belyaev, 1971, pp. 339–342, fig. 7.

Diagnosis: Body length up to 23 mm. Dorsal papillae 3 pairs, 1.0–1.5 mm long. Deposits up to 1.35 mm long, the dorsal ones with axis 0.05–0.09 mm in diam. Axis and arms less tapered and arms less curved than in *E. h. hanseni.*

Records: Idzu-Bonin Trench, 8800–9735 m. 153 specimens.

Elpidia atakama Belyaev, 1971

Belyaev 1971, pp. 345–346, fig. 11.

Diagnosis: Dorsal papillae 5–6 pairs, 2–4 mm long (in specimens 33–46 mm long). Deposits up to 1.50 mm long; diam. of axis 0.05–0.09 mm in dorsal, 0.10–0.15 mm in ventral deposits. Apophyses 20–50 % the length of the deposits.

Records: Peru-Chile Trench, 7720 m. Two specimens.

***Elpidia* sp. 3** Belyaev, 1971

Belyaev 1971, pp. 357–358, fig. 19.

A few skin fragments taken in the Romanche Trench at 7340 m. Deposits up to 0.85 mm long; diam. of axis c. 0.04 mm.

***Elpidia* sp. 4** Belyaev, 1971

Belyaev 1971, p. 358, fig. 20.

A skin fragment taken in the Peru-Chile Trench at 2140 m. Deposits up to 0.71 mm long, as robust as the ventral deposits of *E. atakama*.

III. GENERAL PART

A. THE TAXONOMIC CHARACTERS AND THEIR VARIATION

In order to estimate the importance of the different taxonomic characters the range of variation within each species should be known. An examination of a large number of specimens of many species showed that there was a pronounced variation in most taxonomic characters.

An *individual variation* is unambiguously revealed by differences between specimens from one and the same station. If two stations are involved, the differences might be due to local variation.

The range of individual variation in a taxonomic character may differ from one locality to another. This is clearly shown by the variation in number of dorsal papillae in *Oneirophanta mutabilis*. In the 14 specimens from St. 654 in the Kermadec Trench the papillae were surprisingly constant both in number and arrangement, while in the 30 specimens from St. 716 in the eastern Pacific the papillae varied greatly in number and showed no regular features in the arrangement and type of reduction.

A *local variation* seems to be of common occurrence among the Elasipoda. Striking examples are shown by four species of the Kermadec Trench, in particular *Oneirophanta mutabilis* (p. 243).

A *geographic variation*, i. e. a variation of a larger scale, was found in practically all the widely distributed species known from many specimens.

An *age variation* has been found in a few species only. This may to some degree be ascribed to the almost complete absence of small specimens in the material (p. 10). Specimens smaller than 20 mm were caught in five species only: *Ellipinion galatheae* (17 mm), *Elpidia glacialis* (11–35 mm), *E. theeli* (7–12 mm), *Laetmogone fimbriata* (9–60 mm), and an unidentified species of *Peniagone* from St. 626 (9–10 mm).

The papillae and tubefeet increase in number with advancing age in the species *Laetmogone maculata, L. fimbriata,* and *Orphnurgus glaber*. In *Laetmogone violacea* the papillae increase in number, while the tubefeet number does not increase to any appreciable degree. As a rule, the number of ambulacral appendages increases with the size of the specimens in those species of the Deimatidae and Laetmogonidae in which they are present in a large number.

Juvenile giant crosses are found in *Psychropotes longicauda,* but otherwise an age variation in the calcareous deposits is unknown in the Elasipoda. In many molpadonians the deposits become irregular in shape and decrease in number with the age of the specimens. Similar changes were found in some aspidochirotes (e. g. Mitsukuri 1897a). In the Antarctic dendrochirote, *Staurocucumis liouvillei,* several generations of deposit types were found in specimens ranging from 0.7 to 13 mm in length (Ekman 1927).

The calcareous deposits

The endoskeleton in holothurians consists of isolated calcareous bodies, the *deposits*. Synonymous terms are ossicles, sclerites, and spicules, the latter term usually designating small and pointed bodies, as found in the Elpidiidae and Psychropotidae.

Düben & Koren (1844a, b) were the first to use the deposits consistently in the description of the species. Working on Scandinavian species they found that these could be most clearly distinguished by their deposits. This high evaluation of the deposits as specific characters has been adopted by subsequent authors, sometimes to such a degree that the deposits were the only feature illustrated.