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

#### The calcareous deposits

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

Düben & Koren (1844a, b) were the first to use the deposits consistently in the description of the species. Working on Scandinavian species they found that these could be most clearly distinguished by their deposits. This high evaluation of the deposits as specific characters has been adopted by subsequent authors, sometimes to such a degree that the deposits were the only feature illustrated. The importance of the deposits in characterizing genera and higher categories of holothurians has been differently estimated. Théel (1882), when creating his system for the Elasipoda, attached little generic importance to the deposits, while considerable attention was paid to them in the systems of R. Perrier (1902) and Hérouard (1923). The interrelationship of the different types of deposit and its bearing on the taxonomy of the Elasipoda was discussed by Hérouard (1923) and Ekman (1926).

## 1. Intraspecific variation.

The range of intraspecific variation in the deposits, contrary to that in other taxonomic features, can be estimated from selected body samples only, and not from the examination of whole specimens. It is, therefore, important that the samples are representative of the variation within the specimen. In most species there is a consistent difference between the dorsal and ventral deposits – the ventral ones being more robust. This difference may to some degree be phenotypic.

Differences between deposits from different parts of the dorsum or ventrum are usually of doubtful taxonomic value. The difference is generally smaller than between dorsal and ventral deposits and is seldom refound from one specimen to another. Even when conspicuous differences occur, as in the dorsum of one of the specimens of *Psycheotrephes magna* from St. 234, they are generally incidental. An exception is constituted by *Orphnurgus glaber*, in which the deformed deposits are increasingly robust towards the posterior end of the ventrum.

The deposits of the ambulacral appendages are usually elongated or rod-shaped bodies which are less characteristic specifically than are the fully developed deposits of the dorsum and ventrum. They were as a rule examined in only a few specimens of each species.

Sometimes species, even belonging to different genera, are indistinguishable by their deposits (Oneirophanta setigera and Orphnurgus protectus; Benthogone rosea, B. fragilis, and Laetmogone interjacens; Laetmogone wyvillethomsoni and L. theeli; and some species of Peniagone). Nevertheless, the deposits proved to be the most reliable of the species characters.

The deposits are important also to the study of geographic and local variation.

2. Interrelationship of the different types of deposit.

(1) The primary cross. Most holothurian deposits begin as a rod with a bifurcation at either end – a primary cross. It has been commonly assumed that the types of deposit which cannot be traced back directly to a primary cross are secondarily transformed. Only the wheels of the Apoda have been regarded as a possible exception (Ludwig 1889–1892).

The bifurcation of the primary cross generally continues into successive dichotomous ramifications, leading to the various types of reticulated plates which occur in all five orders of the Holothurioidea. The large and feebly differentiated plates of many Dendrochirota and of the genera *Deima* and *Oneirophanta* within the Deimatidae represent the least specialized type.

Hérouard (1923) considered the reticulated plate such a fundamental type of deposit that he derived even the various spicule types of Elpidiidae from reticulated plates. The arms of the elpidiid spicules, according to Hérouard, represent zigzag-lines of internodia, emerging through alternating reduction of one of the two branches in each ramification. Hérouard divided the spicules in this family into 1) a quaternary type, with the central growing point lying in the middle of an internodium, and 2) a trinary type, with the central growing point at a nodal point. The dual origin of the spicules, according to Hérouard, indicated that, at an early stage, the family separated into two distinct evolutionary trends.

This complicated derivation of simple spicules was based wholly on speculation. No intermediary stages have been observed between reticulated plates and the spicules of the Elpidiidae, and nothing in the morphology of the spicules suggests that their arms are constructed from a line of internodia. Hérouard's ideas of spicule derivations may, therefore, be left out of consideration.

Ekman (1926) rejected the view of the primary cross as the prototype of all holothurian deposits. He maintained that, at least in the Elasipoda and Aspidochirota, some types of deposit were derivatives of a "Spitzstäbchen" – a rod which is primarily undivided. This view led Ekman to remarkable conclusions regarding the taxonomy of the Elasipoda.

As the relationship of the different spicule types is of fundamental importance for an understanding of the phylogeny and taxonomy of the Elasipoda, it seems relevant to discuss Ekman's views.

Deimatidae. According to Ekman, both spicule types are represented. While the reticulated plates and the crosses with spatulated, perforated arm ends were derived from primary crosses, some of the rod-shaped spicules in the ambulacral appendages in species of *Orphnurgus*, *Oneirophanta*, and *Deima* were derived from "Spitzstäbchen".

As an example of a "Spitzstäbchen" in Deima, Ekman reproduced one of the four tentacular spicules illustrated by Ludwig (1894, pl. IX: 1-4) for D. pacificum, disregarding the fact that the three other illustrated spicules are intermediates between rods and reticulated plates.

The pointed, spindle-shaped rods in the ambulacral appendages in species of the other deimatid genera may seem to offer a more convincing example of "Spitzstäbchen". However, the present study showed that they were connected by intermediary stages to rods with terminal ramifications.

Even the amorphous, ellipsoid, and rounded bodies of *Orphnurgus glaber* (Fig. 13) can be traced back to deposits with terminal, dichotomous ramifications.

Laetmogonidae. Ekman stated that "Spitzstäbchen" occur in all the genera, while "Gabelstäbe" (i. e. elongated primary crosses) seem to occur only in *Laetmogone*. Nevertheless, one of the two "Gabelstäbe" illustrated in his paper was from *Laetmophasma fecundum* (= *Pannychia moseleyi*). According to Ekman, it is difficult to make a clear distinction between the two types of spicule as it is often doubtful whether or not the terminal spines of a rod represent bifurcations. In actual fact, all intermediates between pointed rods and rods with bifurcated ends are found in the family.

Elpidiidae. Ekman divided the family into two subfamilies, based solely on the types of spicule. In Elpidiinae, all the spicules were derived from "Spitzstäbchen", while in Peniagoninae both spicule types were represented. The tripartite spicules of *Amperima* and *Achlyonice* (both referred to Elpidiinae) were derived from rods through development of one oblique spine. This derivation was based on the presence of intermediary forms of spicule in *Amperima naresi*.

The presence in *Amperima naresi* (Fig. 76) of regular tripartite spicules together with irregularly shaped spicules, however, does not necessitate a derivation of the former from the latter. In my opinion, the irregular "intermediary" spicules are more likely reduced stages of regular tripartite spicules, which again may derive from a primary cross through reduction of two of its arms.

The rod-shaped spicules of *Scotoplanes* and *Ellipinion* may be derived through reduction of tripartite spicules or directly from primary crosses. Intermediary stages were found in *Scotoplanes clarki* (Fig. 85) and *S. globosa* (Théel 1882, pl. XXXIV: 2).

The spicules of *Elpidia* remain as the only type which cannot be traced back directly to a primary cross. The uniqueness of these spicules is further underlined by their unusual optical features. Schmidt (1925), determining the position of the optical axis in representatives of the five holothurian orders, found that in all deposits which from their morphology could be seen to derive from a primary cross the optical axis was vertical to the plane of the deposit. Only two deposit types had the axis horizontal to the plane: The *Elpidia* spicules and the "Schnallen" (buttons) in some species of the aspidochirote genus *Holothuria*.

The two pairs of obliquely placed arms of the *Elpidia* spicule apparently are not homologous with the arms of a primary cross, but rather represent two pairs of secondary processes on a rod-shaped spicule, vertical to the plane of the original primary cross. Transitional stages between rods and *Elpidia*-like spicules occur in Antarctic specimens of *Scotoplanes globosa*, as evidenced by the spicules illustrated by Agatep (1967b, pl. IV). The spicules included simple rods, as well as rods with two pairs of smooth or spinous arms. The presence of such transitional spicules in a genus related to *Elpidia* is remarkable.

Psychropotidae. Ekman derived the cross-shaped spicules of this family from "Spitzstäbchen", in contrast to the quite similar crosses occurring in a number of species of *Peniagone*. The different derivation was concluded from the fact that primary crosses do not occur in the family, and that the ventral spicules in many of its species include intermediary stages between crosses and rods. However, as in *Amperima naresi*, the intermediary stages are, in my opinion, more naturally regarded as reduced spicules.

The optical axis is vertical to the plane of the

cross, which agrees with a derivation of the latter from a primary cross (see above).

Ekman's derivation of the psychropotid crosses obscures a remarkable similarity between the spicules of Psychropotidae and those of Elpidiidae. In both families all spicules (except the rare wheels of the Elpidiidae) completely lack dichotomous ramifications other than those of the primary cross proper. Only two other examples are known of spicules which apparently lack the tendency of the primary cross to undergo ramification at the ends of the arms, viz. the spinous crosses of Laetmogone violacea and the crosses of the synallactid genus Galatheathuria Hansen & Madsen, 1956. However, in a specimen of Galatheathuria from Galathea St. 450, most of the crosses have terminal arm spines, possibly representing reduced ramifications. The type specimen of G. (Paelopatides) aspera also had the arm ends "slightly enlarged and spinous" (Théel 1886a, p. 158, pl. X: 13). In the specimens described by Hansen & Madsen (1956), terminal arm spines may have been lost through corrosion.

The peculiar similarity between the spicules of the Psychropotidae and Elpidiidae is one of the arguments for uniting these two families (together with the spicule-free, pelagic family, Pelagothuriidae) to form the new suborder, Psychropotina (pp. 206–207).

The absence of dichotomous ramifications in the spicules of the Psychropotina is probably a secondary feature. Spicules which are close to the hypothetical prototype of the Psychropotina spicules have been described as the fossil family Palelpidiidae Mostler, 1968a (p. 208).

(2) Wheels are the prevailing type of deposit in the Laetmogonidae. Only rod-shaped and (in *Laetmogone violacea*) cross-shaped spicules occur in addition. The centre of the wheels consists of a primary cross, or a five- or six-rayed structure deriving from a primary cross.

Ekman (1926) distinguished between two wheel types in the family – the flat wheel with a flat primary cross in the centre, and the concave wheel with a concave primary cross or a concave five- or six-rayed structure in the centre. While the flat wheels were simply regarded as small perforated plates, the concave wheels were supposed to derive from cross-shaped spicules of the type found in L. violacea.

However, apart from its concavity, the central structure of the concave wheel type has no simi-

larity to the spinous crosses of *L. violacea*. Besides, so many intermediates are found between the concave, six-rayed structure and the flat primary cross that a dual origin of the laetmogonid wheels is unlikely.



Fig. 93. Wheels of Elpidiidae. 1, Achlyonice ecalcarea (Galathea St. 663); 2, Amperima rosea (Monaco St. 2994); 3, Elpidia theeli (Galathea St. 602).

In the Elpidiidae, small wheels (Fig. 93) have previously been found as rare, accessory deposits in *Peniagone theeli*, Achlyonice ecalcarea, Amperima rosea, A. velacula, Irpa ludwigi, and Elpidia glacialis.

Examination was made of specimens of three of these species (Achlyonice ecalcarea, Amperima rosea, and Elpidia glacialis), and wheels were found in all of them. The specimens of Amperima rosea included those described by R. Perrier (1902); wheels were previously known only from the specimens described by Hérouard (1923). In Elpidia glacialis, wheels were found in the subspecies glacialis, but not in the other subspecies.

Only two additional species with wheels, Amperima naresi and Elpidia theeli, were found during the present study, which confirms the rare occurrence of this type of deposit in the Elpidiidae. On the other hand, wheels seem to be a rather constant feature in the species possessing them.

The wheels of the Elpidiidae differ from those of the Laetmogonidae by the presence of a calcareous membrane which connects the nave with the rim, and completely or partly fills in the interspaces between the spokes.

The central part of the elpidiid wheel consists either of a primary cross (Peniagone theeli and Achlyonice ecalcarea) or a three-rayed structure (Amperima rosea, A. naresi, A. velacula, Irpa ludwigi, Elpidia glacialis, and E. theeli). It is notable that the type with a central primary cross is found in the genera which have a primitive calcareous ring, whereas the type with a central three-rayed structure is found in genera with a specialized calcareous ring.

The wheels which Théel (1882) recorded for *Elpidia ambigua* (= *Peniagone purpurea* were probably foreign bodies. They were similar to the wheels in *Benthogone* and *Apodogaster* of the family Laetmogonidae.

Hérouard (1923) supposed that the wheels of the Elpidiidae were rudiments from a larval stage. This view is supported by the fact that the wheels occur scatteredly throughout the family – in primitive as well as in specialized genera. The occurrence of wheels in two only distantly related families of Elasipoda even suggests that the wheels are persisting spicules from a larval stage common to all Elasipoda. However, a direct proof of a larval origin of the wheels is still lacking because the larval development of the Elasipoda is completely unknown.

In contrast to the wheels of the Elasipoda, the wheels of the Apoda can be traced back directly to a larval stage. However, a homology between the wheels in the two orders is doubtful, because the wheels of the Apoda in no case possess a central primary cross, or a structure derived from a primary cross.

(3) C-shaped spicules occur in all species of Scotoplanes, Ellipinion, and Amperima (presence not established in A. furcata). The curved rods of Kolga and Irpa are probably homologous with the C-es of the three other genera, although it is uncertain whether they represent degenerate or primitive stages.

The aspidochirote genera *Stichopus* and *Bathyplotes* have C-shaped spicules which are similar in shape to those of the Elpidiidae (the similarity includes the presence of a middle enlargement). However, the aspidochirote C-es are not likely to be homologous with those of the Elasipoda. The fact that C-shaped spicules of similar shape are found also in echinoids and sponges shows that they need not be monophyletic in the Holothurio-idea.

#### The calcareous ring

Two types of calcareous ring are found in the Elasipoda:

1. – Deimatidae. Laetmogonidae, and Psychropotidae. The ring is similar in structure to that of the other holothurian orders, apart from its low degree of calcification. The few detailed descriptions and illustrations which are found in literature indicate conspicuous differences in ring structure. In order to examine the taxonomic value of these differences, the ring was examined in a number of representatives of the three families.

The structure of the ring may be illustrated by the example of *Oneirophanta setigera* (Fig. 94: 1). The five radial pieces each possesses a median slit for the passage of the radial nerve and watervascular canal, and two lateral depressions for the bottoms of the tentacular cavities. The five interradial pieces each possesses a median septum which separates two tentacular cavities.



Fig. 94. Calcareous rings. 1, Oneirophanta setigera (Galathea St. 726); 2, Oneirophanta mutabilis (Galathea St. 716). Both figures show the complete ring, with five radial and five interradial pieces. The lower figure shows the ring in external outline only.

The tentacular cavities form the basal part of the wide water-vascular canals of the tentacles. Each cavity communicates through a slender canal with one of the five broad radial canals issuing from the water-vascular ring. The calcareous ring is formed by calcifications in the connective tissue surrounding the bottoms of the tentacular cavities. The calcification is most pronounced at the base of the cavities and in the septa between them, while the internal and external membranes of the ring are less calcified.

Due to the low degree of calcification, the shape of the ten pieces varies according to the state of contraction of the specimen, and especially to that of the tentacles. Evidently, recorded specific differences in the shape of the calcareous ring should be regarded with reservations. Even if the ring is more strongly calcified, as in a specimen of *Oneirophanta mutabilis* (Fig. 94: 2), the pieces are still irregular in shape.

The degree of calcification may vary rather irregularly in the ring, and the transition from the stronger to the more feebly calcified parts is often so gradual that the ring has no exact delimitation. If the calcification of the external membrane is weak, the ring will show a number of indentations corresponding to the number of tentacles. If, however, the calcifications of the external membrane are so pronounced that the septa between the tentacular cavities are invisible from the outside, the ring will appear as an unsculptured ribbon. Thus, there is no essential difference between the two ring "types".

Treatment with sodium hypoclorite (cf. Théel 1882, pl. XXXVII: 4) may cause the ring to fall into fragments which do not reflect its structure.

The ring in the Laetmogonidae and Psychropotidae seems in general to be even less calcified than in the Deimatidae. Calcifications may even be absent in some species, the ring consisting only of a firm connective tissue (e. g. Benthogone rosea, Benthodytes typica, and Psychropotes longicauda). A specimen of Psychropotes depressa showed a loose calcareous meshwork at the base of the tentacular cavities. These calcifications have no similarity to the five star-shaped ring pieces in the Elpidiidae. Apparently, the feebly developed ring in these families represents a reduction and not, as in the Elpidiidae, an embryonic stage.

2. – Elpidiidae. The ring (Fig. 95), unlike that of all other holothurians, consists of five radial

pieces only, each with two clusters of arms radiating from a common centre.

Hansen (1967) pointed out that a peculiar evolution of the ring had taken place within the Elpidiidae, suggesting a paedomorphic origin of the whole family.

Three types of calcareous ring may be distinguished, derived from each other in the following order:

(1) In Peniagone, Achlyonice, Kolga, and probably Psychrelpidia, the ring pieces are small, delicate, and usually isolated from each other. The number of arms on each piece shows an individual variation (as far as can be judged from the few species of which sufficient material has been examined). The arms may also be irregularly subdivided. This type of ring is reminiscent of the embryonic ring of other holothurians and represents the beginning of the ring's unique evolution within the family.

The ring structure is known in the following species of *Peniagone* (the figures in parentheses indicate the number of arm pairs on each piece): *P. convexa* (c. 7; Fig. 95: 1), *P. azorica* (10–12), *P. affinis* (c. 12), *P. willemoesi* (10–15), *P. papillata* (7–9), *P. japonica* ("numerous"), *P. elongata* (10–14), *P. vitrea* (4–8), *P. purpurea* (c. 8), and *P. diaphana* (c. 7).

The ring may dissolve with advancing age. Thus, the ring was absent in some *P. azorica* from the Kermadec Trench and in one *P. diaphana* from St. 574. Hérouard (1902) similarly stated that the ring was absent in his specimens of *Scotoanassa translucida* (= *P. diaphana*).

The ring of Achlyonice ecalcarea has about 12 pairs of arms on each piece (Théel 1882), whereas A. monactinica has 6 pairs (Ohshima 1915). The ring of A. tui, according to Pawson (1965a), consists of a "fragile network"; the structure of the five pieces was not specifically described.

The ring of *Psychrelpidia*, according to Sluiter with 8 pairs of arms on each piece, probably belongs to the type found in *Peniagone* and *Achlyonice*.

The pieces of the ring in Kolga (Fig. 95: 2–3) are of a delicate structure. Six specimens examined of K. hyalina (four from Ingolf St. 113 and two from Godthaab St. 54) all possessed basically five pairs of arms on each piece, arranged as two anterior and three posterior pairs. Some pieces had some of the arms wholly or partially split. Danielssen & Koren (1882, pl. III: 27–28) illus-



Fig. 95. Calcareous ring pieces of Elpidiidae (all viewed from posterior end of body). 1, Peniagone convexa (Galathea St. 234); 2-3, Kolga hyalina, two pieces belonging to the same specimen (Ingolf St. 113); 4, Scotoplanes globosa (Galathea St. 32); 5, Elpidia glacialis glacialis, three adjoining pieces (Godthaab St. 143).

trated a ring in which the arms on each piece consisted of three anterior pairs (two of which were partially split) and four posterior pairs. A derivation from five basic pairs is not obvious from the illustration. Théel (1882), however, found that K. nana (here considered a synonym of K. hyalina), had five pairs of arms on each piece.

The ring of Kolga resembles the Peniagone-Achlyonice type in having a varying number of arms on each piece. On the other hand, the fact that the basic arm number seems to be constant recalls the conditions in the related genera *Irpa*, *Elpidia*, *Amperima*, *Ellipinion*, and *Scotoplanes*, although in all these genera the arm number is four pairs only.

The five ring pieces in Kolga are isolated from each other, although some of the arms are so long that they almost touch those of the neighbouring pieces. The reduction and partial fixation of the arm number may, as in Amperima, Ellipinion, and Scotoplanes, have taken place during a former continuous state of the ring.

The supposition that the ring of Peniagone and

Achlyonice represents an embryonic stage cannot be proved directly, as no larval stages of Elasipoda are known. However, in some species of Apoda the first rudiment of the ring consists of five radial pieces, each representing a primary cross with successive divisions of the arms. Thus, the ring of Synaptula hydriformis (Lesueur) passes through a stage resembling the ring of Peniagone and Achlyonice (Clark 1907, pl. VI: 9). The ring of Leptosynapta inhaerens (O. F. Müller) begins with the formation of five similarly shaped radial pieces, followed by the formation of five interradial pieces. From the beginning, the interradial pieces seem to consist of an irregular meshwork (Runnström 1928).

Almost nothing is known about the formation of the ring in the other holothurian orders. In *Psolus phantapus* Strussenfelt the ring begins as five radial rod-shaped pieces with some irregular branches, but with no obvious derivation from a primary cross (Runnström & Runnström 1921). In *Cucumaria echinata* v. Marenzeller the ring begins its formation as a diffuse, continuous meshwork (Ohshima 1921). The ring of the molpadonian *Caudina chilensis* (J. Müller) seems to start in the same way (Kitao 1933).

Although the derivation of the radial pieces of the calcareous ring from primary crosses through a *"Peniagone-stage"* has been observed only within the Apoda, it is probably the original derivation also in the groups in which the ring was found to begin its formation as a continuous meshwork.

(2) In Elpidia and Irpa the ring is continuous and of a firm structure. Each piece has four pairs of arms, forming a large posterior and a somewhat smaller anterior cross (Fig. 95: 5). The inner arms of the posterior cross are throughout their length joined firmly to the corresponding arms of the neighbouring pieces. The outer arms of the posterior cross meet the corresponding arms at the tip (or are connected with them by means of connective tissue fibers). Muscle fibers connect the ring with the pharynx. The ring represents a specialized type, derived from the Peniagone-Achlyonice type through an increase in size of the pieces, concomitant to a reduction in the number of those arms which do not take part in the firm construction of the ring.

The ring of *Irpa ludwigi* differs from that of *I. abyssicola* and *Elpidia glacialis* in having a flattened, irregularly shaped process on two pairs of the arms. Although the presence of these

processes was apparently verified for several specimens (von Marenzeller 1893b), they may not represent a constant feature in the species. They belong to the two pairs of arms that take no part in the firm construction of the ring.

The identical, and very specialized, ring structure is a remarkable similarity between the two genera. The simplification and regular formation of the ring pieces apparently evolved as a means of strengthening the construction of the ring, when the latter had regained its continuous state.

(3) In Amperima, Ellipinion, and Scotoplanes (Fig. 95: 4) each piece of the ring possesses four pairs of arms as in Irpa and Elpidia, but the ring is discontinuous and of a delicate structure. Although a derivation of the ring directly from the Peniagone type cannot be excluded, a derivation from the Elpidia-Irpa type seems more likely. A reduced and constant arm number was probably attained in a ring in which each piece performs a definite mechanical function.

The structure of the ring is known in Amperima robusta, Ellipinion papillosum, E. kumai (in this species an additional unpaired arm was present on each piece), Scotoplanes globosa, and S. clarki. Agatep (1967b) described the ring of S. globosa as consisting of "a very fine network of spicules", which apparently refers to incidental spicules, and not to the five distinct segments which are known to be present in this species. Similar descriptions were given of the rings in Scotoplanes facetus (= Ellipinion facetum) and S. angelicus (= E. papillosum).

# The tubefeet and papillae

Conspicuous ambulacral appendages are characteristic of most Elasipoda. The *tubefeet* are locomotory and sometimes provided with a sucking-disc, while the *papillae* are sensory or respiratory. The abundant development of the papillae, which has produced many bizarre animal forms within this order, is connected with the absence of respiratory trees (p. 208).

(1) Tubefeet. The well-defined ventral sole of the Elasipoda is bordered by ventrolateral tubefeet which are usually conspicuous. The midventral tubefeet, on the other hand, are reduced or absent.

In Elpidiidae the ventrolateral tubefeet are large and few in number; in some species of *Peniagone* they border only the posterior part of the ventral sole. As suggested by Hérouard (1923), the presence of few and large-sized tubefeet in this family may be a larval feature.

Large-sized, but more numerous, tubefeet characterize the Deimatidae and Laetmogonidae. As in Elpidiidae, the tubefeet are never fused into a brim.

The communication of the tubefeet, and in some species the papillae, with large water-vascular, dermal cavities is a feature peculiar to the Deimatidae, Laetmogonidae, and Elpidiidae. The cavities are branched in Deimatidae and Laetmogonidae, as well as in the elpidiid genus *Achlyonice*. The remaining Elpidiidae have unbranched cavities. The Psychropotidae may possess similar cavities at the base of the unpaired appendage.

The function of the cavities is considered elsewhere (pp. 205–206).

In most species of Psychropotidae the tubefeet are numerous, pointed, and fused into a brim which surrounds the body. Separate and rather large tubefeet are found along the side of the body in *Psychropotes longicauda*.

(2) Papillae belonging to the two dorsal radii are present in practically all species of Elasipoda. Papillae are present along the ventrolateral radii in the Deimatidae and in the laetmogonid genus *Apodogaster;* in the latter genus the papillae are small and fused into a brim which surrounds the body above the ventrolateral tubefeet.

The papillae and tubefeet not only provide valuable characters in the separation of species, genera, and families. The fact that they present numerical differences makes them especially adequate for the study of intraspecific variation. The geographic subspecies erected for the species *Deima validum, Oneirophanta mutabilis,* and *Elpidia glacialis* are based mainly on differences in number of dorsal papillae. Similarly, the geographic variation found in *Orphnurgus glaber* consists to a high degree of differences in number of papillae and tubefeet.

In view of the importance attached to the tubefeet and papillae as revealing geographic variation it is essential that descriptions of holothurians show the variation in number of these features for each locality.

(3) Velum. The Elpidiidae possess a velum formed by partial fusion of two pairs of large and usually one pair of reduced papillae. The taxonomic value of the velum has been differently estimated. Théel (1882) used its relative size as a generic character, whereas Hérouard (1923) did not even regard presence or absence of a velum as of generic importance. The latter view was confirmed by the present investigation.

It is remarkable that a velum, or papillae homologous with this structure, is present in all the genera of the family, with the exception of Elpidia. Thus, in Rhipidothuria the two most anterior pairs of papillae are placed closely together on an elevation of the skin corresponding in position to a velum. Similarly, the two pairs of minute papillae present in Parelpidia (here synonymized with *Peniagone*) are, like a velum, placed on the anterior part of the dorsum. Scotoplanes has two pairs of large and one pair of reduced papillae. As pointed out by Hérouard (1923), the papillae differ from those of a velum only by the large interspace between the first two pairs. The papillae of Scotoplanes may thus be derived from those of a velum through a process of allometric growth.

The velum may be a rudiment of a swimmingbrim of the type present in the Pelagothuriidae. This view is supported by the presence of a similar brim (composed of dorsal and lateral papillae) in *Psychrelpidia*, a genus which both in the structure of the calcareous ring and the presence of 10 tentacles agrees with the Elpidiidae.

Thus, the absence in *Elpidia* of every trace of a velum is as remarkable as the presence of a unique type of spicule in the same genus. Nevertheless, the fact that *Elpidia* has a specialized calcareous ring similar to that of the velum-bearing genus *Irpa* indicates that the absence of a velum is also in *Elpidia* a secondary feature.

(4) Circum-oral papillae. A ring of often inconspicuous papillae surrounds the tentacle crown in *Deima*, *Benthogone*, and *Benthodytes*. Its (at least partial) presence has been established for all the species, except *Benthodytes superba*.

Circum-oral papillae have not been found outside these three genera. *Ilyodaemon abstrusus*, which also has circum-oral papillae, is here transferred to *Benthogone*, with which it agrees also in the simply shaped wheels and the high tentacle number.

Only one species of *Benthodytes (B. lingua)* was previously known to possess circum-oral papillae. Post-oral papillae were, however, known from a number of species. The present study confirmed that *B. sanguinolenta* has only post-oral

papillae. In all other species the observed postoral papillae probably form part of a complete ring.

A contractile oral membrane is known to accompany the ring of circum-oral papillae in *Deima validum, Benthogone rosea, Benthodytes incerta, B. lingua, and B. typica.* The membrane is inserted on the internal side of the ring of papillae and may be narrowed to a small opening through contraction of a sphincter muscle, thus covering the whole of the tentacle crown. As the membrane is visible only when somewhat contracted, it may be present in all species with circum-oral papillae.

The presence of circum-oral papillae together with a sphincter muscle is a remarkable similarity between these genera which belong to three different families.

#### The tentacles

The tentacles show a variation of taxonomic significance both in number and shape.

(1) Number. The Deimatidae, Laetmogonidae, and Psychropotidae all show a variation of 15-20 tentacles. The whole variation in number may be found within one and the same species (Orphnurgus glaber, Benthogone rosea, Benthodytes typica), but usually the number is species constant. Similarity in number may reflect taxonomic relationship.

All laetmogonids with 15 tentacles belong to *Laetmogone*, in which there are only two exceptions to this number: *L. theeli* (20) and *L. interjacens* (15–17). The latter resembles *Benthogone* (with 15–20 tentacles) also in body form and in the shape of the deposits.

A constant number of 15 tentacles is in *Bentho*dytes combined with the presence of cross-shaped deposits with a bipartite apophysis. Higher tentacle numbers are found in the two species with reduced rod-shaped deposits, *B. typica* (15–20) and *B. sanguinolenta* (18).

The species of *Psychropotes* have 16 tentacles, except *P. depressa* and *P. longicauda*, both with 18 tentacles. The closely related genus, *Psycheotrephes*, has similar tentacle numbers: *P. magna* (16–18) and *P. recta* (16).

Juvenile tentacle numbers are found in two species of Psychropotidae: Psychropotes loveni (10-12) and Psycheotrephes exigua (10). Both species were erected on small-sized specimens, which may not have attained the full tentacle number of the species. Specimens of *Psychropotes depressa* (1.7–12.0 cm long) showed an increase in tentacle number from 10 to 18 (Fig. 44). A similar increase was found in *P. longicauda*.

A juvenile tentacle number characterizes the whole family Elpidiidae. The only exceptions to the number of 10 tentacles are provided by the genus *Achlyonice* (10–12) and the species *Peniagone islandica* (8).

(2) Shape. Differences in the shape of the tentacle discs are probably correlated with different modes of food uptake (p. 196). Besides, they may reflect taxonomic relationship. But unfortunately the tentacle discs are often so contracted that their shape cannot be made out.

Deimatidae. In the present work, a generic importance has been attached to the two distinct types of tentacle in this family (p. 16). Deima and Oneirophanta have rounded tentacle discs with a smooth surface and with the margin smooth or provided with subglobular or digitiform processes (Pl. VIII: 1-3). Orphnurgus has tentacle discs with conspicuous papillae on the surface and branched (but contractile) processes on the margin (Pl. VIII: 5-7). The tentacles of the young of the brood-protecting subspecies Oneirophanta mutabilis affinis (Pl. VIII: 4) resemble those of the genus Orphnurgus.

Laetmogonidae. Although the tentacles show less conspicuous differences than in the Deimatidae, there seems to be some correlation between tentacle type and taxonomic affinity.

In Benthogone rosea and B. fragilis (Pl. VIII: 11) the discs are covered with conspicuous papillae arranged in radial fields which may proceed into marginal processes. Such processes are present in the Indian Ocean specimen of B. rosea from Galathea St. 241 and in B. fragilis from Galathea St. 324. In the examined Atlantic specimens of B. rosea the surface of the tentacle discs is likewise covered with conspicuous papillae, but the margin is more smooth, probably due to retraction of the processes.

In Laetmogone violacea (Pl. VIII: 8), L. wyvillethomsoni, and L. theeli the discs have a smooth surface and a smooth margin.

In L. maculata (Pl. VIII: 9–10), L. fimbriata, and L. biserialis the discs have a smooth surface (although often wrinkled due to contraction). The edge of the disc is smooth or irregularly lobated. The tentacles of *L. ijimai* probably show the same variation.

Pannychia and Apodogaster (the unidentified species from the Kermadec Trench) have tentacle discs with retractile papillae on the surface and well-developed marginal processes.

Psychropotidae. Psychropotes (Pl. VII: 6) and Psycheotrephes have rounded, vaulted discs with subglobular marginal knobs. The discs are of a fixed shape, and two species only (Psychropotes depressa and P. semperiana) show retractility of the discs into the tentacle stalk.

Benthodytes (Pl. IX: 1–7, Fig. 36) has large and flat discs which in all the species are retractile into the tentacle stalk. Species differences are present but difficult to make out because the tentacles are soft and changeable in shape. In addition to the retractility of the single tentacles, the whole crown can be concealed under a contractile oral membrane, present inside the circumoral ring of papillae (p. 191).

Young specimens of *Benthodytes* have more regularly shaped discs, reminiscent of those of *Psy*chropotes and *Psycheotrephes*.

Elpidiidae. *Elpidia* (Pl. X: 11–13) has not only a unique type of deposit but also of tentacle. The discs bear a number of marginal processes of which 1–3 aboral pairs are often extended to a great length.

Kolga (Pl. IX: 8) and Irpa have in common another characteristic type of tentacle with 5–7 marginal lobes, each divided into 3 lobuli.

A third type of tentacle, with a pair of lobes on the aboral margin of the discs, is found in a number of species of *Peniagone* (Pl. X: 1-5, 7-8), *Achlyonice* (Pl. X: 9), *Amperima, Ellipinion*, and *Scotoplanes* (Pl. IX: 9). The lobes are particularly long and slender in *Peniagone diaphana* (Pl. X: 7-8), whereas in other species (e. g. *Amperima naresi*, Pl. X: 6) they are barely distinguishable. The fact that the lobes are usually contractile (cf. the tentacles illustrated for *Peniagone azorica* and *P. convexa*) suggests that bilobed tentacle discs occur in even more species than known at present. However, some species (e. g. *Ellipinion galatheae*, Pl. X: 10) do not possess tentacles of this type.

## The alimentary canal

The Elasipoda, as usual in the holothurians, has a looped intestine consisting of three parts. A remarkable variation in the gross morphology is the highly distensible rectum, usually provided with a large caecum, in most of the elpidiid genera (*Amperima*, Ellipinion, Scotoplanes, Kolga, Elpidia, and Achlyonice).

The caecum is absent in the primitive genera *Psychrelpidia* and *Peniagone*. Of the specialized genera, only *Irpa* seems to have a small rectum devoid of a caecum. The state of the rectum is unknown in *Rhipidothuria*.

Ludwig (1889–1892) suggested that the caecum of the Elpidiidae is a rudiment of a respiratory tree. This view was opposed by Ekman (1926) who pointed out that the origin of the caecum from the ventral side of the rectum, as well as the fact that it is almost without exception stuffed with mud, contradicts such a derivation.

The absence of the caecum in the primitive genera of the family is a further indication that it is not a rudiment but an organ developed within this particular family. The species of the Elpidiidae are notable for their high buoyancy. Possibly, they are unable to keep to the sea floor without a considerable amount of bottom material stored in their intestinal canal. The function of the caecum may be that of increasing the volume of the intestinal canal and thereby the specific gravity of the animals.

#### The mesentery

As already noted by Théel (1882), the mesentery of the Elasipoda differs from that of other holothurians in having a dorsal attachment throughout its length. Ekman (1926) proved that this course of the mesentery was common to all five families of Elasipoda – the three parts of the mesentery being attached to the mid-dorsal, leftdorsal, and right-dorsal interradius, respectively. (Only posteriorly, the third part may have a ventral attachment).

In all other holothurians the three parts of the mesentery are attached to the mid-dorsal, leftdorsal, and right-ventral interradius, respectively. This even applies to the Apoda in which the intestine has almost completely lost its looping.

Ekman (1926) suggested that the dorsal attachment of the mesentery throughout its length serves to increase the oxygen supply to the intestine, which in the absence of respiratory trees is supplied with oxygen mainly from the dorsal body surface. Fig. 96. Oneirophanta mutabilis. Variation in the line of attachment of the mesentery (difference between full-drawn and dotted line) in four specimens from St. 654 (left) and four specimens from St. 716 (right). rd, right dorsal, ld, left dorsal, lv, left ventrolateral, mv, midventral, and rv, right ventrolateral longitudinal muscle.



However, the discovery of the peculiar walkingmechanism in the Elasipoda (p. 205) suggests another explanation of the dorsal attachment of the mesentery: An intestine resting upon the ventral body wall might interfere with the function of the intradermal pockets responsible for the protraction of the tubefeet.

Differences in the course of attachment of the mesentery on the body wall might, according to Ekman, distinguish genera and even species. Ekman illustrated the course in a number of species, but without stating number of specimens examined. The differences illustrated might, therefore, represent individual rather than specific differences.

In order to estimate the range of intraspecific variation in the course of the mesentery, four specimens of *Oneirophanta mutabilis* from St. 654 (Kermadec Trench) and four specimens from St. 716 (eastern Pacific) were examined (Fig. 96). At each station a remarkable variation was found. There was also a small, but possibly consistent difference between the specimens from the two stations.

The first part of the mesentery in all specimens from St. 654 ran in the dorsal midline throughout its length. In the specimens from St. 716 the first part of the mesentery started in the dorsal midline, then approached or even touched the right dorsal longitudinal muscle.

The second part of the mesentery in the St. 654 specimens, after having crossed the left dorsal muscle, either proceeded obliquely forwards towards the left ventral muscle, or followed the left dorsal muscle up to about half its length. In the St. 716 specimens the second part followed the left dorsal muscle from a little more than half, to about 3/4 its length.

The mesentery, after having crossed the left

ventral muscle, passed uninterruptedly across the ventral side of the body wall until it reached the right dorsal muscle. Ekman failed to find this part of the mesentery in *Oneirophanta mutabilis* and suggested that the absence distinguished the family Deimatidae from the Laetmogonidae. Actually, already Hérouard (1902, pp. 34–35) found that the genus *Deima* has an uninterrupted mesentery.

The third part of the mesentery was attached close to the right dorsal muscle for about half its length; then the attachment ran to the right ventral interradius close to the midventral muscle. The course of the third part showed only little variation in the examined *Galathea* specimens.

The mesentery formed a continuous membrane, except for the rectal part, which was disintegrated into single threads. The membrane was perforated throughout its length in the St. 654 specimens. In the St. 716 specimens the mesentery was unperforated, at least in its first part.

The variation in the course of the mesentery in O. mutabilis is almost the largest possible for a three-looped intestine with dorsal attachment of all three parts of the mesentery. In view of this large variation it is not advisable to introduce possible average specific or subspecific differences in the course of the mesentery into the taxonomy of the holothurians. Similarly, the great intraspecific variation in the degree of perforation of the mesentery shows that also this feature is of limited taxonomic value.

The disintegration of the mesentery of the Elpidiidae into single threads throughout its length, in contrast to the membranaceous mesentery in the four other families, remains as the only difference of taxonomic significance shown by the mesentery of the Elasipoda.

Heding (1935, pl. IX) illustrated the course of the mesentery in eleven species of Molpadonia, accepting Ekman's view on the significance of this feature in characterizing species. Ten species were illustrated by one drawing each, with no comments on the possible range of intraspecific variation. The variability in the course of the mesentery in the Elasipoda makes it unlikely that the differences illustrated by Heding are taxonomically valid.

## The external morphology of the gonads

The present chapter deals with the taxonomic significance of the external morphology of the gonads. The reproductive biology of the species is considered elsewhere (pp. 196–204).

Deimatidae (Pl. XI: 1-4). Each of the two gonads consists of a single cluster of unbranched, elongated sac-shaped tubules. By this feature the gonads differ from those of the other elasipod families.

The gonads are similar in the two sexes, except that the tubules are more numerous and slender in the males.

Deima validum has ovaries with 3-7 tubules and testes with 5-15 tubules on each side. Théel (1882) illustrated (for *D. fastosum*) testes with slender tubules possessing a number of globular distensions. Such tubules were not present in any of the *Galathea* specimens.

Oneirophanta mutabilis. The ovaries showed the following variation in number of tubules on each side: Western Indian Ocean (3 specimens), 3-5; Kermadec Trench, Sts. 663 and 664 (4 specimens), 3-5; Kermadec Trench, St. 654 (5 specimens), 5-13; eastern Pacific, St. 716 (11 specimens), 2-4.

Théel (1882) found the variation in number of ovarian tubules to be 3–9 on each side (numbers not specified for each locality).

The testes were examined in one specimen from St. 192, six from St. 654, and 12 from St. 716. At Sts. 192 and 716 the testes consisted of two clusters of numerous slender tubules, usually somewhat dilated at the end. This type was also reported from the *Challenger* specimens.

In the specimens from St. 654 the testes were similar to the ovaries in external morphology. The tubules were thick and few in number (7–10 on each side in specimens 6.0–9.5 cm long, and 4 in a 5.0 cm long specimen). There were no males among the specimens from the two other Kermadec Trench stations.

The gonads in Oneirophanta setigera and Orphnurgus glaber agreed in morphology with those of Deima validum and Oneirophanta mutabilis.

Laetmogonidae (Pl. XI: 9–12). The gonads consist on each side of one or more clusters of branched tubules and thus differ distinctly from the gonads of the Deimatidae. There is also some intra-family variation in the morphology. However, too few species were examined to permit a demonstration of generic or specific differences.

Psychropotidae (Pl. XII: 1-9). The cross-bearing species of Benthodytes have ovaries with a few groups of large and feebly subdivided lobes placed along an undivided duct on each side. B. sanguinolenta and B. typica, which also in other respects stand apart in the genus, have branched ovaries with follicles opening directly into the ducts. Psycheotrephes magna and Psychropotes longicauda have ovaries with a few large, rounded or somewhat elongated sacs opening into an undivided duct on each side. In Psychropotes depressa the sacs are smaller, more numerous, and closely set - the ovary attaining the shape of a corncob. In P. verrucosa, P. belyaevi, and P. semperiana the corncob-shaped fertile part of the ovary is very thick and covered with small, closely set lobules. The ovaries of the Psychropotidae contain the largest eggs known in holothurians (pp. 202-203).

The testes consist of groups of tubules opening into a common duct on each side. The length of the testes may vary within a species. However, the extreme length in *B. sanguinolenta* is probably a specific character.

Elpidiidae (Pl. XII: 10–11). The paired gonads in *Psychrelpidia* and *Peniagone*, in contrast to the unpaired gonads in the other genera (unknown only in *Rhipidothuria*), is one of the features pointing to an original position of these two genera within the family.

The unpaired gonad is probably always the left one. (Due to a strong reduction of the dorsal mesentery its position cannot always be established).

The gonads usually consist of clusters of tubules opening into a duct of varying length. A deviating type is found in the two closely related genera *Kolga* and *Irpa*, in which the gonads consist of a ramified duct ending in long and slender fertile tubules.

In agreement with the small size attained by the eggs, the ovaries resemble the testes in external morphology.

#### Conclusion

The present investigation confirmed the view that the calcareous deposits generally provide the best taxonomic characters. Higher categories such as the suborder Psychropotina and the family Laetmogonidae within the suborder Deimatina are characterized, in particular, by their deposit type. Differences between species are often most clearly shown by their deposits, although different species may have identical deposits. The intraspecific variation is often great, and in many species a geographic and local variation can be distinguished.

Differences in number, shape, and arrangement of tubefeet and papillae may similarly distinguish families, genera, species, and intraspecific categories. For the analysis of intraspecific variation numerical differences are especially important, as this type of variation is generally quantitative rather than qualitative in character. Numerical characters in holothurians are practically only provided by the number of ambulacral appendages and by the spoke number in the wheel-shaped deposits.

The number and shape of the tentacles may distinguish genera and species groups within genera, but are generally of little value in characterizing species. A juvenile tentacle number (10-12) distinguishes the Elpidiidae.

Differences in body shape, including breadth of lateral brim and shape and size of velum, depend on the degree of contraction and state of preservation and should, therefore, be used with reservation in species distinctions.

A highly distensible rectum with a caecum is found in most genera of Elpidiidae. The absence of the caecum in the primitive genera *Psychrelpidia* and *Peniagone* suggests that the caecum is a specialized feature developed in this family. The caecum may serve to increase the specific gravity of these extremely buoyant animals, thus preventing them from being swept from the bottom.

The dorsal attachment of the whole mesentery characterizes the order Elasipoda. Differences in

the course of the mesentery within the Elasipoda are without taxonomic significance.

The external morphology of the gonads may be characteristic of groups of species, and even of a family (Deimatidae). However, their different appearance according to the degree of ripeness makes the demonstration of species differences doubtful.

## **B. BIOLOGY**

#### Feeding

The increasing dominance of the holothurians with depth is accounted for by deposit-feeding forms. The filter-feeding order, Dendrochirota, is almost entirely absent in the deep sea. The faculty of the holothurians of ingesting large amounts of sediment, combined with their low food requirements due to their low content of organic matter, makes this group well fitted for subsisting on the nutrient-poor deep-sea sediments.

The majority of the deep-sea holothurians seem to spend their life upon the surface of the bottom, and not buried within it. This is suggested by their ventrally turned tentacle crown and their flattened ventrum, and it has in recent time been confirmed by deep-sea photography. The surface-dwelling holothurians include probably the whole order Elasipoda, most of the Synallactidae, and *Hadalothuria*, the only hadal representative of the order Molpadonia. *Hadalothuria*, which differs from other Molpadonia in having a ventrally turned tentacle crown, has been photographed crawling on the bottom (Lemche *et al.* in press).

A surface-dwelling habit seems to offer a particular advantage in the deep sea where the nutrients are present as a thin surface layer of the sediments and where it may be necessary to cover a large area in search of food. Life upon the surface is favoured by the scarcity of carnivores, in particular of fishes. The latter are likely to represent the chief potential enemies of holothurians.

The highest degree of adaptation for feeding on large amounts of sediment is reached by the Elpidiidae. Many of these have the lowest content of organic matter in all echinoderms and their alimentary canal is often excessively developed. Their enormous dominance in the trenches is in agreement with the large supply of sediments to this environment. It is interesting that one of the dominating hadal species, *Scotoplanes* globosa (or its close relative, *S. clarki*) is also abundant in the much shallower San Diego Trough (depth 930–1420 m) where similar sedimentary conditions prevail. This trough receives large amounts of sediment through the canyons transecting the southern California continental borderland. Bathyscaphe observations (Barham *et al.* 1967) showed that *Scotoplanes* was particularly abundant (up to  $15/m^2$ ) at the base of the canyons where sediments accumulated.

There is also evidence that the dominance of *Elpidia* at hadal depths is conditioned by a rich supply of sediments (p. 173).

Sokolova (1958) pointed out that differences in the shape of the tentacle discs are likely to be correlated with a different degree of selectivity in food uptake – tentacles with well-developed marginal processes on the discs (e. g. *Elpidia*) being able to pick up single food particles from the bottom, while tentacles with more undifferentiated discs (e. g. *Psychropotes*) convey the surface layer of the sediment indiscriminately to the mouth. Differences in type of intestinal content correlated with the different types of tentacle were, however, not demonstrated.

Samples of the content of the anteriormost part of the gut in 16 species of Elasipoda from the *Galathea* (belonging to all four benthic families and representing the different types of tentacle found in the order) likewise failed to reveal any correlation between tentacle type and type of intestinal content. The intestinal content was mostly fine-grained and undeterminable, except for scattered foraminiferan shells. There was no indication that the Elasipoda are able to select smaller animals, e. g. small crustaceans or molluscs.

A selectivity in food uptake is suggested not only by the different shape of the tentacles, but also by the different degree of filling of the intestine in species living on the same type of sediment. Thus, in *Amperima naresi, Scotoplanes* globosa, and S. clarki the intestine was so stuffed with bottom material that it occupied the entire coelomic cavity, while in *Elpidia glacialis* (taken simultaneously with the two former species) the intestine was much less filled. This suggests a higher nutritive value of the material ingested by *E. glacialis*, which is in agreement with the fact that its tentacles are more specialized than those of the other species mentioned. The tentacles of *Elpidia*, with their long digitiform processes, may be capable of selective feeding, for instance by avoiding the ingestion of larger particles devoid of nutritive value. On the other hand, the supposed differences in the nutritive value of the ingested sediment may also be due to the *Elpidia* specimens grazing on patches on the sea floor with an especially rich flora of bacteria (Lemche *et al.* in press).

#### Reproduction

#### 1. Introductory remarks.

The taxonomic significance of the variation in external morphology of the gonads is considered elsewhere (pp. 194–195). The present chapter deals with the reproductive biology of the species, with special regard to the following aspects:

(1) Developmental types, as indicated by the egg size. Very little direct information is available on the type of larval development in deep-sea animals. Mortensen (1921) reared pelagic larvae from specimens of the echinoid *Laganum diplopora* taken at a depth of 800 m off Japan. He maintained (without stating the egg diameter) that "judging from the character of the eggs, many other deep-sea forms must have pelagic larvae" (l. c., p. 249).

As hardly any direct observations exist, conclusions regarding developmental types have to be made from the egg diameter attained. Thorson (1952) found that in littoral-sublittoral echinoderms eggs measuring 0.04–0.15 mm yield planktotrophic larvae, whereas eggs measuring 0.18–1.00 mm yield lecitotrophic larvae. Eggs of intermediate size lead to either of the two types, or to a combination of both.

Schoener (1972) compared the number and size of the eggs in five species of deep-sea ophiuroids with those of shallow water species with known type of development. One *Ophiura ljungmani* (depth 2178 m) contained 93000 eggs, with a maximum diameter of 0.08 mm. According to Schoener, both number and size indicate that the species has pelagic larvae. The reproductive habits of the other four species were less certain.

A lecitotrophic development does not exclude the possibility of a planktonic stage. Thus, the larva of *Psolus phantapus*, emerging from 0.59 mm large eggs, has been taken in the plankton (Thorson 1946). Ockelmann (1965) similarly demonstrated the presence of three types of larval development in marine bivalves, each type corresponding to a definite interval in egg size: 1) planktotrophic development (egg size 0.040–0.085 mm); 2) lecitotrophic development with a short pelagic stage which is independent of food uptake from the plankton (egg size 0.09–0.14 mm); 3) direct development, often combined with brood protection (egg size 0.15–0.20 mm).

The second type of development predominates among the bivalves of the deep sea (Ockelmann 1965, Knudsen 1970). A direct development seems to be rare, and brood protection even more so.

(2) Histology of the gonads in relation to sexual phase. Histological changes in the gonads in connection with the sexual cycle have been described in detail for various sublittoral species of echinoids and asteroids.

Giard (1877) observed, in the gonads of sea urchins, a peculiar type of large nutritive cells proliferating into the lumen of the gonads after spawning. Each cell contained a large vacuole (erroneously interpreted as a hypertrophied nucleus) and a number of small cytoplasmic globules of reserve which were later utilized by the growing gametocytes.

Caullery & Siedlecki (1903) and Caullery (1925) found that not only did these vacuolated cells perform a nutritive function, but they were also phagocytic, ingesting the eggs and sperm which remain in the gonads after each spawning.

The nutritive-phagocytic cells have subsequently been demonstrated in many species of echinoids and may be universally present in this class. Holland & Giese (1965), by means of an autoradiographic technique, examined the histological changes in the gonads of *Strongylocentrotus purpuratus*, including the functional relations of the nutritive phagocytes.

The nutritive phagocytes, after proliferation into the lumen of the empty gonads, increase in size due to the development of a large vacuole and the accumulation of cytoplasmic globules of reserve. Concurrently with the transfer of nutrients from the cytoplasmic globules to the sexual cells, the nutritive phagocytes shrink, although their vacuoles are usually retained. The tissue in the deglobulated phase has a net-like appearance although it probably still consists of individual, vacuolated cells.

Nutritive phagocytes are also commonly pres-

ent in the gonads of asteroids (Cognetti & Delavault 1962). However, in some species they appear to be absent, their nutritive function being taken over by nutrients stored in the pyloric caeca (Pearse 1965, Mauzey 1966).

Seasonal changes in the gonads of the holothurian *Stichopus japonicus* were described by Tanaka (1958). Although no mention was made of a nutritive-phagocytic tissue, its presence is indicated in a photograph of the ovary in the "recovery stage" (1. c., pl. I: 2).

(3) Reproductive periodicity. This cannot be conclusively demonstrated without samples from one locality throughout the year. The materials collected by the various deep-sea expeditions are, therefore, not well suited for such an examination, and it is not surprising that little information on this subject can be gathered from the literature.

In a population of the sea urchin Allocentrotus fragilis, from c. 150 m depth, Boolootian et al. (1959) demonstrated a distinct breeding-cycle, probably correlated with planktonic larvae utilizing a phytoplankton bloom. This species occurs down to 840 m, but it is not known whether the reproductive periodicity applies to the whole depth range of the species.

Madsen (1961b) stated that, although variations in the annual food supply to the bottom might induce a rhythmic spawning in deep-sea animals, there was still nothing to indicate that this really takes place. An examination of the gonads of the Porcellanasteridae suggested that they produce eggs throughout the year.

Wolff (1962), on the other hand, in a material of North Atlantic bathyal and abyssal isopods, found that the large majority of the females had feebly developed brood sacs. The fact that the specimens were taken mainly during the summer season indicated that most of the species develop their young during the winter months. Wolff suggested that this periodicity of spawning was due to the origin of the North Atlantic deep-sea isopods from Arctic shallow water forms.

George & Menzies (1967) suspected a rhythmic spawning at bathyal and abyssal depths in three Antarctic species of the isopod genus *Storthyngura*. However, too few specimens were examined to permit reliable conclusions.

Schoener (1968) produced evidence for a winter spawning in two North Atlantic species of abyssal ophiurans. Samples taken during the winter contained adult specimens with well-developed gonads, while summer samples from the same locality contained adult specimens with feebly developed gonads together with juvenile specimens.

Sanders & Hessler (1969), on the other hand, found indications of a continuous reproduction throughout the year in the bivalve Nucula cancellata and in a species of the isopod genus Ilyarachna, both from bathyal depths in the North Atlantic.

## 2. The material examined.

The histology of the gonads was examined by means of sections of 23 specimens, belonging to 10 species of Deimatidae, Psychropotidae, and Elpidiidae. The purpose was a comparison with the conditions known from various shallow-water echinoderms (the gonadal histology of deep-sea echinoderms has not previously been examined). A large-scale examination of the histological changes in the gonads accompanying the different sexual phases has not been attempted. The results of such an examination would be of doubtful value in the absence of samples taken from the same population at different seasons. For the same reason, no measurements were made of the size distribution of the eggs in each ovary.

The maximum egg size was established in representatives of all the four benthic families of Elasipoda.

The results permit only few conclusions regarding the presence or absence of a reproductive periodicity. An aperiodic egg production is suggested where the maximum egg size varies conspicuously from one specimen to another. On the other hand, the presence of a reproductive periodicity cannot without further proof be concluded from the presence of eggs of maximum size in all the females of a population.

Deimatidae. The eggs reach a diameter of 0.8-0.9 mm in both *Deima validum* and *Oneirophanta mutabilis*. In *O. setigera* and *Orphnurgus glaber* the eggs measured up to 0.3 mm; but these eggs may not represent the maximum size in the species – the material comprising only two and one adult females, respectively.

Deima validum. Of the total of 19 specimens from the western Indian Ocean, 12 had empty gonads with thin and transparent walls. These specimens, 2.3–12.0 cm long, probably comprised juveniles, as well as adult males and females in an inactive sexual phase. In the remaining seven specimens eggs could be seen on external inspection of the ovaries. The eggs varied in maximum size from one specimen to another (Table 18).

Table 18. Deima validum. Maximum egg size in the egg-bearing females from the Indian Ocean.

Station	Length of specimens cm	Maximum egg size mm
190	5.0	0.1
193	8.0	0.8
217	5.0	0.4
234	6.0	0.1
_	11.0	0.6
235	9.0	0.4
279	5.0	0.1

In all these females the eggs were few and very spaced in position. While ovaries with eggs not exceeding 0.1 mm in diameter might be at the onset of a new sexual phase, ovaries with scattered eggs of larger size were probably at a post-spawning stage, with a few unspawned eggs remaining.

None of the gonads with sexual products were testes. Apparently, all the adult males were in an inactive sexual phase.

The fact that all the specimens from the western Indian Ocean were emptied of sexual products (with the exception of some relict ova in a few specimens) or were at the very beginning of egg development suggests a periodicity of spawning. The specimens were all taken during a relatively short period (3.II-10.IV).

Histological examination was made of the ovaries of four specimens with different maximum egg size: 0.1 mm (St. 234), 0.4 mm (St. 235), 0.6 mm (St. 234), and 0.8 mm (St. 193).

In the ovary with eggs up to 0.1 mm all the eggs were attached to the ovarian wall, being covered with the inner epithelium of the gonad. The lumen of the gonad was empty, except for the presence of inconspicuous patches of a reticular tissue, probably representing remnants of a nutritive-phagocytic tissue similar to that found in echinoid and asteroid gonads.

In the ovaries with eggs up to 0.4 and 0.6 mm (Pl. XIII: 1-2) some of the larger eggs were loose

in the lumen of the gonad. Most of them were necrotic, with the yolk more or less vacuolated and containing fine, basophilic grains, and with disintegrated nuclei. Many of these eggs were invaded by phagocytes either at their periphery, or throughout. The phagocytes had conspicuous, basophilic nuclei and a vacuolated cytoplasm. Patches of a reticular tissue were present in these gonads also.

In the ovary with eggs up to 0.8 mm there was practically no phagocytosis of eggs. Patches of a reticular tissue were present, especially at the distal end of the gonadal tube.

Deima validum thus agrees with the echinoids and most of the asteroids in the role played by the nutritive phagocytes. These cells first ingest the relict ova and afterwards change into a reticular tissue occupying part of the lumen of the gonad.

The lively phagocytosis of the eggs in two of the three ovaries with scattered large eggs confirms that these ovaries were in a post-spawning phase.

Oneirophanta mutabilis mutabilis. The 21 specimens examined comprised 12 females (4.0–10.0 cm long), all of which contained eggs (Table 19), 8 males (5.0–10.0 cm long), and one specimen (5.0 cm long) with feebly developed gonads, indeterminable to sex on external inspection.

Table	19.	Oneiroph	ianta	mutab <b>ili</b>	s mutabilis.
Maxi	mum	egg size i	n the	Galathea	specimens.

Station	Length of specimens cm	Maximum egg size mm
192	8.0	0.8
-	9.0	0.9
217	10.0	0.5
654	4.0	0.07
-	6.5	0.3
_	7.5	0.8
-	7.5	0.9
_	7.5	0.9
663	5.5	0.05
664	5.5	0.2
_	6.0	0.15
	7.0	0.5

Both in the western Indian Ocean and the Kermadec Trench the eggs reach a diameter of 0.9 mm. Sexual ripeness seems to be attained at a body size of 7.5 cm. While five of the six specimens measuring 7.5–10.0 cm had eggs up to 0.9 mm in diameter, the six specimens measuring 4.0–7.0 cm had eggs of smaller maximum size. The latter specimens show an increase in egg size with the size of the specimens, which confirms that they are developing their first batch of eggs.

In the ovaries with maximum egg size up to 0.2 mm the eggs were spaced in position on the ovarian wall. Ovaries with maximum egg size of 0.3 mm and more were usually completely filled with eggs.

The specimens of Oneirophanta mutabilis thus formed a marked contrast to those of Deima validum, in which only one out of eight females had eggs reaching the maximum size in the species and in which none of the ovaries were filled with eggs.

Histological examination was made of the ovary of the specimen from St. 192 in which the eggs measured up to 0.8 mm in diameter (Pl. XIII: 3). Eggs up to 0.4 mm in diameter were present on the ovarian wall. The basophilic egg membrane was strongly developed towards the ovarian wall, and very thin towards the lumen, where it was covered with the inner epithelium of the ovary. Some of the eggs were crowded with phagocytes. Assemblages of phagocytes, apparently from eggs with a disintegrated egg membrane, were seen, in some places, to pass gradually into the fine reticular tissue which filled a large part of the ovarian lumen.

Eggs of a larger size, and some of smaller size, were found loose in the lumen of the ovary. These eggs showed no sign of phagocytosis or disintegration.

Oneirophanta mutabilis affinis. A total of 27 specimens from St. 716, measuring 4.0-9.5 cm, were examined. Specimens larger than 5 cm could be determined to sex on external inspection of the gonads. There were 11 females and 12 males – both sexes ranging in size from 5.0 to 9.5 cm.

As stated previously (Hansen 1968) the specimens from this station are remarkable in having intra-ovarian brood protection.

The young ranged in size from 7 to 30 mm (Table 20). The largest young thus approached the size of the smallest free-living specimens (40 mm).

Mother	Young		
Length mm	Number	Length mm	
50	0	-	
55	0		
60	0	-	
70	6	7–8	
75	0		
75	2	30	
80	2	13–24	
85	4	16-19	
90	0	-	
90	8	15-19	
95	1	10	

Table 20. Oneirophanta mutabilis affinis. Number and size of young in the females from St. 716.

The ovaries with no young were small in size (even in the 75 mm long specimen the tubules were only up to 2 mm long). An exception was the 90 mm long empty specimen, in which the ovarian tubules were up to 20 mm long. This specimen was, probably, in a post-spawning phase, while the other empty specimens were juveniles which had not yet developed their first batch of young. It also differed from the other specimens by its large genital opening – a further indication that it had recently borne its young.

Very scattered eggs were present on the ovarian wall in all the specimens which did not contain any young. In the 90 mm long specimen the eggs were up to 0.2 mm in diameter, while in the other empty specimens they did not exceed 0.1 mm.

The fact that all the adult females had either large young in their ovaries, or had recently borne, suggests a reproductive periodicity at this locality. This was further supported by the histological examination of the gonads (see below). *Galathea* St. 716 was situated beneath the Costa Rica Dome where an intense upwelling takes place from December to May (Smith 1968). The specimens were taken at the end of the upwelling season (on May 6), which indicates that the development of the young is correlated with a period of a rich production in the surface plankton.

The young in their first stages possibly eat up the undeveloping eggs. But since no eggs were found in the examined young-containing ovaries the young before they are 7 mm long apparently change to nutrients secreted into the ovary. The young are not in any way attached to the ovarian wall.

Usually, only one young is present in each sac. However, in the female with eight young, five were contained in the same sac. In all the ovaries some sacs are empty. The young in each ovary are usually rather equal in size, which indicates that they all derive from one fertilization.

Histological examination was made of five ovaries and one testis.

In the 9.0 cm long female with empty ovaries the ovarian wall showed conspicuous proliferations of large, highly vacuolated cells with clearly defined nuclei and distinct cell boundaries (Pl. XIII: 4–5). The vacuolated tissue in some places passed gradually into the connective tissue of the ovarian wall; in other places it was separated from the connective tissue by a distinct boundary. Apparently, the vacuolated cells proliferate from limited places and spread from there over the remaining part of the ovarian wall. The proliferations are covered with the uninterrupted inner epithelium of the ovary.

The extremely scattered eggs were situated between the vacuolated tissue and the inner epithelium. They measured up to 0.2 mm in diameter. The basophilic egg membrane was strongly developed towards the underlying vacuolated tissue. Most of the larger eggs were invaded by phagocytes with a vacuolated cytoplasm; these cells are probably identical with the vacuolated cells of the ovarian wall. There was almost no trace of the fine reticular tissue which was well developed in the specimen of *Oneirophanta m. mutabilis* from St. 192.

The lively phagocytosis of the eggs indicates that the eggs did not belong to a new batch.

In the specimen with young measuring 7–8 mm the ovarian wall likewise showed proliferations of vacuolated tissue (Pl. XIII: 6). However, the cells had to some degree disintegrated, their vacuoli being ruptured. Some of the proliferations had almost completely collapsed; their epithelium, however, was uninterrupted. Most of the few eggs remaining were invaded by phagocytes (the two eggs seen in the photograph are not). The reticular tissue had completely disappeared from the lumen of the ovary.

In the 8.5 cm long specimen with young 16–19 mm long the proliferations had almost completely collapsed and contained practically no vacuolated tissue (Pl. XIII: 7). Phagocytes were present in the very few eggs remaining.

The 6.0 cm long specimen with empty ovaries showed well-developed proliferations. As in the specimen with the smallest young the vacuolated cells of the proliferations had somewhat disintegrated, but none of the proliferations had collapsed.

In the 5.5 cm long female the ovarian wall showed no proliferations of vacuolated tissue.

The vacuolated tissue probably acts as a store which provides nutrients for the growing embryos. It develops shortly after spawning and collapses with the growth of the young. The fact that the proliferations had completely collapsed already in the sections of the ovary with 16–19 mm long embryos does not exclude the possibility that they are still present in other parts of the ovary.

The presence of proliferations with somewhat disintegrated vacuolated cells in the 6.0 cm long female suggests that this specimen was prepared for the development of a batch of young, but had failed to carry it through because of its small size.

Histological sections of a 9.0 cm long male showed testicular tissue in the process of phagocytosis (Pl. XIII: 8–9). Ingested heads of spermatozoa were present in the cytoplasm of many of the vacuolated phagocytes, but no free spermatozoa were present. Thus, also the testes appeared to be in a post-spawning phase.

The developmental stages of the young. The presence of a gradual series of young ranging from 7 to 30 mm in length makes it possible to follow the development of the different features. Already the smallest young possess all types of ambulacral appendages.

Tentacles. Of the six smallest young (7–8 mm long) three possessed 5 tentacles, while the other three possessed 2, 3, and 4 tentacles, with small rudiments of additional ones. The 16–19 mm long young had 5–8 tentacles, whereas the young measuring 24 and 30 mm had 10. Since even the smallest free-living specimens had 20 tentacles, the increase in number from 10 to 20 takes place at a body size of 30–40 mm.

The discs of the tentacles (Pl. VIII: 4) are different in structure from those of adult specimens, having papillae on the surface and incisions on the margin. The tentacles probably function as soon as they are formed, taking up nutrient matter secreted from the ovarian wall. This may explain their different structure. Tubefeet. All the young possessed tubefeet throughout the length of the three ventral radii. Even in the smallest young at least some were provided with sucking-discs. The smallest young had about 5 midventral and 5 pairs of ventrolateral tubefeet. The largest young had about 8 midventral and 14 pairs of ventrolateral tubefeet.

Papillae. Both lateral and dorsal papillae increased in number from about 5 pairs of each in the smallest to 7 pairs in the largest young. While the smallest young had low conical papillae, the two 30 mm long ones had papillae as long as in adult specimens.

Deposits. The two 30 mm long young possessed irregularly branched, delicate rods in the skin. They represent the deeper-lying ramified spicules of adult specimens; the outer, reticulated plates which form a strong armour of the skin in adult specimens had not yet started their formation. (The plates are fully formed in 40 mm long freeliving specimens). Strong rods with somewhat irregular terminal ramifications were present in the tubefeet and papillae.

The young smaller than 30 mm lacked deposits altogether.

Intestine forming a straight tube in the 7–8 mm long young, but already at a size of 16 mm the intestinal loop begins its formation.

Although young have not been found in any specimen of *Oneirophanta m. mutabilis*, there are two features suggesting that brood protection occurs also in this subspecies. Firstly, the minimum size was 3.5 cm both in the *Challenger*, *Galathea*, and *Eltanin* specimens, and smaller specimens have not been recorded from any expedition. Secondly, the subspecies has apparently unusually limited means of dispersal, as evidenced by the pronounced local variation at St. 654 in the Kermadec Trench.

Laetmogonidae. Conspicuous differences in egg size are found in this family, which indicates that different types of larval development are represented.

Laetmogone violacea. The material from Mi-chael Sars St. 76 consisted of 18 females (3.5–12.0 cm long), 16 males (4.0–13.5 cm long), and five juveniles (2.2–3.5 cm long) which could not be determined to sex on external inspection of the gonads. The maximum egg size in relation to body size was examined in the 18 females (Fig.



Fig. 97. Laetmogone violacea. Maximum egg diameter in relation to body length in 18 specimens from Michael Sars St. 76.

97). The growth of the oocytes appears to start at a body length of 5 cm, and already at a body length of 6 cm some of the eggs may have attained the full size of 0.4 mm. Examination of 17 females from other North Atlantic localities confirmed that the maximum egg size in the species is 0.4 mm. The material did not permit conclusions regarding the presence or absence of a reproductive periodicity.

Laetmogone maculata. The specimens from Valdivia St. 202 comprised five females and three males; both sexes ranged in size from 6 to 9 cm. A maximum egg size of 0.15 mm was found both in these specimens and in a specimen from off Tasmania.

Laetmogone fimbriata. A 1.8 cm long female taken off Durban had eggs up to 0.19 mm. Two other examined females had eggs of smaller maximum size.

Benthogone rosea. Of nine examined North Atlantic females (8–16 cm long) two had eggs up to 0.9 mm in diameter, and five had eggs up to 0.7–0.8 mm. The size of 0.9 mm probably represents the full size. This size was attained already in an 8 cm long female.

Pannychia moseleyi. Two examined females (fragmentary) had eggs up to 0.4 and 0.8 mm.

The results indicate a correlation between egg size and depth occurrence:

Laetmogone maculata, 0.15 mm in females from 141–293 m (total depth range 141–732 m).

L. fimbriata, 0.19 mm in a female from 412 m (total depth range 164–1300 m).

L. violacea, 0.4 mm in females from 256–1300 m (total depth range 256–1804 m).

Pannychia moseleyi, 0.8 mm in a female from 915–975 m (total depth range 212–2598 m).

Benthogone rosea, 0.9 mm in females from 2480 m (total depth range 1103-2480 m).

The material does not permit conclusions regarding a possible intraspecific correlation between egg size and depth occurrence. In L. *violacea* the eggs reached the same size in specimens from 256 m and 1300 m; the maximum egg size is not known in specimens from the deeper part of the depth range (1300–1804 m).

Psychropotidae. A very large egg size is characteristic of this family.

Benthodytes typica. The maximum egg size was ascertained for 35 females taken by the Galathea (Table 21).

Station	Length of specimens cm	Maximum egg size mm
186	7	1.6
_	8	0.6
192	7	2.1
217	6	0.4
_	6	0.4
_	6	1.1
-	7	1.6
-	7	0.6
-	7	1.7
-	8	0.3
-	8	1.5
-	8	2.1
-	8	1.6
_	9	0.6
~	9	0.6
~	9	0.2
~	9	1.8
	10	1.9
281	9	0.5
299	5	0.2
-	6	0.4
	6	0.6
~	7	0.1
	7	0.3
-	7	1.7
-	8	0.1
-	8	0.4
~	8	0.2
575	7	1.5
-	7	1.6
-	7	2.2
	8	2.6
-	9	3.0
-	9	1.9
· -	9	2.0

Table 21. Benthodytes typica. Maximum egg size in 35 Galathea specimens.

It is remarkable that all the specimens from St. 575 (Tasman Sea) have eggs of large size, while the specimens from St. 299 (Bay of Bengal) have small eggs, with the exception of one specimen with eggs up to 1.7 mm in diameter. This conspicuous difference in egg size may be due to a periodicity of spawning at these two localities. On the other hand, the great variation in maximum egg size at St. 217 (western Indian Ocean) is more consistent with an aperiodic egg production.

The maximum egg size found in the other species of *Benthodytes* is: *B. incerta*, 1.7 mm (seven females examined); *B. lingua*, 2.0 mm (seven females examined); *B. sibogae*, 1.9 mm (four females examined); *B. sanguinolenta*, 2.2 mm (in Ludwig's specimens).

Psycheotrephes exigua. Maximum egg size in three females from the Galathea: St. 234 (10 cm long), 0.4 mm; St. 234 (28 cm long), 3.6 mm; St. 663 (30 cm long), 3.7 mm.

Psychropotes longicauda. The distribution of the maximum egg size in the 24 females from the

Table	22.	Psych	ropotes	longica	uda.	Maximum
	egg	size in	the Ga	<i>lathea</i> sp	ecim	ens.

Station	Length of specimens cm	Maximum egg size mm
234	12	0.6
_	13	0.4
235	15	0.5
-	18	2.5
601	14	1.0
_	18	3.0
663	6	0.3
-	10	0.5
_	11	0.3
_	14	0.5
-	16	0.9
_	19	4.0
-	20	4.4
-	23	3.9
664	9	1.8
_	13	0.8
-	15	1.0
_	16	2.5
-	17	0.2
_	17	1.1
	18	0.4
_	18	4.1
-	19	4.0
716	21	0.7
		1

Galathea indicates that sexual ripeness is attained at a body length (exclusive of the tail) of about 18 cm (Table 22).

The maximum egg size found in the species of *Psychropotes* with corncob-shaped ovaries is: *P. belyaevi*, 3.6 mm (five females examined); *P. verrucosa*, 3.0 mm (three females examined); *P. depressa*, 1.9 mm (six females examined); *P. semperiana*, 0.5 mm (four females examined).

The eggs of the Psychropotidae are much larger than those of other echinoderms. In bulk, the eggs of *Psychropotes longicauda* (diam. 4.4 mm) surpass those of the hitherto largest known eggs of echinoderms (diam. 1.0 mm) by 85 times.

The fact that a 3.2 cm long specimen of *P.* longicauda was taken in a pelagic net (pp. 124-125) suggests that the enormous egg size in the Psychropotidae is an adaptation which ensures a long pelagic development independent of food uptake from the plankton – thus an adaptation to life in the nutrient-poor deep sea.

A correlation between egg size and depth occurrence is indicated in this family also. Eggs measuring 3–4 mm in diameter were found in the most pronouncedly abyssal species, while eggs of 1.7–2.2 mm were found in the bathyal and bathyal-abyssal species.

Histological examination was made of the ovaries of four specimens, belonging to Psychropotes depressa, P. semperiana, P. belyaevi, and Benthodytes typica.

The wall of the ovary in the three species of Psychropotes consists of a thick layer of highly vacuolated cells. Scattered in this vacuolated tissue are cells with a strongly basophilic nucleus and a cytoplasm stuffed with eosinophilic globules. In the sections of the ovary of P. depressa (Pl. XIV: 1-2) the globulated cells were represented by different stages. In most of them the cytoplasm formed a thin layer around the nucleus, but in others the cytoplasm had increased in bulk, and the nucleus had become eccentric in position. The latter cells were especially abundant near and within eggs under disintegration. At a later stage, vacuoli arise in the cytoplasm, while the globules disappear. The cells in this vacuolated and deglobulated state are probably identical with the vacuolated cells of the ovarian wall, the two cell types representing two phases of the nutritive-phagocytic tissue.

The sections from *P. semperiana* and *P. belyaevi* (Pl. XIV: 3-5) showed a vacuolated tissue inter-

spersed with cells with eosinophilic globules; most of the latter cells had a well-developed cytoplasm. There were no transitional stages between the globulated cells and the vacuolated cells of the ovarian wall, and there were no eggs under disintegration.

In *P. belyaevi* the greater part of the vacuolated tissue had undergone some disintegration, resembling that of the vacuolated tissue accompanying the development of the young in *Oneirophanta mutabilis affinis*.

The abundant development of the vacuolated, nutritive tissue probably forms the basis of the enormous size reached by the eggs in these species.

The sectioned ovary of *Benthodytes typica* showed only a feebly developed nutritive-phagocytic tissue.

Elpidiidae. A maximum egg size of about 0.2 mm was found in *Elpidia glacialis* (both in the Kermadec Trench and in the Baffin Bay), *Scotoplanes globosa, S. clarki, Amperima naresi,* and *Peniagone azorica.* The small diameter of the ovarian tubules indicates that this egg size is not appreciably surpassed in other elpidiids.

Although the eggs are much smaller than those of the other families of benthic Elasipoda, they are still so large that a lecitotrophic development is to be expected.

## 3. Conclusion.

The egg size varies greatly within the Elasipoda, but even the smallest eggs probably produce lecitotrophic larvae. Conspicuous differences in egg size are present between the families: Deimatidae, (0.3–)0.9 mm; Laetmogonidae, 0.15–0.9 mm; Psychropotidae, 1.7–4.4 mm; Elpidiidae, 0.2 mm. In Laetmogonidae and Psychropotidae a correlation was found between egg size and depth occurrence. The eggs of the Psychropotidae, which in bulk surpass the largest hitherto known echinoderm eggs by up to 85 times, may enable the juveniles to spend a long pelagic life independent of food uptake from the plankton.

Brood protection was found in a population of *Oneirophanta mutabilis affinis* at 3570 m off the Pacific coast of Costa Rica. The intra-ovarian development of the young apparently takes place during a period of rich phytoplankton production.

Another example of reproductive periodicity

may be provided by the abyssal populations of *Deima validum validum* in the western Indian Ocean.

Histological examination of the gonads in members of the Deimatidae and Psychropotidae showed various stages of a nutritive-phagocytic tissue resembling that known from the gonads of sublittoral species of echinoids and many asteroids. The cells of this tissue ingest the ova and sperm which remain after a spawning. In the nutritive phase the cells are highly vacuolated. The nutritive tissue is abundantly developed in species of *Psychropotes* with eggs of giant size, and in the brood-protecting *Oneirophanta m. affinis*.

Hermaphroditic specimens have not been found, and neither was there any indication of a change of sex.

#### Swimming and floating

A power of swimming by means of undulatory movements of the body probably exists in many psychropotids and aspidochirotes. Michael Sars (1868, 1877) observed it in specimens of the synallactid *Bathyplotes natans* taken at a depth of 400 m off Lofoten. Pawson (1966) referred to a similar observation on the Caribbean stichopodid *Astichopus multifidus*. Gilchrist (1920, p. 381) mentioned that holothurians (unidentified) from deep water off the South African coasts had been seen swimming after capture.

A photograph of a holothurian (possibly *Psychropotes depressa*) swimming over the bottom at a depth of 1930 m off Baja California was published by Arrhenius (1963). The specimen is seen to eject intestinal content through the anus.

Hansen & Madsen (1956) reported the catch of the synallactid Galatheathuria aspera in the South China Sea at least 700 m above the bottom. The species in external appearance is reminiscent of the cuttlefish Sepia, having a compact, lenseshaped body surrounded by a brim. Possibly, Galatheathuria also swims like a Sepia – by undulatory movements of the brim.

Östergren (1938) pointed out that most of the species of the Psychropotidae and some species of the synallactid genus *Paelopatides* are more darkly coloured ventrally than dorsally. Thus, the dark (in some species almost blackish) colour of the ventral side may conceal the swimming animal from enemies looking from below, while the lighter colour of the dorsal side may conceal it when seen on the background of the bottom. It is noteworthy that *Galatheathuria aspera*, which swims in the free water masses, is uniformly dark all over.

Juvenile stages of deep-sea holothurians have on a few occasions been caught in pelagic nets. This applies to a 13 mm long specimen of *Benthodytes typica* (p. 93), to specimens up to 30 mm long of *Peniagone diaphana* (pp. 154–155), and to a 32 mm long specimen of *Psychropotes longicauda* (pp. 124–125). The latter was by Belyaev & Vinogradov (1969) recorded as a new genus and species, *Nectothuria translucida*.

The four juveniles (9–10 mm long) of *Penia*gone (p. 155) taken in a bottom trawl west of New Zealand (St. 626, depth 610 m) are also likely to have been pelagic. This is indicated not only by the gelatinous and transparent state of the specimens, but also by the shallow depth, which is unusual for a member of this genus.

These pelagic juvenile specimens drift with the currents, sometimes at a great distance from the bottom. Their specific gravity is close to that of the water, and they have little power of active locomotion. They seem to be important to the dispersal of various bathyal and abyssal species of Elasipoda (p. 238).

#### Function of the water-vascular dermal cavities

The ambulacral appendages of the Elasipoda are not, as in most other echinoderms, connected with water-vascular ampullae suspended in the coelomic fluid. In Elpidiidae, Deimatidae, and Laetmogonidae, the water-vascular canals of the tubefeet, and usually also of the papillae and the velum, communicate with large intradermal cavities (p. 190).

The intradermal ambulacral cavities were first described by Théel (1877) for *Elpidia glacialis*, and later (Théel 1882) for a considerable number of species of Elpidiidae, Deimatidae, and Laetmogonidae. Danielssen & Koren (1882) described them for *Kolga hyalina*. No descriptions are found in the subsequent literature.

The first attempt to explain the function of these peculiar ambulacral cavities was made by Östergren (1938), who suggested that they facilitate the passage of oxygen through the skin, thus compensating for the lack of respiratory trees in the Elasipoda.

Hansen (1972) pointed out that recent deep-sea photographs of Scotoplanes suggest another function of the cavities. Walking specimens of Scotoplanes show a series of transverse constrictions along the length of the body, indicating peristaltic movements of the muscles of the body wall. The peristaltic movements were supposed to press fluid from the dermal cavities into the tubefeet which are greatly extended during walking. Ampullae of the normal type do not seem to be adequate instruments for the protraction of the few and very large tubefeet characteristic of the Elasipoda. The replacement of the ampullae by dermal cavities permitted an increase in capacity, and at the same time made possible the application of the powerful muscles of the body wall in the protraction of the tubefeet.

During walking the tubefeet act as stilts which raise the body of these very buoyant animals from the substratum. Walking on stilt legs, known also from deep-sea crustaceans and pycnogonids, is apparently an adaptation to movement on the soft deep-sea bottom.

Deep-sea photography has also revealed the presence of body constrictions in walking specimens of *Peniagone* (Lemche *et al.* in press).

Only in soft-skinned forms like Scotoplanes and Peniagone the peristaltic movements of the circular musculature of the body wall are probably accompanied by externally visible constrictions of the skin. However, the cavities are equally well developed in forms with a rigid and armoured skin (Oneirophanta, Deima, Elpidia), which indicates that the muscles of the body wall here perform a similar strong pumping action. This is confirmed by photographs of specimens of Elpidia (Lemche et al. in press) in which the tubefeet show a considerable extension despite their strong armature of spicules.

The function of the ventral, intradermal cavities is likely to be facilitated by the entirely dorsal attachment of the alimentary canal (p. 193).

The velum is connected with similar intradermal cavities which may cause changes in its size and position. Deep-sea photographs (Lemche *et al.* in press) show that at least two species of *Peniagone* are able to bend the velar papillae over the head, reaching the bottom with their tips. One of the species (*P. purpurea*) has a flattened body with a velum consisting of two pairs of long, slender papillae; the papillae can be moved independently, searching the surrounding water, as well as the surface of the bottom. The other photographed species (probably *Peniagone azorica*) has a velum of normal shape and position. It is remarkable that also in this species the velum may reach the bottom in front of the animal, thus apparently performing a sensory function.

The long papillae of many deimatids and laetmogonids may perform a similar sensory function. However, as yet there is no photographic evidence of such a function.

In addition to the locomotory or sensory function, the ambulacral appendages may have a respiratory function, as they increase the surface area of the body. This function may be further facilitated by the rapid exchange of fluid in their water-vascular canals due to the pumping action of the ambulacral, dermal cavities.

## C. SYSTEMATICS, RELATIONSHIP, AND ADAPTATION

## Monophyletic origin

Elasipoda are usually easy to recognize due to their conspicuous and often strangely shaped ambulacral appendages and flat ventral sole bordered by large tubefeet, or by a brim of fused tubefeet.

Common to all Elasipoda are two anatomical features - the absence of respiratory trees and the dorsal attachment of the mesentery throughout its length. Two other features, although not common to all the five elasipod families, may be taken as a further indication of a monophyletic origin of the whole group. One feature is the occurrence in a number of elpidiid species of accessory wheel-shaped deposits of the type otherwise characteristic of laetmogonids. The other feature is the replacement in the Elpidiidae, Deimatidae, and Laetmogonidae of the tubefeet ampullae by intradermal ambulacral cavities - a unique feature in echinoderms. These similarities between Elpidiidae and Deimatidae-Laetmogonidae are remarkable, as the Elpidiidae are otherwise more closely related to Psychropotidae and Pelagothuriidae.

The presence of a ring of circum-oral papillae in one genus of each of the families Deimatidae (Deima), Laetmogonidae (Benthogone), and Psychropotidae (Benthodytes) also points to a common elasipod ancestor.

## **Evolutionary trends**

The Elasipoda seem at an early stage to have branched into two evolutionary lines, here proposed as the suborders Deimatina and Psychropotina.

In the following, the relationship between the two suborders and their families is discussed. The division of the families into genera is dealt with in the Systematic Part.

Deimatina, comprising the families Deimatidae and Laetmogonidae, is characterized by the large and generally numerous papillae, and by the ventral sole being bordered by large, separate tubefeet. While the two families cannot always be distinguished from each other by external features, they differ distinctly in the deposits and in the morphology of the gonads.

Deimatidae. The deposits are reticulated plates, which may change into spatulated crosses or rods, or into rounded or amorphous bodies. Wheelshaped deposits are absent.

The reticulated plates represent a primitive type of deposit. The type is especially characteristic of the Dendrochirota; within the Elasipoda the type is confined to the Deimatidae.

The different forms of the plates and their transformations are a poor guide to the evaluation of the affinities of the genera. The occurrence of two distinct types of tentacle, however, suggests that the family evolved along two lines, one (*Orphnurgus*) comprising bathyal, the other (*Deima*, *Oneirophanta*) primarily abyssal species.

The gonads consist of unbranched tubules (sacshaped in the females).

Laetmogonidae. The deposits are wheel-shaped in all the species. In addition, simple rods or (in *Laetmogone violacea*) spinous crosses occur.

The wheels are similar in type to those occurring scatteredly in the Elpidiidae, which suggests that also in Laetmogonidae they are persisting larval deposits. However, apart from the doubtful feature of the wheel-shaped deposits, the Laetmogonidae show no indication of retained larval features.

The gonads in both sexes consist of branched, slender tubules.

Psychropotina comprises the families Psychropotidae, Elpidiidae, and Pelagothuriidae. The close relationship between the families appears from the combination of features in the genus *Psychrelpidia*, and from the presence in the Psychropotidae and Elpidiidae of a deposit type which is unknown in other holothurians (p. 185). (Deposits are absent in the Pelagothuriidae).

Psychrelpidia has an anterior brim composed of dorsal and ventrolateral papillae - a similarity to Psychropotidae and Pelagothuriidae. As in Pelagothuriidae, the brim is clearly distinct from the free ventrolateral tubefeet and it includes approximately the same number of papillae (14 in Psychrelpidia, 12-16 in the Pelagothuriidae). Further similarities to Psychropotidae are the numerous ventrolateral tubefeet, which almost form a brim, retractility of the tentacles (as in Benthodytes), and the violet body colour. The deposits are cross-shaped as in Psychropotidae and a number of species of Peniagone. Similarities to Elpidiidae further include the type of calcareous ring, the absence of midventral tubefeet, and the number of 10 tentacles.

Hérouard (1923) erected *Psychrelpidia* to accommodate the species *P. discrepans*, originally referred to *Peniagone*. He regarded it as belonging to the Psychropotidae, while Ekman (1926) transferred it to the Elpidiidae. In the present paper it is likewise reckoned among the Elpidiidae, although a reference to the Psychropotidae or Pelagothuriidae would be equally justified.

The brim of *Psychrelpidia* and the Pelagothuriidae may be homologous with the anterior part of the brim in the Psychropotidae, the presence of an anterior brim being apparently an original feature in the suborder Psychropotina. It seems likely that the velum of the Elpidiidae is a reduced anterior brim. A velum (or, in *Scotoplanes*, papillae deriving from a velum) is present in all the elpidiid genera except the most specialized one, *Elpidia*.

Psychropotidae. The family is characterized by the brim of fused tubefeet which surrounds the body. The deposits are cross-shaped, or reduced to rods.

Elpidiidae. The family possesses a number of features indicating its origin by paedomorphosis: The short and ovoid body form, the presence of only ten tentacles, the low number of tubefeet, the presence, in some species, of scattered wheelshaped deposits, and the unique morphology of the calcareous ring.

The large size of the tubefeet, and their connection with intradermal ambulacral cavities, is a similarity to the Deimatidae and Laetmogonidae (pp. 205–206). The velum, as suggested above, probably derives from an anterior brim, the latter still being present in *Psychrelpidia*.

The interrelationship of the elpidiid genera may be inferred from several features: The morphology of the spicules and the calcareous ring, the presence or absence of a velum, and a double versus a single gonad. *Peniagone* occupies, with regard to all these features, an original position within the family. The absence in this genus of a rectal caecum is also likely to be a primitive feature.

Pelagothuriidae. This pelagic family lacks deposits and calcareous ring, the relationship to the two other families being shown by the external morphology. The anterior brim is a swimming or floating organ. The family probably originated through paedomorphosis from pelagic juveniles of some benthic Psychropotina.

Madsen (1961b) suggested a paedomorphic origin of the whole order Elasipoda and of the family Porcellanasteridae among the Asteroidea. As evidence of a paedomorphic origin of the Elasipoda he adduced that the stone canal communicates with the exterior even in adult specimens, and that the deposits (of Elpidiidae and Psychropotidae) resemble initial stages of other holothurian deposits. However, the most peculiar feature of the Psychropotina deposits is not their feeble development, but the fact that they have lost the tendency to develop bifurcations other than those of the primary cross proper. These deposits, therefore, can be cited neither in favour of paedomorphosis, nor of primitiveness.

# The adaptation of the Elasipoda to the deep-sea environment

The Elasipoda have sometimes been cited as an ancient and primitive group which, in the uniform and stable environment of the deep sea, has survived up to the present time (Zenkevich & Birshtein 1960). This view is contradicted by the present study of their morphology and biology. The majority of the features of the Elasipoda appear to be adaptations to the deep-sea environment. Some features are highly specialized, while none can be pointed out with certainty as being primitive. Alleged primitive features in the family Elpidiidae appear to be paedomorphic rather than primitive.

The dominance of the Elasipoda in the deep

sea is due, in particular, to their faculty of subsisting on the nutrient-poor sediments (p. 195).

The flat ventral sole and the ventrally turned tentacle crown are features connected with the surface-dwelling habit (p. 195).

The absence of respiratory trees may be correlated with the excessive development of the papillae. It seems more natural to animals which have their whole body surface exposed to water to use the body appendages for respiratory purposes than to have intestinal respiration. Respiratory trees probably arose as an adaptation to a burrowing life. It is uncertain whether their absence in the Elasipoda is a primary or a secondary feature.

The replacement of the tubefeet ampullae by water-vascular cavities in the ventral skin in the Deimatidae, Laetmogonidae, and Elpidiidae is connected with a peculiar mechanism of protraction of the tubefeet, developed as an adaptation to walking on the soft deep-sea bottom (pp. 205– 206).

The entirely dorsal attachment of the mesentery may be an adaptive feature, as it prevents the intestine from interfering with the function of the water-vascular cavities of the ventral skin (p. 193).

The rectal caecum present in most of the elpidiid genera may have the function of increasing the specific gravity of these extremely buoyant animals (p. 192).

The deposits in the suborder Psychropotina are highly specialized, lacking every trace of dichotomous ramifications other than those of the primary cross proper. But the adaptiveness of this specialization is not evident. The perforated plates of the Deimatidae are unspecialized, resembling deposits found in the Dendrochirota, which is a shallow water group. The wheels of the Laetmogonidae may represent a specialized or paedomorphic feature.

The communication of the stone canal with the exterior may be primitive or paedomorphic.

The unique development of the calcareous ring in the Elpidiidae is based on paedomorphosis. The highly specialized ring in *Irpa* and *Elpidia* is derivable from a normal holothurian ring only through a renewed start from an embryonic ring, as present in *Peniagone* and *Achlyonice* (p. 189). Other paedomorphic features in the family are the short and vaulted body form, the few and large tubefeet, and the number of ten tentacles. The enormous amount of yolk in the eggs of the Psychropotidae may permit juvenile stages to spend a long pelagic life independent of food uptake from the plankton – a particular advantage in the nutrient-poor deep sea (p. 203).

The highly evolved adaptations of the Elasipoda to the deep-sea environment suggest that the group originated in the deep sea and never occurred in shallow water.

#### The evidence of paleontology

The firm dermal skeleton of most echinoderms has made this group one of the best known from fossil records. Unfortunately, the holothurians are the exception to the rule. The fact that the dermal skeleton of holothurians consists of separate and usually small deposits which are scattered after the death of the animal prevents paleontologists from reconstructing fossil specimens. Moreover, the same deposit type may occur in unrelated forms. The fossil "families" of holothurian deposits distinguished by paleontologists (Frizzell & Exline 1955), therefore, can only in a few cases be ranged into the system of the recent Holothurioidea. Frizzell et al. (1966) reckoned the fossil families Theeliidae and Protocaudinidae among the Elasipoda. However, the deposits of the Theeliidae (wheels with a solid centre) refer the family to the Apoda, and not to the Elasipoda. The deposits of the Protocaudinidae (wheels with a primary cross or a similar structure in the centre) resemble those of the recent family Laetmogonidae. But similar wheels are found in e.g. the Antarctic dendrochirote, Staurocucumis liouvillei (Ekman 1927, fig. 8: k). The wheels of the Protocaudinidae are known from Devonian to Jurassic.

Mostler (1968b) erected the family Palelpidiidae for the species *Palelpidia norica* from the upper Triassic of Austria. The family was referred to the Elasipoda because of the similarity of the deposits (primary crosses with five, vertical apophyses) to those of *Elpidia rigida* (= *Peniagone rigida*). However, the arms of the crosses have broad, perforated ends. The deposits, therefore, lack the distinctive feature of those of the suborder Psychropotina and are not referable to the Elasipoda, as defined by the recent forms. Nevertheless, the deposits of *Palelpidia* are very remarkable as they do represent the type from which the Psychropotina deposits are to be derived (p. 185). The deposits of the fossil Praeeuphronides multiperforata Mostler (1968a, b), likewise from the upper Triassic of Austria, have four arms with broad, perforated ends, and a central apophysis. They resemble those of Synallactes aenigma (order Aspidochirota) and bear only a superficial similarity to those of Euphronides (Psychropotes).

The deposits of the Psychropotina are so characteristic that they permit a reliable identification to this suborder. The remarkable absence of Psychropotina deposits from the known fossil sediments (which are all from shallow seas) confirms that at least this suborder of the Elasipoda has its origin in the deep sea.

It may not be possible to determine the geological age of the Elasipoda, because holothurian deposits in deep-sea sediments tend to dissolve shortly after the death of the animal (Frizzell & Exline 1955).

Madsen (1961b) similarly noted that the absence of fossil records of the Porcellanasteridae indicates that also this group evolved exclusively within the deep sea.

# Relationship to the other orders of the Holothurioidea

While several features indicate that the Elasipoda is a monophyletic group, the evidence of its relationship to the other orders of Holothurioidea is doubtful.

A relationship between the Elasipoda and Aspidochirota has been supposed from the presence of shield-shaped tentacles in both groups, and from the similarity in external appearance between the Psychropotidae and various genera of the aspidochirote family Synallactidae. However, the fact that the calcareous deposits are entirely different suggests that the similarities in external appearance are due to convergent evolution. The union of the two orders into a subclass, Aspidochirotacea, as proposed by Pawson & Fell (1965) is, therefore, not adopted in the present work.

## **D. BATHYMETRIC DISTRIBUTION**

## Degree of exploration in relation to depth

In the discussion of the bathymetric distribution and depth preference of the species it should be noted that the different bathymetric zones have not been equally well explored. The data on the



Fig. 98. Number of benthic deep-sea stations with published records of holothurians, in relation to depth.

bathymetric distribution should, therefore, be compared with Fig. 98, which shows the distribution of benthic deep-sea stations in relation to depth. The figure includes all stations with published records of holothurians. Due to the omnipresence and abundance of holothurians in the deep sea, the distribution is fairly representative of the exploration of the deep sea in general.

The area of the sea bottom occupied by the different bathymetric zones should also be taken into account when the degree of exploration is illustrated by the number of stations. Thus, the

Table 23. Number of stations with published records of holothurians in relation to area in three depth intervals.

Depth interval (m)	1000 2000	2000 6000	6000 11000
Percentage area of sea floor (Kossinna 1921)	3.4	78.4	1.3
Number of stations	254	267	58
Number of stations per unit of area	74.7	3.4	44.6



Fig. 99. Bathymetric distribution of the Deimatidae and Laetmogonidae.

number of stations per unit of area is much higher in the hadal than in the abyssal zone (Table 23). Out of the total of 58 hadal stations, 40 belong to the Russian expeditions, from which only the genera *Myriotrochus* and *Elpidia* have so far been worked up.

### Bathymetric distribution of the species

Figs. 99 and 101–103 show the bathymetric distribution of the Elasipoda. All published records are included, each station being indicated by a line. This method was preferred to a pure statement of the range of bathymetric distribution because it provides some information on the depth preference of the species. It should, however, be remembered that a dense lining does not necessarily indicate a frequent occurrence of a species. It may reflect a high degree of exploration (Fig. 98).

## Bathymetric zonation of the deep sea

The pronounced changes in the composition of the marine fauna with depth have led to a division of the sea into bathymetric faunal zones. There is some disagreement as to where the limits between the zones should be drawn, and there is also disagreement in terminology. The present work follows the terminology used by Bruun (1957), who divided the deep sea into a bathyal, an abyssal, and a hadal zone.

The division of the sea into bathymetric faunal zones has often been based on changes in environmental factors of supposed biological significance, rather than on actual changes in the composition of the fauna. As a matter of fact, a discussion of the environmental factors responsible for a zonation should not be made until the limits of the zones have been determined through an analysis of the distribution of the species.

The transition between two bathymetric zones will show a concentration of upper and lower limits of distribution of species (Fig. 100). On the other hand, a concentration of distributional limits is not always indicative of a faunal change. It may be due to a high degree of exploration or to a large total number of species inhabiting the depths in question. The lower limits of distribution of the species of Elasipoda show a concentration at 900-1400 m.

The marked decrease in number of lower limits beyond a depth of 1400 m may reflect a decrease in total number of species, as well as a decrease in intensity of exploration.

The gradual increase in number of lower records towards depths of 5000–6000 m is remarkable in view of the decreasing exploration with depth. Further exploration is likely to show even more clearly that a majority of the abyssal species penetrate to depths close to 6000 m.

The scarcity of lower records at depths beyond 6000 m is not due to insufficient exploration, as these depths have more stations per unit of area than the abyssal depths. It is in part due to the fact that only some of the species of the abyssal zone get the opportunity to go deeper down. However, a change in ecological conditions is also important, as shown by the fact that only







Fig. 102. Bathymetric distribution of the Elpidiidae (I).

three out of a total of 18 species of holothurians taken at the deep-abyssal *Galathea* stations in the Kermadec Trench (4410–5900 m) penetrate deeper than 6000 m.

The absent abyssal species are not to any larger degree replaced by species peculiar to the hadal zone. This may not be due to extreme conditions of life at hadal depths, but rather to a young geological age of the trenches, which has not permitted the evolution of a species diversity comparable to that of the abyssal zone (p. 219). The upper limits of distribution of the Elasipoda show some concentration at 1800–2600 m (and especially at 2400–2600 m). Conversely, the depths of 1200–1800 m show a low number of upper limits; this is remarkable because these depths are better explored and probably also contain a higher number of species than the depths of 1800–2600 m. Apparently, the rather large number of upper records between 1800 and 2600 m indicates the upper boundary of the abyssal fauna.

The depths of 1800–2600 m show no concentration of lower limits of distribution corresponding to that of the upper limits. Apparently, the species of the bathyal zone are less uniform in their vertical range than are those of the abyssal zone. This is probably due to the greater diversity of environment in the bathyal zone and the correspondingly greater diversity in the ecology of its species.

The concentration of upper limits of distribution at about 4000 m may reflect a deep-abyssal faunal element. Madsen (1961b) found that the Porcellanasteridae showed a change in species composition at a depth of 4000–5000 m, and suggested that the change was correlated with the beginning undersaturation of the water with calcium. However, this view finds no support in the holothurians which even at the greatest depths of the trenches are able to store abundant amounts of calcium in their deposits (p. 241).

A vertical zonation of the deep-sea fauna is indicated not only by the concentration of upper and lower limits of species distributions, but also



Fig. 103. Bathymetric distribution of the Elpidiidae (II).

by similarities in the range of bathymetric distribution of the different species and in the range of their preferred depths.

As seen in Figs. 99 and 101–103, most of the species occurring deeper than 2600 m have a wide bathymetric range in the abyssal zone, while few of them ascend to depths less than 1800 m. Among the exceptions are *Psychropotes depressa* and *Benthodytes lingua*, both of which mainly occur in the bathyal-abyssal transition zone. *Deima validum* varies in bathymetric range from one region to another (p. 17).

The preponderance of records between 3200 and 6000 m in Oneirophanta mutabilis and Psychropotes longicauda confirms that the deeper part of the abyssal zone contains characteristic faunal elements.

The upper boundary of the bathyal zone is not clearly defined, owing to the pronounced differences in the vertical range of the bathyal species. It is, however, remarkable that very few bathyal species have their upper limit at depths of less than 200 m. Similarly, there are only few instances of sublittoral species descending deeper than 400 m. This agrees with the view of Sanders & Hessler (1969) that the shelf-slope transition is the most pronounced bathymetric boundary in the sea.

The vertical zonation of the deep-sea fauna, as indicated by the present study of the Elasipoda, differs on essential points from that found by Vinogradova (1962a). Based on concentrations of upper and lower limits of distribution of 1144 species of benthic invertebrates from depths exceeding 2000 m she found that in all the examined groups abrupt changes in faunal composition occurred at certain depths. In some groups (including holothurians) the changes occurred at 2500-3000 and 4000-4500 m, in others at 3000-3500 and 4500-5000 m. In contrast to the present findings the transition zones were indicated by a simultaneous concentration of upper and lower limits of distribution. In holothurians, isopods, and sponges the transition zones showed, in addition, maxima in number of species, but in most other groups the number of species showed a continuous decrease with advancing depth.

The present investigation of the Holothurioidea, like an earlier investigation of the Isopoda Asellota (Wolff 1962), gave no evidence of a change in faunal composition at 4000–4500 m, nor of any maxima in number of species. Wolff suggested that the results obtained by Vinogradova were due to the inclusion of species known from one record only. The inclusion of such species may result in a coincidence of upper limits, lower limits, and species maxima.

Conclusion. The present data on the bathymetric distribution of the Elasipoda support a division of the deep sea into a bathyal, an abyssal, and a hadal zone.

The bathyal zone, comprising depths from 200/400 to 1800/2600 m, shows more varied ecological conditions than the remaining deep sea. In consequence, the bathyal species show little uniformity in bathymetric range; the boundaries of the zone are, therefore, not clearly indicated by upper and lower limits of distribution.

The abyssal zone, comprising depths from 1800/2600 to approximately 6000 m, shows uniform conditions, and many of its species range throughout the zone. The interval of 1800-2600 m is much more pronounced as an upper boundary of the abyssal fauna than as a lower boundary of the bathyal fauna.

The hadal zone, with depths beyond 6000 m, is characterized by the absence of the great majority of the abyssal species, rather than by elements peculiar to the hadal depths. The abrupt decrease in number of species at about 6000 m seems primarily to be correlated with the abrupt decrease in the total area of the sea floor and with the instability and young geological age of the trench environment, which may have permitted only a low faunal diversity.

The hadal zone is considered in detail elsewhere (pp. 239-243).

# Bathymetric distribution and taxonomic relationship

The bathymetric faunal zones are characterized not only by having their own species, but also by the presence or dominance of higher taxonomic categories. The taxonomic revision of the Elasipoda showed that the relationship of species and genera, with few exceptions, is closest between forms living in the same bathymetric zone. This pronounced tendency of the sublittoral, bathyal, and abyssal zone to develop their own taxonomic categories is a general feature of the Holothurioidea.

Order Elasipoda. The order is confined to the deep sea and comprises almost half of the known

species of deep-sea holothurians. Five species are known from depths of less than 200 m: *Laetmo*gone maculata (141–732 m), *L. ijimai* (130–900 m), *L. fimbriata* (164–1300 m), *Amperima velacula* (131–4850 m), and *Elpidia glacialis* (70–9043 m).

Deimatidae. All four species of Orphnurgus are bathyal. Oneirophanta has two abyssal species, O. mutabilis and O. setigera. A third species, O. conservata, known from a single specimen taken at 1315 m, may actually be an Orphnurgus (p. 36).

Deima comprises only one species, D. validum. In some regions it ranges throughout the greater part of the bathyal and abyssal zones, while in other regions it is confined to either of the two (p. 17).

Laetmogonidae is pronouncedly bathyal, containing only three abyssal species: Laetmogone wyvillethomsoni, L. theeli, and Apodogaster sp. (p. 75).

L. wyvillethomsoni has sometimes been confused with L. violacea. Re-examination of a large number of specimens showed that the two species are distinct and that all bathyal records refer to L. violacea, while all abyssal records belong to L. wyvillethomsoni. Its closest relative is probably not L. violacea, but L. theeli.

Psychropotidae is abyssal, with the exception of *Benthodytes lingua* and *Psychropotes depressa*, which are lower bathyal to upper abyssal. No species are restricted to the bathyal zone.

Benthodytes sanguinolenta has an unusually wide vertical distribution (768–7250 m). The name, however, may cover more than one species.

Elpidiidae. *Peniagone*, comprising almost half of the species of the family, is pronouncedly abyssal; only three species have been recorded from the bathyal zone: *P. vignoni* (400 m, Antarctic), *P. japonica* (1135–1669 m, Japan), and *P. azorica* (1385–2252 m off the Azores, otherwise 2320–8210 m).

The other genera are likewise abyssal, although less markedly so than *Peniagone*. Three species are known from the bathyal zone only: *Ellipinion kumai* (500 m) and *Achlyonice tui* (1170 m) are known from one locality each and may, therefore, not be restricted to the bathyal zone, while *Irpa ludwigi* (755–1292 m) is known only from the Mediterranean, where a distinction between a bathyal and an abyssal zone can scarcely be made.

Scotoplanes globosa and Elpidia glacialis are bathyal-abyssal-hadal (p. 196), while Ellipinion *delagei* is one of the few species of Elasipoda which is common to the lower bathyal and the upper abyssal zones.

Order Aspidochirota. The order comprises three families:

Holothuriidae. No species occur deeper than 250 m. Gastrothuria, recorded from a depth of 564 m, is more rightly placed in the Synallactidae (Hansen 1967).

Stichopodidae has one bathyal species, *Stichopus tremulus*, with a bathymetric range of 240–1918 m (off the Scandinavian coasts it ascends to only 20 m). *Stichopus regalis* ranges from 30–470 m (in the Mediterranean: 5–834 m, and possibly deeper). Otherwise, the family is strictly littoral-sublittoral.

Synallactidae is restricted to the deep sea. It comprises approximately 140 species, which is more than one-third of the known species of deep-sea holothurians. Like the Laetmogonidae among the Elasipoda, the Synallactidae are especially characteristic of the bathyal zone.

The following genera are exclusively bathyal: Gastrothuria, Bathyplotes, Amphigymnas, Dendrothuria, Meseres, Filithuria, and Kareniella. Pseudothuria (1660–2600 m) touches the upper abyssal.

No genera are confined to the abyssal zone. Synallactes, Paelopatides, Benthothuria, Mesothuria, Capheira, and Pseudostichopus are bathyalabyssal. Most of them are too little known for an evaluation of a possible correlation between taxonomic affinity and depth range of their species. But such a correlation is evident in Synallactes, the best known genus. It comprises 20 species, which may be separated into an upper bathyal (102–1018 m) and an abyssal (1669–4064 m) group.

Bathyal species of Synallactes:

nozawai Mitsukuri, 1912 102–805 m
multivesiculatus Ohshima, 1915 195–844 m
ishikawai Mitsukuri, 1912 200–500 m
monoculus (Sluiter, 1901a) 310-462 m
<i>mollis</i> Cherbonnier, 1952 366 m
heteroculus (Heding, 1940) 371 m
discoidalis Mitsukuri, 1912 450-650 m
viridilimus Cherbonnier, 1952 530 m
triplax Clark, 1920 545 m
alexandri Ludwig, 1894 585–1018 m
chuni Augustin, 1908 650–1000 m
challengeri (Théel, 1886a) 1007 m

Abyssal	species	of	Synallactes:
1			

gilberti Ohshima, 1915 1669-	-1715 m
anceps Koehler & Vaney, 1910	2098 m
crucifera R. Perrier, 1902	2212 m
aenigma Ludwig, 1894 2404-	-4064 m
profundus (Koehler & Vaney, 1905)	2989 m
horridus Koehler & Vaney, 1905	3178 m
rigidus Koehler & Vaney, 1905	3498 m
robertsoni Vaney, 1908	4409 m

The shallowest recorded species of the abyssal group, S. gilberti, was taken off Japan at a temperature of  $2.4-2.7^{\circ}$  C. It may constitute one of the few examples of deep-sea holothurians ascending to shallow depths in colder seas.

A close relationship between the abyssal species is indicated by the presence of fungiform papillae (otherwise present only in a few species of *Bathyplotes*, but absent in all bathyal species of *Synallactes*), a cartilaginous skin which, at capture, tends to separate from the muscular coat, the few and single-rowed ventrolateral tubefeet, the exclusively quadri-partite tables, and the reduced state of the rods of the papillae.

Order Molpadonia. The order comprises four families:

Gephyrothuriidae, comprising the abyssal genus Gephyrothuria (probably monotypic) and the hadal genus Hadalothuria (monotypic).

Eupyrgidae, with one genus, *Eupyrgus*. Two species are distinguished, the Korean *E. pacificus* (60–65 m) and the Arctic *E. scaber* (7–480 m).

Caudinidae. Caudina, Paracaudina, and Acaudina are littoral-sublittoral, while Hedingia is bathyal to upper abyssal. The five species of Hedingia are: H. albicans (491-3200 m), H. californica (864-2887 m), H. ludwigi (1131 m), H. fusiforme (600 m), and H. planapertura (349 m).

Molpadiidae, with three genera: Ceraplectana, with one species, C. trachyderma (3188-6580 m). Heteromolpadia, with three species: H. marenzelleri (25-1260 m), H. tridens (330-462 m), and H. pikei (370-504 m). Molpadia, with about 30 species. Two are abyssal, M. blakei (c. 2000-5220 m) and M. granulata (syn. M. bathybia) (2692-5820 m). The remaining are bathyal, and only two descend to the upper abyssal zone: M. parva (756-2695 m) and M. musculus (36-3580 m). The Galathea took the latter species on several occasions at depths exceeding 3000 m, but never deeper than 3580 m. The two abyssal species, *M. blakei* and *M. granulata*, are closely related, as shown by the rudimentary state of the tail, the absence of phosphatic bodies in the skin, the similar type of deposit, and the absence (*blakei*) or reduced state (*granulata*) of the tentacle ampullae. The two species which replace each other geographically (p. 246), are so distinct from the other species of *Molpadia* that they might be considered as a separate genus.

Order Dendrochirota. The members of this order, being predominantly suspension feeders, are poorly represented in the deep sea. Of the three families, the Phyllophoridae are littoral-sublittoral Nine species of Psolidae are known from the bathyal zone, and three from the bathyal-abyssal transition: *Psolus pourtalesii* (2236–2327 m), *Psolidium disjunctum* (2798 m), and *P. panamense* (2309 m). No true abyssal species are found in the family.

Cucumariidae includes two deep-sea species, Abyssocucumis abyssorum (1645-4064 m) and Sphaerothuria bitentaculata (227-4058 m), both belonging to monotypic genera. Abyssocucumis is most closely related to Staurocucumis and Ekmocucumis, each with one sublittoral Antarctic species (p. 234). Sphaerothuria is of uncertain relationship.

Order Apoda. The order comprises three families:

Myriotrochidae, with three genera: Trochoderma, with one species, T. elegans (Arctic, 9– 350 m). Acanthotrochus, with one species, A. mirabilis (Arctic Basin, 1090–2030 m). Myriotrochus, with 14 species. Six are hadal, two are abyssal (M. bathybius and M. giganteus, both known from 3645 m off Peru), and six are confined to the sublittoral and upper bathyal of Arctic and Subarctic seas (only one of these, M. theeli, was found as deep as 2000 m). The hadal species, reviewed by Belyaev (1970), show different types of relationship with the sublittoral forms. Thus, the genus exhibits no clear correlation between bathymetric occurrence and taxonomic relationship.

Chiridotidae, with nine genera, is littoralsublittoral and mainly tropical and subtropical. Three species are known from the deep sea: *Chiridota abyssicola* (1891–2870 m), *Achiridota profunda* (2700 m), and *A. inermis* (466–772 m). *Chiridota*, in addition to the single upper-abyssal species, comprises twenty-odd sublittoral species. Achiridota comprises only the two species mentioned.

Synaptidae, with 15 genera. All deep-sea records belong to the genus Protankyra, and all abyssal records to the species P. abyssicola (syn. P. brychia). The species was taken at numerous Galathea stations at 2550-5160 m; possibly, all bathyal records of this species are due to erroneous identification. The interrelationship of the species of Protankyra remains to be clarified.

Conclusion. All Holothurioidea, except to some degree the Apoda, show correlation between taxonomic affinity and bathymetric distribution. This correlation exists even at the sub-generic level: In bathyal-abyssal genera, the species are often segregated into a bathyal and an abyssal group.

The true abyssal species of Apoda belong to two genera which are mainly sublittoral: Protankyra which, in addition to numerous sublittoral warm-water species, has eight bathyal and one abyssal representative; and Myriotrochus whose sublittoral species are Arctic or Subarctic.

The evolutionary implications of the patterns of bathymetric distribution are dealt with in a later chapter (pp. 243-244).

## Number of species and individuals in relation to depth

The faunal change with increasing depth is not only qualitative in type. There is also a change in the number of species and individuals, and in the quantitative representation of the holothurians in relation to other groups.

Fig. 104 shows the number of species of holothurians known to inhabit the different depths, illustrated by intervals of 500 m. While the Elasipoda have the maximum number of species in the abyssal zone, holothurians as a whole show a continuous decrease in number from the sublittoral to the hadal zone.

Fig. 105 shows the number of species taken at each of the Galathea deep-sea trawling stations, with different signatures for each type of gear. As appears from the station list (Bruun 1958), the duration of haul was, on an average, the same in the three bathymetric zones. The number of spe-



Fig. 104. Number of species of holothurians in relation to depth. The Elasipoda are shown in black.



cies is, therefore, a measure of the species diversity. The increase in diversity from the bathyal to the abyssal zone takes place in spite of a decrease in total number of species. From the abyssal to the hadal zone there is a decrease both in diversity and in total number of species.

The number of individuals per species shows yet another pattern (Fig. 106). There is a continuous increase in ratio from the bathyal to the hadal zone. The fact that the high number of species at the abyssal stations is accompanied by high numbers of individuals of each species indicates a dominance of holothurians at the expense of other groups. The enormous number of individuals per species at hadal depths may only to a small degree be due to the individuals being distributed on fewer species. A high number of individuals per species is not as a rule found in the hadal animal groups. A dominance of holothurians has been found throughout the hadal zone in all trenches investigated (Wolff 1970). It applies both to the number of specimens and to the biomass. Thus, the Elasipoda constitute 75-90  $^{0}/_{0}$  of the biomass at a depth of 8000-10000 m in the Kurile-Kamchatka Trench (Zenkevich & Birshtein 1960).

The present findings regarding the number of species and individuals in relation to depth have some bearings on the discussion on the faunal diversity in the deep sea.

Hessler & Sanders (1967) quite remarkably found that the faunal diversity (as defined by the absolute number of species in any single environment) in the deep sea equalled the diversity in equivalent environments from tropical shallow water and greatly surpassed that found in temperate shallow water. Similar results were obtained for Cumacea (Jones & Sanders 1972) and meiobenthic Copepoda (Coull 1972). The authors believed that the high diversity was the result of the great stability of the deep-sea environment throughout the year as well as through geological time.

The presence of a large number of species of holothurians at the abyssal stations is in agreement with the view of a high species diversity in the abyssal zone – although it may to some degree be a consequence of the large number of specimens taken: The higher the density of animals the higher percentage of the total number of species co-existing at a locality will be taken in a single haul. Sanders (1968) developed a "rare-



Fig. 106. Average number of specimens per species of holothurians at each trawling-station of the *Galathea*. Abscissa in logarithmic scale.

faction method" to make possible a comparison of the species diversity in samples of different size.

Unfortunately, the bathyal *Galathea* samples are so small that a reasonable estimate of their species diversity is scarcely possible.

The hadal samples, on the other hand, clearly reveal a low species diversity compared to the abyssal samples: The species decrease in number despite the fact that the hadal samples are exceedingly rich in number of individuals.

The low species diversity at hadal depths may not be due to extreme conditions of the environment. Indeed, only the hydrostatic pressure seems to present an increase in the extremeness of the conditions compared to the abyssal zone. The hadal zone, however, differs from the abyssal zone by its more unstable and geologically younger environment (p. 240). The low diversity at hadal depths, like the high diversity at abyssal depths, is thus consistent with the above-mentioned stability-time hypothesis.

A comparative investigation of the species

diversity at hadal and abyssal depths, comprising other groups than the extremely dominating holothurians, is desirable.

## E. GEOGRAPHIC DISTRIBUTION

# The exploration of the different geographic regions

The treatment of a collection originating from all the three main oceans involves a comparison with the materials described from all previous deep-sea expeditions. Such a comparison of faunas from different geographic regions is especially important in view of the fact that reports from regional expeditions often pay too little attention to species described from other oceans.

The degree of exploration varies strikingly from one region to another. The distribution maps of the species (Figs. 109–125) should, therefore, be compared with the maps showing the density of stations in the different geographic regions (Figs. 107–108).



Fig. 107. Distribution of deep-sea stations with published records of holothurians. Depth 1000-2500 m.

## The bathyal fauna

This fauna comprises practically all the Laetmogonidae, and the genus *Orphnurgus* in the Deimatidae. The centre of distribution is the archipelago of East Asia where the continental slope is very long and consists of isolated areas round the numerous islands. Three species are endemic to the Indonesian seas: *Benthodytes sibogae, Benthogone abstrusa*, and *Laetmogone interjacens*.

The northern boundary of this rich bathyal fauna lies off Japan in the region of convergence between the Kuroshio and Oyashio Currents. This coincidence suggests that the species have pelagic larvae, the distribution of which is obstructed by the southgoing Oyashio Current (p. 238). Only the deepest living species, *Pannychia moseleyi*, goes beyond this boundary.

To the south, the fauna is to some extent distributed to New Zealand and southern Australia.

The Hawaiian Islands possess four bathyal elasipods. Orphnurgus vitreus is endemic. Panny-

chia moseleyi ranges round the coasts of the Pacific. Orphnurgus glaber and Laetmogone biserialis are also found in southeastern Asia and have their northern boundary at the Kuroshio-Oyashio convergence. The occurrence of O. glaber and L. biserialis off the Hawaiian Islands may be due to transport of pelagic larvae by bathyal currents running from Japan to the western part of this archipelago (p. 238). Pannychia moseleyi, which goes much deeper, may have reached the Hawaiian Islands by way of the chain of submarine mountains which connects these islands with Kamchatka.

The eastern Pacific, in addition to *P. moseleyi*, has only one bathyal elasipod, *Laetmogone scotoeides*, taken off Baja California.

The low number of bathyal elasipods along the eastern coast of the Pacific may be due not only to inability to penetrate north of the Oyashio-Kuroshio convergence, but also to unfavourable conditions for soft-bottom bathyal animals along this steep continental slope.



Fig. 108. Same. Depth 2500-6000 m (•) and 6000-11000 m (+).

The coasts of southern and equatorial Africa are almost unexplored at bathyal depths, which may explain that only two species have been recorded: *Benthogone rosea* (off East Africa) and *Laetmogone fimbriata* (off Natal).

The two North Atlantic bathyal laetmogonids, Laetmogone violacea and Benthogone rosea, are both distributed towards the east to Japan and New Zealand. While B. rosea has its northern limit of distribution in the North Atlantic west of Ireland, L. violacea proceeds along the southern slope of the North Atlantic ridge to west of Greenland. The absence along the east coast of America of this otherwise widely distributed species may be due to adverse currents (p. 238).

The only bathyal elasipod known to occur in the western Atlantic is the West Indian deimatid Orphnurgus asper.

## The abyssal fauna

The abyssal Elasipoda show no preponderance in number of species in any region, apart from very limited regions such as off the west coast of Central America and the abyssal depths of the Kermadec Trench. Moreover, the various abyssal species have so few distributional features in common that they cannot form the basis of a division of the abyssal zone into larger zoogeographic regions. Distinctive abyssal faunas may be found in basins with low sill depths (as the Mediterranean and the Arctic Basin) but are rare in the remaining deep sea. At the present time only one such region can be pointed out, viz. a narrow region off the west coast of Central America.

Ekman (1953) proposed a division of the abyssal fauna into four major zoogeographic regions: An Arctic, Antarctic, Atlantic, and Indo-pan-Pacific region.

Madsen (1961b) agreed that the Arctic and Antarctic seas are distinct zoogeographic regions. However, he divided the remaining abyssal deep sea into an Atlanto-Indian(-West Pacific) and a main Pacific region, with a transition zone extending from southern Japan to east of New



Fig. 109. Records of Deima validum.

Zealand. The mid-Pacific deep sea with its sparse food resources was assumed to form the barrier for distribution. Besides, a possible correlation was pointed out between the major abyssal zoogeographic regions and the type of sediment. The Atlanto-Indian region is mainly covered with Globigerina ooze, the main Pacific region with abyssal clay, and the Antarctic region with diatom ooze. The Elasipoda give no conclusive evidence of the faunal interrelationship of the different oceans. This may in part be due to insufficient exploration. The deep-sea fauna of the South Atlantic is so little known that a comparison of the Atlantic and Indo-Pacific faunas actually means a comparison of the well-explored North Atlantic with the rest of the world ocean. Similarly, the greater part of the abyssal Pacific Ocean



Fig. 110. Records of Oneirophanta.

is too little explored to allow conclusions regarding the faunal relationship of this ocean as a whole.

A division of the world ocean into large regions characterized by sediment types finds no support in the distribution of the Elasipoda, which seem to be independent of the usually distinguished types of sediment (p. 235).

The zoogeographic divisions proposed by Vinogradova (1959) are contradicted by the distribution of the Elasipoda. The divisions were largely based on the view that submarine ridges may act as distributional barriers to abyssal animals (p. 238).

The object of the following review of the abyssal elasipod faunas is to point out regions with more or less characteristic faunas, and of underlining similarities and dissimilarities between different faunas and different species.

## 1. World-wide distributions.

Although the demonstration of synonymy has extended the known range of geographic distribution of many species, it is surprising how few species have a world-wide distribution.

The two most widely distributed species are Oneirophanta mutabilis and Psychropotes longicauda. The remarkable similarity in the pattern of distribution (Figs. 110 and 118) may be explained by the fact that both have their main vertical range at 3200-6000 m. They have been found in almost every region investigated at these great depths.

The remaining five species with a world-wide distribution seem to be absent in some regions:

Benthodytes typica, which ranges throughout the abyssal zone, has an almost equally wide distribution as the two above-mentioned species. The absence of records from the Antarctic Ocean is remarkable, as it is known to occur off the coast of South Africa and in the Tasman Sea.

Deima validum seems to be absent from a number of regions, including the Antarctic Ocean. The species shows striking differences in bathymetric distribution from one region to another (p. 17).

*Elpidia glacialis* is of common occurrence in the Arctic and Antarctic deep sea (in the Kara Sea it ascends to a depth of 70 m). Outside these regions it is confined to the hadal depths of a number of trenches.

Psychropotes depressa, an inhabitant of the deeper bathyal and the upper abyssal zone, may also be world-wide in distribution. The lack of records from the Indian Ocean may be due to insufficient exploration of the depths inhabited by this species.

Scotoplanes globosa occurs in the Southern Ocean, the South Atlantic, and the Pacific, including a number of West Pacific trenches. The absence of records from the North Atlantic is remarkable.



Fig. 111. Records of Orphnurgus.



Fig. 112. Records of Benthogone and Pannychia.

2. The Antarctic Ocean.

Ekman (1953), Vinogradova (1959), and Madsen (1961b) deal with the Antarctic abyssal deep sea as a distinct zoogeographic region. This view finds little support in the distribution of the Elasipoda.

Nine abyssal species of Elasipoda are known only from the Antarctic region. *Peniagone incondita* has been taken on several occasions, while the remaining eight species (*Peniagone mossmani*, *P. wiltoni*, *P. affinis*, *P. incerta*, *P. willemoesi*, *Elli*- pinion facetum, Amperima insignis, and Psychropotes scotiae) are known from one station each.

The Antarctic deep sea is characterized by its low temperature, which in large areas is below zero. But in contrast to the Arctic deep sea there is a gradual transition to regions with normal abyssal temperatures. Thus, although an endemic abyssal fauna dependent on very low temperatures may exist, a well-defined boundary between such a region and the remaining deep sea cannot be expected.



Fig. 113. Records of Laetmogone (1).

Fig. 114. Records of Laetmogone (2).



Nine species and one subspecies of Antarctic Elasipoda are known also from other seas. Oneirophanta mutabilis and Psychropotes longicauda are world-wide. Scotoplanes globosa occurs also in the South Atlantic and in the western and northern Pacific. Laetmogone wyvillethomsoni is known from the Kermadec Trench and from off the coast of Chile; although not exclusively Antarctic, it may be restricted to the Southern Ocean. Peniagone vitrea is also known from the Gulf of Panama, Amperima naresi from the Gulf of Panama and the Sunda Trench, A. robusta from the Kermadec Trench, Ellipinion papillosum from the South Atlantic, and Elpidia glacialis sundensis from the Sunda Trench. Kolga hyalina, also found in the Arctic Basin and the adjoining part of the North Atlantic, is the only example of a bipolar distribution among holothurians.

The problem of the existence of deep-sea elements in the Antarctic sublittoral fauna is considered elsewhere (pp. 233-234).

## 3. The North Atlantic.

Although the best explored of the oceans, the stations are so unevenly distributed that erroneous



Fig. 115. Records of Benthodytes (1).



Fig. 116. Records of Benthodytes (2).

conclusions regarding the distribution of the species are liable to be drawn. The deeper part of the abyssal zone (3000/4000-6000 m) is well explored only in a region between the Bay of Biscay and the Azores. This might explain why the two otherwise widely distributed deep-abyssal species, Oneirophanta mutabilis and Psychropotes longicauda, are known only from this part of the Atlantic. The third species of the region, Amperima rosea, although not recorded from elsewhere, may have a much wider distribution within the deep-abyssal zone than indicated by the few finds.

Among the species recorded more than once, only two have not been recorded from other oceans. One is the above-mentioned Amperima rosea, the other A. furcata which is known from two records from the bathyal-abyssal transition zone (1846 and 2320 m).

Of the eleven species which the North Atlantic has in common with other oceans, five (Oneirophanta mutabilis, Deima validum, Benthodytes



Fig. 117. Records of Psychropotes (1).

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Fig. 118. Records of Psychropotes (2), Psycheotrephes, Psychrelpidia and Rhipidothuria.

typica, Psychropotes longicauda, and P. depressa) are world-wide. Three (Peniagone azorica, P. diaphana, and Ellipinion delagei) range to the southwestern Pacific. Peniagone wyvillii is also known from the Central Pacific, Benthodytes lingua from the South Atlantic, and Psychropotes semperiana from the western Indian Ocean.

The similarities between the holothurian faunas of the North Atlantic and the southwestern Pacific suggest a conveyance of pelagic larvae or juveniles by deep currents (p. 238).

Some otherwise widely distributed species have not been recorded from the North Atlantic (Amperima naresi, Scotoplanes globosa, Benthodytes sanguinolenta, and Psychropotes vertucosa).

According to Deichmann (1930), deep-sea species of holothurians are usually found at shallower depths in the western than in the eastern North Atlantic. However, the Elasipoda show only two examples: *Deima validum* is bathyal off the West Indies, but exclusively abyssal in the eastern North Atlantic. *Benthodytes typica* is bathyal in the western Atlantic, but otherwise abyssal. No species of the pronouncedly abyssal family Elpidiidae are known to ascend into the West Indian bathyal region.

While the North Atlantic deep sea as a whole differs from the other oceans by few faunistic features, distinctive deep-sea communities might exist in places within this ocean. The remarkable occurrence of a species of *Elpidia* at the base of the continental slope off the coast of North-West Africa indicates unusual conditions, possibly correlated with a rich upwelling (p. 173).

4. The South Atlantic.

A few deep-abyssal stations in the equatorial part and a number of upper-abyssal stations along the coast of the Gulf of Guinea do not permit a discussion of zoogeographic relationships.

5. The Indian Ocean.

Explored at abyssal depths off South and East Africa, as well as in the Arabian Bay and the Bay of Bengal.

Out of a total of 16 species of abyssal Elasipoda recorded from the Indian Ocean, seven have not been found elsewhere. However, only three of these have been recorded more than once: Psychropotes belyaevi (3 stations between Madagascar and East Africa), Benthodytes plana (southwest of Ceylon and off South Africa), and Peniagone convexa (southwest of Ceylon and off East Africa). Of the eight species recorded from other oceans, four are world-wide, two (Psychropotes verrucosa and Benthodytes sanguinolenta) have wide Indo-Pacific distributions, one (Peniagone rigida) is known from the northwestern Pacific, and one (Psychropotes semperiana) from the Atlantic.

Deima validum occurs at bathyal and abyssal depths (1224-4320 m) in the northern Indian Ocean. The region has no records of Elpidiidae from less than 3194 m and of Psychropotidae from less than 2738 m.

## 6. The Indonesian seas.

Explored by stations in the bathyal and the bathyal-abyssal transition zone, and in the hadal zone of the Banda Trench.

The two species recorded from the Banda Trench (Benthodytes sanguinolenta and Psychropotes verrucosa) are both widely distributed.

Another two are examples of an ascent of abyssal forms into shallower depths: *Deima validum*, recorded from 724–1158 m (Strait of Macassar, south of Celebes, Banda Sea), and a *Peniagone* (*Scotoanassa incerta* Sluiter) from 538–724 m (Strait of Macassar, southwest of Celebes), an exceptionally shallow occurrence for the genus *Peniagone*.

Mortensen (1923) found that in the region round the Kei Islands "a rich and genuine abyssal fauna", including "various Elasipoda", occurred at only 200-300 m depth. Similar observations were made on the *Challenger* and the *Siboga*. But a study of Mortensen's material showed that the Elasipoda cannot be adduced as evidence of an ascent of deep-sea species to shallow depths in this region. Three species of Elasipoda were taken – *Orphnurgus glaber* (245-352 m), *Laetmogone maculata* (225-245 m), and *L. fimbriata* (245 m). They are, however, upper bathyal also outside this region, and their occurrence off the Kei Islands is not exceptionally shallow.



Fig. 119. Records of Peniagone (1).



Fig. 120. Records of Peniagone (2).



Fig. 121. Records of Achlyonice and Amperima.



Fig. 122. Records of Ellipinion.



Fig. 123. Records of Scotoplanes, Kolga and Irpa.

## 7. The Pacific Ocean.

The abyssal depths are very little explored, apart from the southwestern part (the Tasman Sea and north of New Zealand) and a region extending from California to Peru. A number of trenches have been investigated at abyssal and hadal depths.

The faunal similarities between the southwestern Pacific and the North Atlantic have already been mentioned. Otherwise, the fauna of the southwestern Pacific consists of species with a world-wide or wide Indo-Pacific distribution or with an Antarctic or southern distribution.

The abyssal fauna off the west coast of Central America and northern South America is remarkable for its richness in number of species and individuals, and for its taxonomic relationship. Some widely distributed species are here represented by endemic subspecies or by closely related species (p. 246).

The characteristic features of this fauna are likely to be correlated with the rich supply of nutrient matter caused by upwelling and possibly also by turbidity currents and mud slides due to the steep gradient of the continental slope. The poor food conditions of the Central Pacific may have caused the extinction of species from this region, cutting off the eastern Pacific populations from the main distributional area of the species. In some cases (e. g. *Oneirophanta mutabilis*) the eastern Pacific population may have regained contact with the other populations, although still preserving its characteristic features.

The region extends northward to about  $30^{\circ}$  N, where it is replaced by a Californian abyssal fauna of a different composition (Parker 1964). Parker suggested that the change in faunal composition was due to convergent deep-sea currents in combination with submarine ridges. The southern boundary of the region has yet to be determined.

Remarkable similarities are found between the abyssal faunas of the eastern Pacific region and the Kermadec Trench. Both regions are rich in number of species as well as in individuals, and the dominating species are often the same, or



Fig. 124. Records of Elpidia glacialis.



Fig. 125. Records of Elpidia (other than E. glacialis).

closely related forms. An abyssal fauna of a rather similar composition may be characteristic of the Antarctic region, of which the dominating elasipods are *Oneirophanta mutabilis*, *Psychropotes longicauda*, *Scotoplanes* globosa, and *Elpidia* glacialis (Agatep 1967b).

The fact that the dominating species of the three faunas are among the most widely distributed species of Elasipoda indicates that the faunal similarities are ecologically rather than geographically determined. Probably, the similarities are due to a rich supply of nutrient matter in all three regions.

## 8. The Arctic Basin.

The Arctic Basin (including the Norwegian Sea) is very poor in species. The families Deimatidae and Psychropotidae are absent, and the Elpidiidae is represented by three species only (Elpidia glacialis, Kolga hyalina, Irpa abyssicola). The elpidiid genera Peniagone, Amperima, Ellipinion, and Scotoplanes, all abundantly represented in the remaining deep sea, are absent from the region. It is noteworthy that the three elasipod species of the Arctic Basin belong to closely related genera.

One of the Arctic species (Irpa abyssicola) is known only from the type specimen. The other member of the genus (I. ludwigi) is known only from the Mediterranean deep sea. Elpidia glacialis is represented by the endemic subspecies E. g. glacialis. Kolga hyalina occurs also in the northernmost North Atlantic and the Antarctic Ocean.

The Arctic Basin is separated from the Pacific Ocean by extensive sublittoral areas, and from the Atlantic Ocean by the North Atlantic Ridge, with sill depths of about 500 m. The absence of many species and taxa in the Arctic Basin may be due to inability to cross the North Atlantic Ridge, rather than to the negative temperature.

The deep-sea elements in the Arctic sublittoral fauna are considered elsewhere (pp. 234–235).

#### 9. The Mediterranean.

Apart from three dredgings deeper than 3000 m (Marion 1883) the few deep-sea stations are

all from less than 1445 m (von Marenzeller 1893b, 1895, Hérouard 1923).

The Mediterranean is separated from the Atlantic by a sill with a depth of about 400 m. The deep water, deriving from the surface, remains constant at c.  $13^{\circ}$  C. below a depth of c. 1000 m. In spite of this, the Mediterranean deep-sea holothurians belong to the usual deep-sea groups (p. 235).

## The ranges of geographic distribution compared with those of other groups

Wide geographic distributions are characteristic not only of holothurians. They have been shown in porcellanasterids (Madsen 1961a) – and may apply to all echinoderm groups – in molluscs (Knudsen 1970), ascidians (Millar 1970), and polychaetes. The polychaete species are probably the most widely distributed of all deep-sea animals, as indicated by the world-wide distribution of many of the hadal species (Kirkegaard 1956).

Restricted distributions appear to be the rule in the Pogonophora, a deep-sea group inhabiting regions close to the coast (Ivanov 1963).

Also some groups of Crustacea have been considered to have remarkably restricted species distributions. Barnard (1961) found this to be the rule in the deep-sea benthic Amphipoda, and proposed the explanation that the species were recent immigrants to the deep sea and/or had a slow rate of dispersion. The species known from widely separated localities proved to be either eurybathic or to have special mechanisms of dispersal.

Wolff (1962) similarly found that the species of the abyssal Isopoda were remarkable for their restricted distributions.

Jones & Sanders (1972) showed that a narrow bathymetric range and a pronounced regional endemism are characteristic of the Cumacea.

# F. DISTRIBUTION IN RELATION TO ENVIRONMENTAL FACTORS

In the uniform environment of the deep sea the influence of the physical factors on animal distribution would seem to present a less complicated pattern than in shallow water. It is surprising, therefore, that the geographic and bathymetric distribution of the Elasipoda can hardly ever be correlated with parameters of the physical environment.

## Temperature

The temperature has generally been regarded as the main factor determining the bathymetric distribution of deep-sea animals. This view was also held by Bruun (1957), who pointed out that the abrupt change in temperature between the warm thermosphere and the cold psychrosphere agrees fairly well with the change in faunal composition from the sublittoral to the bathyal zone. The change in temperature usually takes place at about  $10^{\circ}$  C.

According to Bruun, also the bathyal-abyssal boundary was mainly determined by the temperature, coinciding with the isotherm of  $4^{\circ}$  C. The abysso-hadal boundary, on the other hand, does not coincide with a change in temperature. Due to adiabatic heating the temperature in the hadal zone shows a slight increase with depth.

The fact that the sublittoral-bathyal and the bathyal-abyssal boundaries largely coincide with isotherms does not imply that the faunal changes are determined by the temperature. In order to examine a possible influence of the temperature, the bathymetric distribution of the species should be investigated in regions where the said isotherms are closer to the surface (Antarctic and Arctic seas) or are entirely absent (the Mediterranean).

1. Faunal similarities between the polar sublittoral regions and the deep sea.

(1) The Antarctic. A number of sublittoral and abyssal stations have been operated, while the bathyal depths are almost unexplored. A possible ascent of deep-sea species has to be concluded from the existence of bathyal and abyssal elements in the sublittoral Antarctic fauna.

The present investigation confirms the view held by Ekman (1925) that the Antarctic sublittoral echinoderm fauna contains very few deepsea elements. In the Antarctic seas, at depths less than 600 m, the deep-sea groups of holothurians are represented by the following species:

Elasipoda. Peniagone vignoni, taken at 400 m in the Antarctic, is the shallowest recorded member of the genus. Its close relative, P. japonica, is the next shallowest recorded species (Japan, 1135–1669 m; temp.  $2.6-3.4^{\circ}$  C.). Amperima velacula is known only from the Antarctic (131-4850 m). It is the shallowest recorded member of the genus.

Apodogaster alcocki, taken at 385 m in the Antarctic, is otherwise known from the Bay of Bengal at 1026 m and  $7.2^{\circ}$  C. The shallow occurrence in the Antarctic is apparently not determined by the low temperature.

Aspidochirota. Three species of the family Synallactidae have been recorded from the Antarctic sublittoral. (A fourth species, Synallactes carthagei Hérouard, in my opinion is a synonym of the dendrochirote, Ekmocucumis turqueti).

Pseudostichopus mollis Théel is known from the Antarctic and southern Chile at 137–400 m. It is otherwise recorded from the eastern Pacific (Gulf of Panama to California) at 245–3436 m and  $2.2-12.7^{\circ}$  C., which indicates that the shallow Antarctic occurrence is not due to low temperature.

Bathyplotes moseleyi (Théel) has been recorded from the Antarctic and southern Chile at 100-627 m, and from off Japan at 127-805 m and  $1.8-13.5^{\circ}$  C. These widely separated areas are not likely to be connected through a deepsea occurrence. (Apart from the record of *B.* reptans from 2212 m off the Canary Islands, no member of the genus has been taken deeper than 1300 m). Probably, the northern and southern records of *B. moseleyi* refer to different species.

Mesothuria bifurcata Hérouard is recorded from a juvenile Antarctic specimen taken at about 450 m. A specimen from 2337 m depth south of Iceland was only tentatively referred to the same species (Heding 1942). The record at 450 m is not especially shallow in the genus.

Molpadonia. *Molpadia antarctica* (Théel) was recorded from off southern Chile at 220-631 m. The depth range is not unusual in this predominantly bathyal genus.

Dendrochirota. Abyssocucumis abyssorum (Théel) is a widely distributed abyssal species, recorded from depths of 1645-4064 m. The Antarctic record from 385 m (Ekman 1927) refers to a juvenile specimen (4 mm long) which might have been misidentified.

The two Antarctic sublittoral dendrochirotes, Staurocucumis liouvillei (Vaney) and Ekmocucumis turqueti (Vaney), both belonging to monotypic genera, are most closely related to the abyssal genus Abyssocucumis. Apoda. The Antarctic sublittoral members of Apoda are not related to deep-sea forms.

(2) The Arctic. The absence in the Arctic Basin of practically all the abyssal holothurians of the North Atlantic indicates that in high latitudes abyssal species in general do not ascend to shallow depths. The temperature (c.  $4^{\circ}$  C.) at the top of the North Atlantic Ridge would not prevent a migration of North Atlantic deep-sea species into the Arctic Basin.

The Arctic sublittoral has one species (*Elpidia* glacialis) in common with the Arctic deep sea. However, it is remarkable that the sublittoral records are from the Kara Sea, a region where special conditions prevail (p. 173). Usually, the species in the Arctic does not ascend to depths smaller than 400 m.

The following deep-sea holothurians ascend to shallow depths in northern latitudes:

Laetmogone violacea ranges from 256-1804 m and from  $2.2-10.2^{\circ}$  C. All records from less than 654 m are from Greenland waters.

Psychropotes depressa. The shallowest record is from south of Iceland (957 m). The temperature was probably  $3-4^{\circ}$  C., which is in the warmer part of its normal range (1.6-4.2° C.). The next shallowest record (1158 m) is from the eastern Atlantic at about 7° C. – the only known occurrence of the species at temperatures higher than 4.2° C. Thus, the shallow records do not coincide with low temperatures.

Scotoplanes globosa has been recorded twice from depths of less than 2000 m off Japan (545 and 970 m), both stations with "abyssal" temperatures ( $2.2^{\circ}$  and  $1.6^{\circ}$  C.). However, bathyscaphe observations of Scotoplanes globosa (or the closely related abyssal species, S. clarki) in the San Diego Trough (depths 1060 and 1243 m, temp.  $3.0^{\circ}$  C.) indicate that the ascent of Scotoplanes to shallow depth depends primarily on sedimentary conditions (p. 196).

Bathyplotes natans, which in the eastern North Atlantic occurs at 600–1600 m, ascends along the Norwegian coast to 200 m. This is the only example of a synallactid ascending to shallower depths in northern latitudes.

No deep-sea species of Dendrochirota, Molpadonia, or Apoda ascend to shallower depths in northern latitudes.

A taxonomic relationship between the deep sea and the Arctic sublittoral is shown by the Myriotrochidae (order Apoda), which occur at shallow depths only in high northern latitudes (p. 216).

(3) Conclusion. Almost no deep-sea holothurians are known to ascend to shallower depths in polar seas.

A faunal relationship between the polar sublittoral regions and the deep sea is shown at a higher taxonomic level. Two species of Antarctic sublittoral Dendrochirota are closest related to deep-sea forms, and the species of Myriotrochidae are found either in the Arctic sublittoral or in the deep sea.

The fact that the deep-sea fauna has entirely different relationships to the sublittoral faunas of the Arctic and Antarctic indicates that the migration was from sublittoral depths into the deep sea, and not the opposite way. An ascent of deep-sea species to shallow depths would probably have resulted in similarities in the representation of deep-sea elements in the Arctic and Antarctic sublittoral faunas.

2. Penetration of species into the Mediterranean deep sea.

The constant temperature prevailing below a depth of 1000 m in this sea would make it possible to eliminate the temperature factor in the study of the vertical zonation of the deep-sea fauna. Unfortunately, the Mediterranean deep-sea fauna is practically unexplored apart from that of the upper bathyal zone (pp. 232–233).

The Mediterranean deep sea has one endemic holothurian, the elasipod *Irpa ludwigi*. The other five species known from the Mediterranean deep sea occur also in the North Atlantic deep sea. The known depth ranges are:

Mesothuria verrilli (Théel). Mediterranean: 280–1103 m. Atlantic Ocean: 618–4165 m.

Mesothuria intestinalis (Ascanius). Mediterranean: 390-1445 m. Atlantic Ocean: 20-1400 m.

Pseudostichopus occultatus v. Marenzeller. Mediterranean 415–3624 m. Atlantic Ocean: 232– 2984 m.

Stichopus regalis (Cuvier). Mediterranean: 5– 834 m. Atlantic Ocean: 30–470 m.

Molpadia musculus (Risso). Mediterranean: 50–200 m. Cosmopolitan: 36–3580 m.

Thus, only S. regalis is known to penetrate deeper in the Mediterranean than in the Atlantic Ocean. Strangely enough, the opposite holds good of M. musculus which seems to be restricted to the sublittoral zone in the Mediterranean, while in other regions it penetrates into the abyssal zone.

3. Comparison with other groups.

A general lack of dependence on temperature in the vertical distribution of the species is not confined to exclusive deep-sea groups, such as the various taxa of deep-sea holothurians. The bivalves, in which the sublittoral species are apparently rather easily adapted to the deep-sea environment, show no preference for a descent into the deep sea in Arctic or Antarctic regions (Knudsen 1970).

Wolff (1962), on the other hand, found that in the Isopoda the bathyal-abyssal boundary was indistinct in high latitudes, owing to the presence of many eurybathic cold water species.

## Sediments and nutrient conditions

The vertical zonation of the sea according to biological principles agrees fairly well with the commonly used zonation according to type of sediment. While the littoral and sublittoral zones are covered with terrigenous sediments and the abyssal zone with pelagic sediments, the bathyal zone is covered with a transitional type, the hemipelagic sediments, which contain a decreasing amount of terrigenous material towards the abyssal zone.

Nevertheless, it is doubtful whether a causal relationship exists between the usually distinguished sediment types (terrigenous sediments, Globigerina ooze, diatom ooze, pteropod ooze, abyssal clay) and the vertical and horizontal distribution of animal species. No elasipods known from more than one station have been recorded only from diatom ooze, pteropod ooze, or abyssal clay. Even the most widely distributed abyssal sediment, the Globigerina ooze, shows only three species with more than one record which have not been recorded from other types of sediment as well: Benthodytes plana (two stations), Psychropotes belyaevi (four stations close to each other), and Amperima rosea (three stations close to each other).

This absence of correlation suggests that the usually distinguished sediment types are based on criteria which are biologically irrelevant.

Investigations on animal communities from shallow water confirm that the relationship between animal distributions and sediment types is not of a simple nature. Sanders (1958) found that the occurrence of the two dominating species, Nucula proxima and Nephthys incisa, in a sediment-eating association in Buzzards Bay depended on a clay content of  $10-20 \ 0/0$  in the sediment, rather than on the texture of the sediment as a whole. The organic matter bound to the clay particles (which are less than two microns in diameter) appeared in this sediment to be presented in a way which agreed with the feeding biology of these particular species.

Ursin (1960) showed that the distribution of echinoderm species in the North Sea only to a small degree depended on the texture of the sediment. Buchanan (1963) similarly found that the distribution of three animal communities off the Northumberland coast was poorly correlated with the texture of the sediments: Similar sediments could be associated with very different faunas, and conversely, a mixture of sediment types was not necessarily accompanied by a mixing-up of the animal communities.

Ekman (1947), on the other hand, found that the distribution of various invertebrates in the Gullmarfjord and the Skagerrak was partly correlated with the compactness of the sediments.

Sanders et al. (1965), studying the faunal assemblages along the transect from Gay Head (Massachusetts) to Bermuda, found that the density of animals on the sea floor showed no clear correlation with the content of organic matter in the sediment. This was ascribed to the fact that the analytical techniques (Kjeldahl analysis and determination of organic carbon) did not differentiate between labile and refractory organic matter. The abyssal sediments with their smaller supply of organic matter, according to the authors, might show a higher percentage of refractory matter than the bathyal sediments. Furthermore, the greater faunal density in the bathyal zone might lead to a greater mixing of the sediments and thus to a quicker burial of refractory matter.

Thus, neither grain size nor organic content of the sediment seem to directly influence the distribution of animal species. The features on which they depend are more complicated. As almost nothing is known of the vertical and horizontal distribution of these features in the deep sea, it is not to be expected that usual expedition materials should reveal correlations between sediment types and animal distributions.

While the organic content of the sediments is

a doubtful indicator of their nutritive value, a better indication of the food conditions might be gained through a knowledge of the amount of organic matter supplied from the euphotic zone. Sokolova (1972), based on organic surface productivity, divided the world ocean into eutrophic and oligotrophic regions. Eutrophic conditions prevail in the peripheral and equatorial parts of the oceans. Vast oligotrophic regions are found in the northern and southern Pacific.

The supply of organic matter is especially high in places where upwelling occurs. The rich fauna at St. 716, situated beneath the Costa Rica Dome, is likely to be conditioned by a rich surface production due to upwelling. The only known instance of brood protection in deep-sea holothurians (in *Oneirophanta mutabilis*) is from this station. The young seem to be developed during the upwelling season. This suggests that seasonal variations in the surface production may be reflected to a depth of at least 3600 m (p. 200).

Turbidity currents and mud slides may in some regions play a major role in the food supply to the deep-sea bottom. Heezen et al. (1955) suggested that they may not only convey large quantities of nutritive matter for the abyssal fauna, but that they may also involve mass burial of animals on the abyssal sea floor, which again may lead to oil-forming deposits. An indication that turbidity currents exert a great influence on animal life in restricted localities is provided by the investigations of Griggs et al. (1969) in the Cascadia Channel off the Oregon coast. The channel, which is richly supplied with terrestrial detritus conveyed by turbidity currents, has an animal density four times higher than the surrounding abyssal plain. Besides, the turbidity currents could be shown at times to have led to a complete destruction and burial of the benthic fauna.

Turbidites may be responsible for the formation of the smooth "abyssal plains" (Johnson 1964), and both turbidites and sediments derived from mud slides are probably brought to the bottom of the trenches in large quantities down their steep slopes (p. 240). Thus, Anikouchine & Ling (1967) demonstrated that the sediments of the Java and Mindanao Trenches are mostly turbidites, and that even the sediments of the oceanic Mariana Trench contain significant additions of turbidites. An abundant supply of sediments to the trenches probably forms the basis of the rich fauna of Elpidiidae at hadal depths (pp. 195–196).

The similarity in species composition of the rich abyssal holothurian faunas of the eastern Pacific region, the Antarctic, and the Kermadec Trench may be due to a rich supply of organic matter in all three regions (pp. 231–232).

If a region with an abundant food supply is bordered by barren regions, a geographic isolation of species may result. The distinctive features of the eastern Pacific region (p. 231) may be due to such type of isolation.

Russian workers (Vinogradova 1962b, Zenkevich et al. 1971) have done an extensive work in mapping the distribution of biomass in the oceans. An analysis of the species composition in relation to the variations in biomass might yield interesting results. It should, however, be emphasized that the biomass, or standing crop, is not a direct measure of the organic production. In shallow water communities a high biomass may represent many years' production, while a smaller biomass composed of shortlived species may be combined with a high organic production.

While variations in the food supply to the bottom seem to exert a great influence on the geographic distribution of deep-sea species, an influence on the bathymetric distribution seems more doubtful. It might be assumed that deep-sea species ascend to shallower depths in regions with a poor food supply, while in regions with a rich supply shallow water species would penetrate deeper. However, no such correlation can be demonstrated in the bathymetric distribution of the Elasipoda. Thus, in the barren region off the West Indies only two species of Elasipoda, Benthodytes typica and Deima validum, ascend to shallower depths. The occurrence of D. validum at equally shallow depths in the rich eastern Pacific region suggests that the range of bathymetric distribution in this species is not determined by food conditions alone.

The rich eastern Pacific region shows no example of holothurians descending to unusually great depths.

Deep-sea species of holothurians thus generally remain at their preferred depths also in regions where the temperature or food conditions might induce them to extend their distribution to other bathymetric zones. This does not, however, prevent that the two factors in combination exert an influence on the bathymetric distribution of many species.

The possibility that the abyssal fauna is conditioned by a combination of low temperature and poor food supply might be checked in cold regions with a poor food supply. An example of an Arctic region with poor food conditions is provided by the Kara Sea, where many deep-sea forms (including *Elpidia glacialis*) ascend to shallow water. But the Kara Sea is also remarkable for the darkness of its water (p. 173). Actually already Moseley (1880) suggested that the occurrence of deep-sea animals at shallow depth in the Arctic is not only due to the low temperature, but also to the darkness of the water during most of the year.

## Hydrostatic pressure

A number of physiological and biochemical reactions have been observed in the laboratory when shallow water organisms were exposed to high hydrostatic pressure: Changes in protoplasmic viscosity, pseudopodia formation, ciliary movement, cell division, enzyme activity, etc.

Knight-Jones & Morgan (1966) maintained that the influence of high hydrostatic pressure on living systems is so profound that it is not surprising that the hadal fauna is poor in species. Flügel & Schlieper (1970) similarly regarded the high pressure as one of the factors responsible for the absence of some invertebrate groups at depths exceeding 4000 m. Wolff (1970), in his recent review of the hadal fauna, maintained that the gradual change in faunal composition at depths exceeding 6000 m is primarily caused by increased hydrostatic pressure.

It should be emphasized that the laboratory experiments deal with the pressure reactions of single specimens and have little bearing on the problem whether a species through a multitude of generations may develop genetic adaptations to increased pressure. Actually, there is no indication that inability to pressure adaption has prevented animal groups from penetrating into the deep sea. The few groups which are absent or poorly represented at the greatest depths seem to be prevented by their feeding habits. The low species diversity at hadal depths may be due to the low geological age of the trenches rather than to unfavourable conditions of life at the great depths (p. 219).

The significance of the hydrostatic pressure for the bathymetric distribution of animals is still obscure.

#### Currents

The distribution of some bathyal and a few abyssal species of Elasipoda seems to be related to ocean currents. This suggests the presence of a pelagic phase in their development, or a faculty of leaving the bottom as adults.

Juvenile and adult benthic holothurians have sometimes been taken in pelagic nets (pp. 204–205). On the other hand, there is no proof of a special, pelagic larval stage of benthic deep-sea holothurians. The eggs in all the families of Elasipoda are so large that possible pelagic larvae are likely to be independent of the plankton for food uptake – thus serving only the dispersal of the species.

Current-dependent distributions are suggested in the following cases:

(1) In the region of Newfoundland where north- and southgoing currents meet. The northgoing currents, which can be traced to a depth of 4000-5000 m, would seem to present an effective barrier to a southward migration of bathyal species with pelagic larvae.

Laetmogone violacea (Fig. 113), which is of common occurrence along the northern and eastern continental slopes of the North Atlantic, might have been obstructed in its southward migration in the western Atlantic by this barrier.

(2) Off Japan a similar boundary exists between north- and southgoing currents, comprising the water masses of the upper 1500 m (Sverdrup *et al.* 1942, fig. 205). The boundary may form a distributional barrier to bathyal species with pelagic larvae or juveniles.

Laetmogone violacea, L. maculata, L. fimbriata, L. biserialis, and Orphnurgus glaber are known from Japan up to this boundary, while they have never been taken along the northern and eastern coast of the Pacific. Two of the species (L. biserialis and O. glaber) have reached the Hawaiian Islands, possibly by way of pelagic larvae or juveniles conveyed by bathyal currents from Japan. It is noteworthy that the Hawaiian specimens of O. glaber are more similar to those from Japan than to those from South-East Asia. Of the bathyal species of Elasipoda known from the western Pacific, only the deepest living, *Pannychia moseleyi* (Fig. 112), extends north of this point of convergence. It has been found down to 2600 m.

(3) The existence of some degree of similarity between the abyssal holothurian faunas of the North Atlantic and the southwestern Pacific (p. 227) recalls a pattern of distribution demonstrated by Sewell (1948) for pelagic deep-sea Copepoda. Sewell pointed out that the faunal similarities might be due to transport by deep ocean currents. At depths of 1500–4000 m, the water moves from the North Atlantic southward, giving off a water mass that flows eastward south of the Cape of Good Hope and proceeds across the southern part of the Indian Ocean to the southwestern Pacific.

Three of the species of Elasipoda common to the two regions (Benthodytes typica, Psychropotes longicauda, and Peniagone diaphana) have been taken as juveniles in pelagic nets.

## Topography

Vinogradova (1959) distinguished a number of zoogeographic regions and subregions in the deep sea, separated to a great extent by submarine ridges. The importance of these ridges as distributional barriers, according to Vinogradova, was shown by the existence of an inverse correlation between the depth of the habitat of the species and the wideness of their geographic range. The deep-sea species with most restricted distributions (apart from the trench species) were held to be the stenobathic abyssal species.

The justification of Vinogradova's conclusions cannot be fully evaluated owing to lack of detailed information on the distribution and taxonomic status of the total of 1031 species on which they were based. The present revision of the Elasipoda, however, led to completely different zoogeographic conclusions. The two stenobathic deep-abyssal species, *Oneirophanta mutabilis* and *Psychropotes longicauda*, belong to the very few cosmopolitan species of Elasipoda, while even the most widely distributed bathyal species are far from being cosmopolitan.

The topography of the ocean floor at abyssal depths seems to have very little influence on the distribution of the Elasipoda. The faunal composition of some deep-sea basins which are separated from the main ocean by ridges or elevations with low sill depths may partly be determined by inability of some species to cross the topographical barrier. However, the fact that these ridges at the same time exert a pronounced influence on the hydrographic conditions in the basin, makes it difficult to demonstrate a direct influence of the topography on the distribution. Thus, a possible absence in the Mediterranean of a North Atlantic abyssal species may be due to the high temperature of the Mediterranean deep sea, rather than to inability of the species to cross the barrier at the entrance.

On the other hand, the absence in the Arctic Basin of practically all the Elasipoda of the North Atlantic is not likely to be due to failure to adapt themselves to the negative temperatures of this basin. Equally low temperatures prevail in the Antarctic deep sea which has a diversified fauna of Elasipoda. Apparently, the North Atlantic Ridge forms an insurmountable barrier to the species.

#### Conclusion

The known distribution of the Elasipoda can only to a very small extent be correlated with parameters of the physical environment. The deepsea environment is so uniform that it is difficult to imagine distributional barriers for the species. Yet, hardly two species have the same distribution, and only few species approach a cosmopolitan distribution.

The influence of the physical environment on the distribution of the species probably consists in changing the conditions of competition. Absence of a species from certain regions is apparently due to inability to compete successfully rather than to inability to exist under the particular physical conditions. However, our present knowledge does not permit a discussion of the distribution of the species in terms of biological relationship. The zoogeography of the deep-sea holothurians (as of other deep-sea groups) is still little beyond the descriptive stage.

### G. THE HADAL FAUNA

The term *hadal* was introduced by Bruun (1956) to designate the depths of 6000-11000 m. Apart from some ocean basins with depths slightly

exceeding 6000 m, hadal depths are found only in the deep-sea trenches. Bruun regarded the hadal depths as an ecological zone equal in rank to the bathyal and abyssal zones. Wolff (1960), speaking of "the hadal community", adhered to the same view; he found that the hadal fauna differed from the abyssal fauna not only in its composition, but also in a number of morphological peculiarities of its species. Although summarizing the knowledge of all the species occurring deeper than 6000 m, Wolff (l. c.) held that the abysso-hadal boundary would be more correctly placed at 6800-7000 m. (A lowering of the abysso-hadal boundary from 6000 m to 6800-7000 m increases the number of exclusively hadal species from 58  $^{0}/_{0}$  to 74  $^{0}/_{0}$ ).

Belyaev (1966) again reviewed the fauna living deeper than 6000 m (by Russian workers termed the *ultra-abyssal* fauna) and discussed its specific features.

Menzies & George (1967) questioned that the fauna of the hadal depths differed from the abyssal fauna by any morphological or biological features. The term *trench floor fauna* was preferred, because it did not imply the existence of a biological zone comparable to the abyssal and bathyal zones.

Wolff (1970), induced by the criticism advanced by Menzies & George, provided further arguments in support of his views. Both Wolff and Menzies & George based their views especially on a study of Isopoda, a fact which makes their different opinions even more remarkable.

In the following, the composition of the hadal fauna and the characteristics of its species is reviewed with special regard to the holothurians. The investigation confirmed the existence of a number of features peculiar to the hadal fauna. The features are probably not related to the depth, but rather to the topographical, geological, and sedimentary conditions of the trench environment.

## The hadal environment

The hadal zone is characterized by the following features:

(1) Small total area. While  $78.4 \, {}^{0}/_{0}$  of the sea has depths of 2000–6000 m, only  $1.3 \, {}^{0}/_{0}$  has depths of 6000–11000 m. The abrupt decrease in area takes place in the interval of 6000–7000 m. (2) Geographic discontinuity. While the abyssal depths, with few exceptions, form a continuous geographic unit, the hadal depths consist of a number of geographically isolated trenches and basins.

(3) Geological instability. In contrast to the stable and uniform abyssal environment the deep-sea trenches are influenced by tectonic instability and, in coastal trenches, by an often high rate of sedimentation. Thus, Moore (1972) presented evidence that a deep-sea trench bordering the continental shelf of the eastern Bering Sea was uplifted during Cretaceous to be superceded by the Aleutian Trench in the earliest Tertiary.

There is evidence that a fairly recent (possibly Quaternary) decrease in depth of the Japan Trench has led to the extermination of three deep-hadal species of holothurians (p. 242).

(4) Ecological conditions. Most of the trenches are situated close to the coast and may benefit from the rich production of the coastal plankton. In addition, the steep slopes allow turbidity currents and mud slides to reach the bottom of the trenches, conveying a supply of organic material (p. 236). The rich accumulation of sediments in the trenches may be the most important ecological factor distinguishing the hadal from the abyssal zone.

The temperature in the trenches is usually between  $1.5^{\circ}$  and  $2.5^{\circ}$  C. Due to adiabatic heating the temperature increases by about  $1^{\circ}$  C. from 5000 to 10000 m.

The water renewal is probably sufficient to ensure that oxygen is no limiting factor for hadal animal life.

The undersaturation of the water with calcium at depths beyond 5000 m has not prevented the existence of strongly calcified forms at hadal depths (p. 241).

The high hydrostatic pressure is still of unknown importance to the bathymetric distribution of deep-sea animals (pp. 237–238).

## General features of the hadal fauna

A comparison between the hadal and the bathyalabyssal faunas involves a number of questions. In the following these are considered in relation to the physiographical and ecological conditions in the hadal zone.

(1) Number of species per locality. The present investigation indicates that the hadal zone has a

low faunal diversity compared to the abyssal zone. This may be due to the unstable and geologically young environment, rather than to extreme conditions of life at great depths (p. 219).

(2) Number of species per trench. A low faunal diversity in the hadal zone will tend to reduce the number of species occurring in each trench. This may to some degree be counterbalanced by the considerable diversity of habitats due to the irregular topography of the slopes.

(3) Total number of hadal species. The division of the hadal zone into geographically isolated trenches tends to increase the total number of hadal species. Nevertheless, the species number decreases abruptly at 6000-7000 m. This may be due to the abrupt decrease in area at this depth and to a low faunal diversity in the hadal zone.

(4) Number of individuals per species. The fact that holothurians (Elasipoda in particular) are highly adapted for life at great depths, combined with their low species diversity in the hadal zone, has led to exceptionally high numbers of individuals per species, compared to other groups (p. 218).

(5) Composition of the hadal fauna. Concurrently with the increasing abundance of the holothurians with depth a change takes place also in the relative representation of other groups. Wolff (1960, 1970) pointed out that the hadal fauna is characterized by the absence (Decapoda, Brachiopoda) or poor representation (fishes, Cirripedia, Bryozoa) of some groups, while other groups (Polychaeta, Holothurioidea, Isopoda) are dominant. These faunal changes indicate an increasing dominance of deposit feeders at the expense of filter feeders and carnivores. The poor representation of carnivores is not unexpected. The large biomass in the trenches is accounted for by elpidiids, which have a very low food value.

The decrease in number of filter feeders may to some degree be apparent only. Sokolova (1959) pointed out that the slopes of the trenches in some places are swept by currents which may create favourable conditions for filter-feeding animals. This has been confirmed by deep-sea photographs revealing a rather rich representation of crinoids and other filter feeders in places with hard bottom at hadal depths (Lemche *et al.* in press). Due to difficulties in fishing on this type of bottom the filter-feeding fauna of the trenches is little known. No filter-feeding holothurians are known from hadal depths.

Menzies & George (1967) rightly pointed out that the groups which are poorly represented at hadal depths are also poorly represented at abyssal depths. The change in faunal composition is gradual with depth, and, therefore, cannot motivate the distinction of an abysso-hadal boundary.

The authors further held that the dominant groups are not the same in different trenches, or at different levels in each trench. But actually, the holothurians are dominant at all levels in all trenches (p. 218).

Menzies & George (1967) also pointed out that the nomination of a group to be dominant depends very much on the mesh-size of the gear. With fine-meshed gear the isopods would increase in dominance and with even finer meshes the Foraminifera would be the dominant group. However, this does not invalidate the finding that the holothurians increase in dominance with depth compared to other groups of similar body size.

(6) Morphological characteristics. Birshtein (1957) and Wolff (1956a, b, 1960, 1962, 1970) found that gigantism in Crustacea is most often met with in the deep sea, and in particular in the hadal zone. Menzies & George (1967), on the contrary, held that gigantism in the Isopoda is not correlated with depth.

The holothurians lend no support for the view of deep-sea gigantism. Although the abyssal species are often large-sized, they are generally not larger than the bathyal and sublittoral species. The hadal species of holothurians, as a rule, are smaller in size than the abyssal species. Thus, none of the large-sized species from the abyssal stations in the Kermadec Trench (Oneirophanta mutabilis, Psychropotes longicauda, Psycheotrephes magna, Mesothuria candelabri, Abyssocucumis abyssorum, Molpadia blakei) descend into the hadal zone. This decrease in average size, however, has no direct relation to the depth. It is due to the fact that the dominance of the holothurians at hadal depths is accounted for, in particular, by the Elpidiidae.

The only hadal example of a change in morphological features with depth is shown by the genus *Elpidia* in which there is a tendency to increasing calcification with depth. This is the more remarkable as the high hydrostatic pressure and the low temperature cause dissolution of calcium in the sediments at depths beyond 5000 m. Evidently, undersaturation of the water with calcium does not prevent animals from storing large amounts of calcium in their skeletons. This was also noted by Zenkevich (1963) who pointed to the fact that the echinoderms are extremely abundant in the brown mud of the Kara Sea, in spite of the total dissolution of calcium in this sediment.

An increased calcification with depth is also found in *Deima validum*, in which the deposits are more robust and strongly calcified in abyssal than in bathyal specimens.

(7) Endemism in the trenches. Belyaev (1966) stated that of the known hadal species  $68 \ 0/0$  had so far never been taken outside the hadal zone.

Menzies & George (1967) argued that this percentage was not at all remarkable. Comparing the isopod faunas of two abyssal localities which were rather close to each other and not separated by any topographic barrier they found that both localities had a higher percentage of "endemic" species than that distinguishing the hadal zone from the remaining deep sea. According to these authors a species is "endemic" to locality A if absent in locality B, irrespective of its remaining distribution. However, this type of "endemism" has no bearing on the problem in question, which deals with the percentage of hadal species that have not been found outside the hadal zone in any part of the world ocean.

In order to avoid confusion of terms, the word "endemic" in the present work is used in the meaning "endemic to one trench system". Species recorded from the hadal zone only (whether from one or from several trenches) are called "exclusively hadal".

Out of the total of 22 species of holothurians known from the hadal zone, 13 are exclusively hadal.

Nine exclusively hadal species are endemic to one trench system:

Ellipinion galatheae: Philippine Trench (9820–10000 m).

*Elpidia longicirrata:* Kurile-Kamchatka Trench (8035–8345 m).

Elpidia atakama: Peru-Chile Trench (7720 m). Paroriza grevei: Banda Trench (6650–7280 m). Myriotrochus kurilensis: Kurile-Kamchatka

Trench (7795–8430 m).

Myriotrochus longissimus: Japan and Idzu-Bonin Trenches (6475–7190 m). Myriotrochus mitis: Kermadec Trench (8927–9174 m).

Myriotrochus kermadecensis: Kermadec Trench (8927–9174 m).

Hadalothuria wolffi: New Britain Trench (8920 m).

There is photographic evidence (Lemche *et al.* in press) of the occurrence *Hadalothuria* (wolf-fi?) in the New Hebrides Trench.

Three exclusively hadal species are common to the Kurile-Kamchatka and Idzu-Bonin Trenches, but seem to be absent in the interjacent Japan Trench: *Elpidia hanseni* (8610–9735 m), *E. birsteini* (8060–9345 m), and *Myriotrochus zenkevitchi* (8135–9715 m). Only one of the species (*E. hanseni*) has developed subspecific differences between the two populations. As pointed out by Belyaev (1971), this suggests that in fairly recent time (possibly as late as the Quaternary) the Japan Trench was deep enough to permit a continuous distribution of these deep-hadal species. At present, the Japan Trench is less than 8000 m deep, with the exception of a local deep (8412 m) in its southern part.

One exclusively hadal species, Myriotrochus bruuni, is common to several trenches: Philippine, Japan, Mariana, New Britain-Bougainville, Kermadec, Tonga, and Sunda Trenches. Total depth range 6458–10710 m.

The example of *M. bruuni* is remarkable, since species exclusive to the hadal zone are otherwise with almost no exception restricted to one single trench system (Belyaev 1966). However, the absence of taxonomic differences between the trench populations of *M. bruuni* (Cherbonnier 1964, Belyaev 1970) suggests that the populations are, in actual fact, connected through an abyssal occurrence. The species, therefore, may constitute no exception to the rule.

The non-exclusively hadal species of holothurians often penetrate into several trenches. Thus, the four non-exclusively hadal species of holothurians from the Kermadec Trench all seem to occur in other trenches as well. *Elpidia* glacialis has been dredged in a number of trenches, and there is photographic evidence (Lemche *et al.* in press) that also the other three species occur in additional trenches: *Penia*gone azorica (New Britain and Romanche Trenches), *Scotoplanes globosa* (New Britain and New Hebrides Trenches), and *Pseudostichopus* villosus (New Britain Trench). The Banda Trench provides an exception, as none of its four non-exclusively hadal species of holothurians are known to penetrate to hadal depths in other trenches (Hansen 1956). This may be due to ecological and zoogeographic conditions particular to this isolated trench which is completely surrounded by shallow seas.

Apart from the species of the Banda Trench, only one non-exclusively hadal holothurian seems to penetrate into one trench only (*Amperima* naresi in the Sunda Trench).

(8) Evolution in the trenches. A species which has become restricted to hadal depths in a number of trenches may be subject to a divergent evolution. In the course of time, a geographic subspeciation or even speciation may result, leading to endemic trench species.

Examples of geographic subspeciation due to isolation in trenches are provided by the hadal populations of *Elpidia glacialis*. This species had probably a wide abyssal distribution during the Glacial Age. The subsequent extinction of the species at abyssal depths outside the polar regions resulted in its isolation in a number of trenches, where it developed into endemic subspecies. *Elpidia atakama* from the Peru-Chile Trench may represent one such population which has reached species level.

A geographic subspeciation has also taken place in *Elpidia hanseni*, in which, according to Belyaev (1971), the populations of the Kurile-Kamchatka and Idzu-Bonin Trenches differ at the subspecies level.

The fact that the exclusively hadal species are almost all endemic to one trench system suggests that the evolution in the trenches has often proceeded to species level. On the other hand, the present restriction of a species to the hadal depths of a single trench is no proof of its origin in situ. It may represent a relict occurrence of a former abysso-hadal distribution. An indication that isolation in trenches has led to speciation might be found in cases in which hadal species from different trenches together form a superspecies. As yet, such superspecies have not been described for any group. Among the holothurians, a hadal species pair, as mentioned, may be represented by Elpidia glacialis, inhabiting the trenches of the western Pacific, and E. atakama from the Peru-Chile Trench.

(9) Taxonomic variation within trench populations. The irregular topography of the trenches may lead to isolation and taxonomic segregation of populations. Four species of the Kermadec Trench exhibit a pronounced local variation. In *Oneirophanta mutabilis* the specimens from St. 654 have very peculiar features in common, indicating a pronouncedly stationary population. *Psychropotes longicauda* shows differences in body colour between the specimens from St. 663 and those from St. 664. In the two abysso-hadal species, *Scotoplanes globosa* and *Peniagone azorica*, a correlation is indicated between taxonomic variation and bathymetric occurrence.

Belyaev distinguished four species of *Elpidia* in the Kurile-Kamchatka Trench. The shallowest living, *Elpidia kurilensis* (= *E. glacialis kurilensis*) (6710-8100 m), was regarded as the ancestor of the deep-hadal *E. longicirrata* (8035-8345 m) and *E. birsteini* (8060-9345 m). The deepest living, *E. hanseni* (8610-9530 m), is likely to be of the same ancestry. The four species differ in number and size of the dorsal papillae. Besides, they show an increasing calcification with depth.

The existence in the Kurile-Kamchatka Trench of four closely related species of *Elpidia* suggests that populations isolated in parts of a trench may develop into subspecies and even species.

Conclusion. The features which characterize the hadal fauna are correlated with the trench environment, rather than with the great depths. In point of fact, there would be no reason to distinguish a particular zone for the depths of 6000–11000 m if these depths were not restricted to trenches.

A large supply of sediments forms the basis of the overwhelming abundance of holothurians (elpidiids in particular) and may be the most important ecological factor in the hadal zone.

Geological instability and low age may have permitted only a low faunal diversity, as indicated by the low number of species per station in the hadal holothurians.

The small total area combined with a low faunal diversity may explain the abrupt decrease in total number of species at the abysso-hadal transition.

Geographic discontinuity has led to subspeciation, and probably speciation, in former abysso-hadal species which have become restricted to a series of trenches. This may to some degree counterbalance the low total number of species in the hadal zone. The irregular topography may bring about isolation and taxonomic segregation of populations within the single trenches. The existence in the Kurile-Kamchatka Trench of four closely related species of *Elpidia* raises the question whether such populations may evolve further into distinct species.

## H. EVOLUTIONARY ASPECTS

The deep-sea environment, apart from the trenches, is characterized by its great uniformity from one region to another, and its stability throughout the year and through geological time. Three consequences of evolutionary significance have already been considered: The low total number of species in the deep sea due to the geographic uniformity, the high faunal diversity in abyssal communities due to the stability of the environment, and the low holothurian (and probably faunal) diversity in the unstable hadal environment.

The present chapter deals with the evolutionary processes in the deep-sea fauna, as revealed by the taxonomy and distribution of the Elasipoda. A thorough knowledge of the taxonomy of a group is indispensable to such a study. A group should preferably be revised on a world-wide basis to minimize the risk that regional faunas are described with too little attention being paid to the faunas of other geographic regions.

The hadal zone in several respects offers conditions for its fauna which are different from those of the abyssal and bathyal zones. The evolutionary problems in the hadal zone were, therefore, discussed in connection with the other problems of the hadal fauna (pp. 239–243).

## Evolution within the deep sea versus immigration from shallower depths

New species may be added to the deep-sea fauna either through speciation within the deep sea or through immigration from the sublittoral zone. The relative role played by the two phenomena differs greatly from one animal group to another. In groups which have been restricted to the deep sea during a long geological time the species have probably arisen mainly through speciation within the deep sea. In groups where the deep-sea species are closely related to sublittoral forms new species may also have been added to the deep-sea fauna through a relatively recent immigration from sublittoral depths. Groups restricted to the deep sea are especially well suited for the study of the conditions of evolution in this environment. It has already been emphasized that the holothurians constitute a pronounced example of such a group, and that at least one of the elasipod suborders, Psychropotina, seems to have evolved entirely within the deep sea (p. 209).

The echinoderms have produced several exclusive deep-sea groups (stalked crinoids, the families Porcellanasteridae, Benthopectinidae, Brisingidae, and Zoroasteridae among the Asteroidea, the Echinothuridae and Aspidodiadematidae among the Echinoidea). At least some of these groups do not follow the rule of the holothurians that the relationship is closest between species from the same bathymetric zone. Thus, Alton (1966) found that in Goniasteridae and Zoroasteridae "the replacement of species belonging to the same genus with depth was strongly exhibited". As examples were mentioned bathyal species which were replaced by closely related abyssal species.

No polychaete families are restricted to the deep sea. The molluscs (apart from the Monoplacophora) possess only one family restricted to the deep sea, the bivalve family Galatheavalvidae. The only species of the family, Galatheavalva holothuriae Knudsen, 1970, lives as a commensal in the oral cavity of Psychropotes belyaevi.

Some families of crustaceans are restricted to the deep sea (Neotanaidae among the Tanaidacea, Eryonidae and Homolodromiidae among the Decapoda). In general, however, the crustaceans of the deep sea seem to exhibit a close relationship to sublittoral forms. This has been stressed both for Amphipoda Gammaridea (Barnard 1961) and Isopoda (Wolff 1962).

## **Geographic variation**

It is generally agreed that in terrestrial animals speciation is almost exclusively brought about by geographic isolation (Mayr 1963). There is less evidence of the importance of geographic isolation for speciation in marine animals, although polytypic sublittoral species are known from a number of groups (Rensch 1947, Mayr 1954). Hardly anything is known about the types of geographic variation in deep-sea animals. Yet it would be highly desirable to acquire a knowledge of the conditions of geographic speciation in the stable and uniform environment of the deep sea, with its remarkable absence of distributional barriers or abrupt changes in ecological conditions.

The omnipresence of geographic variation in marine animals is revealed almost whenever a sufficient number of specimens are examined from different localities. A striking example among sublittoral echinoderms was provided by Vasseur (1952), who studied populations of the sea-urchins *Strongylocentrotus droebachiensis* and *S. pallidus* from three localities along the Norwegian coast. A geographic variation was present in all the characters examined: Colour of the test, colour and structure of the spines, number of ocular plates reaching the periproct, shape of the pedicellariae, number of pore-pairs, relative weight of the lantern, ecology, and sperm agglutination.

Madsen (1961a), in his revision of the deep-sea Porcellanasteridae, also found that the species differed taxonomically from one population to another.

Knudsen (1970), on the other hand, found that the abyssal bivalves showed a remarkable lack of geographic variation.

The existence of a geographic variation has often been obscured due to the tendency of taxonomists to describe specimens from widely separated localities as distinct species, even when they are only slightly different. Thus, Clark (1907, p. 69) stated that "on a priori grounds, it is to be assumed that a species from the Atlantic Ocean is distinct from its nearest allies in the western Pacific. Even slight differences, if they are constant, may be used to distinguish species from widely separated areas". This subjective element in species determination was also pointed out by Madsen (1961b, p. 204), who illustrated it by the example of his own decision (Madsen 1956) to erect a new species, Primnoella krampi, for a gorgonarian from the Kermadec Trench. The species so much resembles the North Atlantic species P. jungerseni that "had they been found in the same area there should have been little objection in considering them individual variants of the same species".

These cautious measures taken by taxonomists

have the advantage that premature conclusions regarding synonymies and types of geographic variation are avoided. On the other hand, it is important that a specialist calls attention to the species in his material which might represent geographic forms of other species, and to the part of the intraspecific variation which might prove to be of a geographic type. Usually, only a specialist will be able to point out such possibilities.

A material from a large number of stations is required to make out whether a character changes gradually with distance or by abrupt changes at definite boundaries. With our present limited knowledge such an analysis is tentative only, even in the case of the most well-investigated species.

In the following is discussed the role played by the different types of geographic variation in the better-known species of Elasipoda.

#### 1. Clines.

Clines, or character-gradients, are known to be wide-spread in continental species (Mayr 1963). They arise as adaptations to changes in the environment, and are smoothed through the action of gene flow. The widely distributed species of the deep sea, living in an environment which gradually changes with distance, are likely to show this type of geographic variation.

In Orphnurgus glaber the extensive variation in number of dorsal papillae and in shape of the deposits seems primarily to be of a clinal nature.

## 2. Local variation.

While a clinal variation is difficult to demonstrate, the presence of marked differences between closely situated populations is more easily recognized. Almost every species known from a reasonably large number of specimens could be shown to vary taxonomically from one locality to another. A pronounced local variation may develop in trenches, apparently due to their irregular topography (pp. 242–243).

#### 3. Polytypic species.

The fact that geographic segregation plays a major role in speciation lends a special interest to the demonstration of discontinuous geographic variation. The description of this type of variation in terms of polytypic species serves the dual purpose of clarifying the presentation of geographic variation and of pointing out geographic regions with characteristic populations which may eventually evolve into new species.

The usefulness of the subspecies concept in describing intraspecific geographic variation has been questioned by various taxonomists. It has been held that the application of subspecific names to local populations encumbers the literature with nomenclature and tends to confuse rather than clarify the presentation of geographic variation, and, furthermore, that division of a gradually changing species into subspecies gives a false impression of discontinuity in the variation.

However, although the subspecies concept is not adequate in describing all types of geographic variation, it has the advantage of pointing out, also to the non-specialist, regions inhabited by especially characteristic populations. Comparison of taxonomic works on different groups may in this way reveal geographic regions which are, or have been, centres of species formation.

Subspecific names have been used only to a very small extent in the description of benthic deep-sea invertebrates, and in most cases only to designate specimens which, in one or more respects, differ from the "typical" form of the species. Actually, the subspecific name often replaces the "variety" of older descriptions, and is not intended to cover a distinct geographic form of the species. These subspecies are usually known from too few specimens to allow a decision as to their taxonomic status.

The subspecies concept has here been applied to three species, Oneirophanta mutabilis, Deima validum, and Elpidia glacialis. The subspecies erected conform with the 75  $^{0}/_{0}$  rule proposed by Mayr et al. (1953, p. 145): The overlap is so small that at least 75  $^{0}/_{0}$  of the specimens of subspecies A are distinguishable from 97  $^{0}/_{0}$  of the specimens of subspecies B.

The subspecies of *Elpidia glacialis* are probably geographically isolated from each other. The eastern Pacific subspecies of *Deima validum* may be geographically isolated at the present time, the nearest finds of the main subspecies being off Japan. The two subspecies of *Oneirophanta mutabilis* apparently adjoin each other by a narrow zone of intergradation; possibly, they have met subsequent to a former isolation.

The only example of geographic subspeciation in abyssal bivalves similarly comprises a widely distributed and an eastern Pacific subspecies (Knudsen 1970).

## 4. Superspecies.

The region off the Pacific coast of Central America and northern South America not only possesses endemic geographic subspecies, but also endemic species which replace closely related species from other regions. *Scotoplanes clarki* in this region apparently replaces the closely related and widely distributed *S. globosa*. A similar example may be provided by the widely distributed *Laetmogone wyvillethomsoni* and the eastern Pacific *L. theeli*, the only two abyssal species of the genus.

The Molpadonia present a species pair with a similar distribution. *Molpadia blakei* (Théel, 1886b), previously known from the North Atlantic, was taken by the *Galathea* in the South Atlantic, the Indian Ocean, the Tasman Sea, and the Kermadec Trench. The closely related *M.* granulata (Ludwig, 1894) seems to be confined to the eastern Pacific. The specimens which Sluiter (1901b) and Koehler & Vaney (1905) referred to this species (i. e. to *Trochostoma granulatum*) were probably misidentified. The two species are the only true abyssal species of *Molpadia*. They are more closely related to each other than to any of the bathyal species of the genus (p. 216).

Knudsen (1970) mentioned two examples of geographic replacement in abyssal species of bivalves. Both comprise a widely distributed species and a closely related species from the eastern Pacific region.

#### The alleged antiquity of the deep-sea fauna

Since the beginning of deep-sea exploration it has been widely believed that the great depths of the ocean have acted as a refuge for primitive animal groups. As examples of ancient survivors have, in particular, been cited animal groups which are restricted to, or are dominant, in the deep sea.

In recent time this view has been opposed by various authors (Menzies & Imbrie 1958, Menzies *et al.* 1961, Madsen 1961b, Clarke 1962). On the other hand, Zenkevich & Birshtein (1956, 1960) maintain that the deep sea is dominated by ancient (i. e. mesozoic) groups.

The Elasipoda are among the groups which have been cited as evidence of great antiquity. But this view finds no support in the present investigation. The features peculiar to the Elasipoda are either adaptations to life in the deep sea (pp. 207–208) or they are paedomorphic, like various features of the Elpidiidae (p. 207). Nor is there any evidence that the deep-sea representatives of the four other holothurian orders are more primitive than their shallow-water relatives.

The view that the deep sea harbours exceptionally many ancient and primitive groups has been based not only on the supposed phylogenetic relationship of the deep-sea groups, but also on theoretical considerations regarding the influence of the deep-sea environment on the evolutionary processes.

It has been argued (Zenkevich & Birshtein 1960, Carter 1961, Friedrich 1965) that the great stability and homogeneity of the environment has delayed the process of evolution and thereby made possible a survival of ancient groups. However, although the evolutionary processes may be slow in the stable deep-sea communities, it should be remembered that the deep sea is not a closed environment. Shallow water groups which are able to develop the necessary adaptations may continually introduce new species into the deep sea to compete with the "ancient" groups. In actual fact, there is evidence that the stable and homogeneous abyssal environment has led to the development of highly diversified communities with a keen competition between the species (p. 218).

The idea of a low level of competition in deepsea communities led Parker (1961) to the view that groups which are no longer able to compete successfully in shallow water may avoid extinction through emigration to the deep sea. However, there is no reason why a group should postpone its penetration into the deep sea until it can no longer survive in shallow water.

A less keen competition in the less diversified hadal communities might seem to provide better conditions for the survival of primitive forms. However, the low faunal diversity at hadal depths seems to be connected with a low geological age of the environment (p. 219), which in itself prevents the trenches from being refuges for ancient forms. Actually, the hadal fauna bears no primitive or ancient stamp.

In short, there is no evidence that the deep-sea environment is especially favourable for the survival of ancient and primitive forms. The composition of the deep-sea fauna, like that of the sublittoral fauna, is determined by the ability of the species to compete successfully under the particular conditions. Thus, the increasing dominance of the holothurians at great depths, which Zenkevich & Birshtein (1960) regarded as one of the indications of the antiquity of this group in the deep sea, is rather due to their highly evolved adaptation to the deep-sea environment.

Bruun (1956) and Bruun & Wolff (1961) held that the bathyal fauna includes a number of ancient animal groups, whereas the present abyssal fauna is on the whole of a fairly recent date. A cooling of the abyssal zone due to the formation of the polar ice caps during the Pleistocene glaciation was believed to have exterminated the Tertiary abyssal fauna, with the exception of eurybathic and eurythermic species. The bathyal zone, which at the present time has temperatures similar to those of the Tertiary abyssal zone, on the contrary offered conditions for the survival of an ancient deep-sea fauna.

As examples of ancient bathyal groups were mentioned the stalked crinoids, the hexactinellid sponges, the eryonid crustaceans, and the coelacanth fish *Latimeria* (which, however, is sublittoral). The two first-mentioned groups are filter feeders and thus poorly adapted for abyssal life. The eryonid crustaceans are represented in the abyssal zone by the genus *Willemoesia* and are thus not strictly bathyal.

A post-Tertiary origin of recent bathyal and abyssal faunas may apply to groups in which there is a close taxonomic relationship between the faunas of the different bathymetric zones. The absence of such a relationship in the Holothurioidea points to an evolution within the bathyal and abyssal zones of a magnitude which could hardly have been brought about since Tertiary time.

Moreover, the fact that the temperature does not seem to be of paramount importance for the bathymetric distribution of the holothurians makes it unlikely that the extremely slow process of cooling at the end of the Tertiary should have exterminated the abyssal fauna of this group.

The stable deep-sea environment has been thought to favour not only the survival of ancient forms but also the evolution of extreme specializations which would be dangerous in a more changing environment. As an example has been adduced the Elasipoda with their "fantastic modications of the form of the body" (Carter 1961).

However, it seems very doubtful whether there is any correlation between the great array of body forms in the Elasipoda and the stability of the environment. The modifications of the body are caused by the peculiar development of the ambulacral appendages, notably the papillae of the dorsal and ventrolateral ambulacra. In the absence of respiratory trees the papillae have taken over the respiratory function. It seems quite natural that this function has been fulfilled in different ways: By increase in number or size, or by excessive delopment of some of the papillae. The great variation in number, size, and arrangement of the papillae is not surprising in animals which have their whole body surface exposed to the water and in which the papillae act as respiratory organs. A similar evolution has taken place in the shallow water opisthobranch molluscs, in which an excessive development of the body appendages is combined with absence of mantle cavity and true gills. Apparently, this evolution may take place both in a stable and in a changing environment.

Thus, the Elasipoda do not support the view that the deep-sea environment has favoured the survival of primitive groups or the evolution of groups with extreme specializations.

The influence of the deep-sea environment on the rate of evolution cannot be illustrated by the example of the Elasipoda. Although at least the suborder Psychropotina probably evolved exclusively within the deep sea, its geological age is unknown due to lack of fossil records from the deep-sea bottom (p. 209).

# **IV. SUMMARY**

The class Holothurioidea comprises about 1100 species, 380 of which are from the deep sea, i. e. from depths exceeding 200–400 m. Among the five orders, the Elasipoda are unique in being confined to the deep sea.

The knowledge of the Elasipoda was founded by the Challenger Expedition 1872–1876 (Théel 1882). Also the subsequent exploration of the group was based on the collections from the great deep-sea expeditions.

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