sublittoral fauna, is determined by the ability of the species to compete successfully under the particular conditions. Thus, the increasing dominance of the holothurians at great depths, which Zenkevich & Birshtein (1960) regarded as one of the indications of the antiquity of this group in the deep sea, is rather due to their highly evolved adaptation to the deep-sea environment.

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

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

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

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

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

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

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

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

IV. SUMMARY

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

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

The material collected by the Galathea Expedition 1950–52 is larger than that of any previous expedition. This is due to the use of large collecting gear, as Herring Otter Trawl, and Sledge Trawls with 3 and 6 m wide openings. Large gear is especially suited for the catch of holothurians, which, owing to their high buoyancy, often escape the openings of smaller nets. Its effectiveness is shown by the fact that only one out of a total of 80 soft-bottom stations at depths greater than 1000 m failed to bring up holothurians.

The present work describes the Elasipoda collected by the *Galathea,* as well as a small number of Elasipoda collected by the late Dr. Th. Mortensen. In addition, the work is based on a re-examination of the material from most of the previous deep-sea expeditions.

The Systematic Part includes all the known species of the four benthic families of Elasipoda (the pelagic family, Pelagothuriidae, is omitted). The number of recognized species is reduced from 165 to 106, despite the erection of 11 new species. The order is being divided into two suborders, Deimatina and Psychropotina, the foundations of which are presented in the General Part.

The General Part deals with the morphology, biology, and distribution of the Elasipoda. Special chapters are devoted to the problems of the hadal fauna and to the evolutionary processes in the deep sea, as viewed from our present knowledge of the Elasipoda.

A. The taxonomic characters and their variation

The *calcareous deposits* (sclerites, spicules) of the skin as a rule provide the best species characters, although they may be almost identical in species belonging to different genera, or even families. A geographic or local variation is often present.

The present investigation contradicts the views of Hérouard (1923) and Ekman (1926) regarding the phylogeny of the deposits. Instead, it is pointed out that in the Psychropotidae and Elpidiidae the deposits have a feature in common which is unique among holothurians: They completely lack dichotomous ramifications, apart from the two bifurcations of the primary cross proper.

The *calcareous ring* in the Elpidiidae consists of five star-shaped pieces and resembles the embryonic ring in other holothurians. The most original state is represented by the ring of *Psychrelpidia, Peniagone,* and *Achlyonice,* in which the pieces are small, separate, and composed of a varying number of arms. From this type may be derived the firm and continuous ring of *Elpidia* and *Irpa.* In these genera the ring pieces possess four pairs of arms only, two pairs of which are joined to the corresponding arms of the neighbouring pieces. The reduction and fixation of the arm number probably happened subsequent to the re-attainment of a firm and functional structure of the ring. In *Amperima, Ellipinion,* and *Scotoplanes* each piece likewise has four pairs of arms, but the pieces are small and isolated from each other. This type of ring may be derived from the *Elpidia-Irpa* type through reduction of the five pieces.

Thus, the morphology of the calcareous ring in the Elpidiidae bears evidence not only of a paedomorphic origin of the family, but also of the interrelationship of its genera.

The ring in the Deimatidae, Laetmogonidae, and Psychropotidae is of the usual holothurian type, apart from its low degree of calcification. Due to its soft consistency the ring is changeable in shape and, therefore, of hardly any taxonomic value.

The *tubefeet* in the Psychropotidae are small and usually fused. The other three benthic families have large tubefeet which are usually few in number. They communicate with large water-vascular cavities of the ventral skin, a unique feature connected with a peculiar type of walking (see below).

The *papillae* are often large, numerous, and of a peculiar shape. The unpaired appendage in *Psychropotes* and the velum in the Elpidiidae consist of fused dorsal papillae. The velum seems to be an original feature in the Elpidiidae.

The abundant development of the papillae, like the absence of respiratory trees, is a feature connected with the surface-dwelling habit. In animals with the whole body surface exposed to the water it seems more natural to make use of the body appendages for respiratory purposes than to use intestinal respiration. A similar evolution is known from the shallow water opisthobranch molluscs, in which the abundant development of the body appendages is connected with the absence of mantle cavity and true gills.

Differences in number of tubefeet and papillae are important to the study of intraspecific variation. The geographic subspecies of *Elpidia glacialis, Deima validum,* and *Oneirophanta mutabilis* are based in part on such differences.

Circum-oral papillae are present in all species of *Deima, Benthogone,* and *Benthodytes (B. sanguinolenta* has only post-oral papillae), which represent three different families. A contractile membrane, which may completely cover the tentacle crown, is in all three genera present inside the ring of circum-oral papillae.

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

The *alimentary canal* is in most genera of the Elpidiidae provided with a large rectal caecum. Its absence in the primitive genera *Psychrelpidia* and *Peniagone* indicates that it is not a rudimentary respiratory tree but an organ originating in the Elpidiidae. The mud-filled caecum may act as a ballast tank, increasing and regulating the specific gravity of these extremely buoyant animals.

The *mesentery* in the Elasipoda, contrary to other holothurians, has a dorsal attachment throughout its length. This is apparently an adaptive feature connected with the peculiar mechanism of protraction of the tubefeet (see below).

Ekman (1926) held that differences in the course of the attachment of the mesentery on the body wall might characterize species, and even genera. But in *Oneirophanta mutabilis* it was found that even at a single station the variation may approach the highest possible for a mesentery with an entirely dorsal attachment.

The *external morphology of the gonads* may contribute to the characterization of genera, and even higher categories.

B. Biology

Feeding. The Elasipoda subsist on the surface layer of the substratum, which they graze by means of their ventrally turned tentacle crown. A different degree of selective feeding is indicated by the considerable variation in the shape of the tentacle discs. In *Elpidia* the highly specialized tentacles are combined with a very slender intestine, both features indicating a high degree of selective feeding. Two other dominant genera of the hadal zone, *Scotoplanes* and *Amperima,* have feebly differentiated tentacle discs and a heavily filled intestine.

Differences in gut content related to the different tentacle types could, however, not be demonstrated.

Reproduction. The larval development of the Elasipoda is unknown. However, even the smallest eggs (0.2 mm in diameter in the Elpidiidae) are so large that a lecitotrophic development is to be expected. Pelagic larvae, if any, will thus be independent of food uptake from the plankton, at least in their initial stages.

The largest eggs (1.7–4.4 mm in diameter) were found in the Psychropotidae. In bulk, they surpass the largest hitherto known echinoderm eggs by up to 85 times. The large size seems to be correlated with a long pelagic life of the juveniles. Thus, *Psychropotes longicauda* (egg diameter 4.4 mm) is known to spend its life in the plankton up to a body length of at least 32 mm.

A positive correlation between egg size and depth occurrence was found in the Laetmogonidae and Psychropotidae.

Brood protection was found in a population of *Oneirophanta mutabilis affinis* from 3570 m off the Pacific coast of Central America. The young are retained in the ovaries up to a length of 30 mm, representing one-third to almost half the length of the mother. The fact that the young are born at the end of a period of rich phytoplankton production suggests that a seasonal variation in the surface production may induce a reproductive periodicity at abyssal depths.

A reproductive periodicity is also indicated in abyssal populations of *Deima v. validum* from the western Indian Ocean. A definite proof of reproductive periodicity, however, requires samples from the same locality at different seasons of the year. The phenomenon may be more widespread in the deep sea than indicated by the two examples.

The gonads of the Deimatidae and Psychropotidae contained a nutritive-phagocytic tissue similar to that previously known from a number of sublittoral echinoids and asteroids. The cells ingest the sperm and ova which remain after each spawning, and later transfer nutrients to the next batch of sexual products. The tissue is abundantly developed in the Psychropotidae and in the brood-protecting *Oneirophanta mutabilis affinis.*

Hermaphroditic specimens have not been found, and there was no indication of a change of sex.

Swimming and floating. Many psychropotids and synallactids probably have the power of swimming over the bottom by means of undulatory movements of the body. The synallactid *Galatheathuria* swims in the free water masses, apparently by means of undulatory movements of the brim. Juvenile specimens of some psychropotids and elpidiids have likewise been caught a great distance above the bottom.

Function of the water-vascular dermal cavities. The water-vascular ampullae of the tubefeet and papillae are in the Deimatidae, Laetmogonidae, and Elpidiidae replaced by large water-vascular, dermal cavities. These are emptied into the tubefeet and papillae by means of peristaltic movements of the muscles of the body wall. Photographs show that the protracted tubefeet may act as stilts which raise the ventral surface of the walking animal above the substratum. Walking on stilt legs is otherwise known from various abyssal crustaceans and pycnogonids. The papillae of the velum have been observed, in some species of *Peniagone,* to be extended sufficiently to reach the substratum in front of the animal, thus acting as tactile organs.

The pumping action of the cavities may also further the circulation of fluid in the tubefeet and papillae, thus increasing the respiratory exchange through the skin.

C. Systematics, relationship, and adaptation

Monophyletic origin. The absence of respiratory trees and the exclusively dorsal attachment of the mesentery are common to all Elasipoda. Further indications of a monophyletic origin are found in three features shared by families or genera belonging to each of the two suborders: (1) Large tubefeet connected with water-vascular dermal cavities are common to the Deimatidae, Laetmogonidae, and Elpidiidae. (2) Circum-oral papillae in combination with a sphincter muscle are found in one genus of each of the families Deimatidae, Laetmogonidae, and Psychropotidae. (3) The wheel-shaped deposits found in some species of Elpidiidae are of the type otherwise characteristic of the Laetmogonidae.

Evolutionary trends. The Elasipoda appear to have separated at an early stage into two evolutionary trends, here proposed as the suborders Deimatina and Psychropotina.

Deimatina, comprising the families Deimatidae and Laetmogonidae, are, with few exceptions, characterized by their numerous and often long papillae. The two families differ distinctly in their calcareous deposits. The Deimatidae have reticulated plates (or derivatives of such plates), the most primitive type of holothurian deposit. The Laetmogonidae have wheels of a type otherwise found only as rare, accessory deposits in a few species of Elpidiidae and may represent a retained larval feature.

Psychropotina comprises the families Psychropotidae, Elpidiidae, and Pelagothuriidae. A common descent is indicated partly by the very specific similarity between the deposits of the Psychropotidae and those of the Elpidiidae (absent in the Pelagothuriidae), and partly by the fact that *Psychrelpidia* (here reckoned among the Elpidiidae) combines features of all three families.

The Elpidiidae and Pelagothuriidae are probably paedomorphic. Paedomorphic features in the Elpidiidae include the ovoid body form, the few and large tubefeet, the number of ten tentacles, the structure of the calcareous ring, and the occasional presence of scattered wheel-shaped deposits. The Pelagothuriidae may originate from pelagic juveniles of some benthic Psychropotina.

The most primitive elpidiid genus (apart from *Psychrelpidia)* is *Peniagone,* which possesses the basic elpidiid type of deposits and calcareous ring.

The adaptation of the Elasipoda to the deep-sea environment. The present investigation contradicts the view of the Elasipoda being primitive survivors in the deep sea. The majority of the features peculiar to the Elasipoda are adaptations to the particular environment of the deep sea. Some features are highly specialized, none appear to be primitive. Alleged primitive features of the Elpidiidae are paedomorphic rather than primitive.

The dominance of the holothurians in the deep sea is determined above all by their feeding-biology. Their faculty of ingesting large amounts of sediment, combined with a low food requirement due to their low content of organic matter, makes them well-fitted for subsisting on the nutrient-poor deep-sea sediments.

The surface-dwelling habit of the Elasipoda, which may be conditioned by the scarcity of carnivores (fishes in particular) in the deep sea, represents a further advantage. The food, which is confined to a thin surface layer of the bottom, becomes more easily accessible, and an extensive area may be searched by the animals.

Features correlated with the surface-dwelling habit are the flat ventral sole, the ventrally turned tentacle crown, the absence of respiratory trees, and the utilization of the papillae for respiratory purposes.

The peculiar mechanism of protraction of the tubefeet in three of the families is an adaptation to walking over the soft bottom. Part of the same mechanism is the entirely dorsal attachment of the mesentery, which prevents the intestine from interfering with the function of the ventral water-vascular cavities.

The elpidiids have among all holothurians the lowest content of organic matter in relation to body size. This makes them so buoyant that even slight water movements may sweep them off the bottom. As suggested above, the rectal caecum may be an organ compensating for the low specific gravity of the body.

A further adaptation to the deep-sea environment is the enormous eggs of the Psychropotidae, which apparently permit the juveniles to spend a long pelagic life independent of food uptake from the meagre deep-sea plankton.

The calcareous deposits of the Psychropotina are highly specialized, in spite of their simple structure.

The paedomorphic evolution of the Elpidiidae included the development of a unique and specialized calcareous ring.

The high degree of adaptation to the deep-sea environment and the absence of primitive features indicate that the Elasipoda originated in the deep sea and never occurred in shallow water.

The evidence of paleontology. Fossil deposits referable with certainty to Elasipoda are not known. Deposits of the fossil family Protocaudinidae (Devonian to Jurassic) resemble those of the recent Laetmogonidae. However, similar deposits occur in the Dendrochirota.

The deposits of the Psychropotina are sufficiently specific to permit a reliable identification of fossil remains. Their absence in fossil sediments confirms that at least this suborder never occurred in shallow water.

Relationship to other orders of the Holothurioidea. There is only doubtful evidence of the position of the Elasipoda within Holothurioidea. Relationship to the Aspidochirota is indicated by external features only, the deposits being entirely different.

D. Bathymetric distribution

Bathymetric distribution of the species. In Figs. 99 and 101–103 each record of a species is indicated by a line. This method of representation gives some idea of depth preferences, if the different degree of exploration is taken into account (Fig. 98).

Bathymetric zonation of the deep sea. A division of the sea into bathymetric faunal zones should be based on changes in faunal composition and not on changes in environmental factors of supposed biological significance. A transition between two zones may be indicated by a concentration of upper and lower limits of distribution of species and by a change in dominance of larger groups.

The upper and lower distributional limits of the species of Elasipoda (Fig. 100) supports the distinction of an abyssal zone with an upper limit at 1800–2600 m and a lower limit at 5000–6000 m. A bathyal zone, on the contrary, is not clearly delimited. Due to the more varied ecological conditions at these depths, the species exhibit considerable differences in bathymetric distribution, and few species range from the lower limit of the sublittoral to the upper limit of the abyssal zone.

The scarcity of lower limits at depths exceeding 6000 m may, in part, be due to the fact that not all abyssal species have the opportunity to go any deeper. However, only few of the many abyssal holothurians of the Kermadec Trench descend into the hadal zone, which indicates that there is also a change in ecological conditions.

The replacement of larger taxonomic units is most strongly exhibited at the sublittoral-bathyal transition. This is the upper boundary of the Elasipoda and the Synallactidae, which together comprise the greater part of the known species of deep-sea holothurians.

Bathymetric distribution and taxonomic relationship. In holothurians the taxonomic relationship is generally closest between forms living in the same bathymetric zone. Apparently, the sublittoral, bathyal, and abyssal zones developed their own groups of holothurians with little admixture of species from other zones.

Number of species and individuals in relation to depth. While the Elasipoda show a maximum in number of species in the abyssal zone, the holothurians as a whole continuously decrease in species number with depth (Fig. 104).

The number of species per station is highest in the abyssal zone (Fig. 105). This agrees with the view advanced by Hessler & Sanders (1967) that the stable abyssal environment has favoured the evolution of a high faunal diversity. Conversely, the low number of species per station in the hadal zone may be due to a young geological age and a lack of stability of the hadal environment.

The number of individuals per species (Fig. 106) continuously increase from the bathyal zone to the bottom of the trenches. The combination in the abyssal zone of a high number of individuals per species and a high number of species per station indicates a dominance of holothurians at the expense of other groups. This dominance is even more pronounced in the hadal zone where, in spite of the decrease in number of species, the total number of individuals per station is much higher than in the abyssal zone.

E. Geographic distribution

The *bathyal species* include almost all laetmogonids and the species of the deimatid genus *Orphnurgus*. None of the bathyal species even approach a cosmopolitan distribution.

The *abyssal species* are often widely distributed, although few are world-wide. The ranges of geographic distribution increase with depth throughout the bathyal and abyssal zones.

Due to the many individual differences in the geographic distribution of the species, the Elasipoda lend no support to a division of the deep sea into larger zoogeographic regions. Characteristic faunas are found in basins with a low sill depth (e. g. the Arctic Basin). A zoogeographic abyssal region may be distinguished along the Pacific coast of Central America.

F. Distribution in relation to environmental factors

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

Temperature has usually been regarded as the main factor determining the bathymetric distribution of deep-sea animals and the zonation of the deep sea. However, no sublittoral holothurians are known to descend into the Mediterranean deep sea, in spite of its high temperature (c. 13° C.). Similarly, the great majority of deep-sea holothurians remain within their usual depth range in the polar seas where the isotherms approach the surface.

A faunal relationship between the deep sea and the polar sublittoral regions is shown at a higher taxonomic level. *Myriotrochus* (order Apoda) is common to the deep sea and the Arctic sublittoral, and the monotypic, abyssal genus *Abyssocucumis* (order Dendrochirota) is closest related to two monotypic genera of the Antarctic sublittoral. The fact that the two polar regions exhibit completely different types of relationship with the deep sea indicates that the migration was from sublittoral depths into the deep sea, and not the opposite way. A migration from the deep sea would probably have resulted in some degree of similarity between the deep-sea elements of the Arctic and Antarctic sublittoral faunas.

Sediments and nutrient conditions. The distribution of the Elasipoda seems to be independent of the usually distinguished types of deep-sea sediment. This is hardly surprising as investigations in shallow water have shown that there is no simple correlation between animal distributions and the structure and organic content of the sediments.

A correlation is rather to be expected between animal distributions and the amount of nutrients supplied to the deep-sea floor through downsinking from the surface and through turbidity currents and mud slides. The similarities between the faunas along the west coast of Central America, the Antarctic, and the Kermadec Trench may be due to an abundant supply of nutrients in the three areas. The similarity is shown by the presence of identical or closely related species, as well as by the richness in number of individuals.

A correlation between bathymetric distribution and food supply could not be demonstrated. There is no indication that species descend to greater depths in regions with an abundant supply of food, or that deep-sea species ascend to shallower depths in nutrient-poor regions.

Although the bathymetric distribution of the holothurians seems to be largely independent of both temperature and nutrient conditions, the two factors in combination may exert an influence: The deep-sea fauna may depend on a combination of low temperature and poor food supply.

Hydrostatic pressure. Numerous observations have been made on the physiological and biochemical reactions of animals to increased hydrostatic pressure. These observations, however, do not throw light on the question whether a species through a multitude of generations is able to adapt itself to an increased pressure.

Almost all marine animal groups are represented in the deep sea. The poor representation of some groups, and the dominance of others, may be explained without introducing the hypothetical factor of pressure adaptation.

Currents. The distribution of a few bathyal and abyssal species shows a dependency on ocean currents, which indicates that they possess a pelagic larval or juvenile phase, or that they may leave the bottom as adults. In actual fact, juvenile and adult benthic Elasipoda were on a few occasions taken in pelagic nets.

A zoogeographic boundary for bathyal species may exist off Newfoundland where north- and southgoing currents meet. The northgoing current possibly prevented *Laetmogone violacea* from migrating southward along the east coast of North America.

A similar boundary off Japan seems to coincide with the northern limit of a number of bathyal species, including *L. violacea.*

Similarities between the abyssal elasipod faunas of the North Atlantic and the southwestern Pacific may be due to conveyance of pelagic stages with deep currents.

Submarine ridges, according to Vinogradova (1959), may act as distributional barriers, in particular to the deep-abyssal fauna. The present investigation, on the contrary, showed that the most widely distributed species are those of the deeper part of the abyssal zone.

G. The hadal fauna

The present study of the Elasipoda confirmed the justification of distinguishing a hadal zone comprising the depths exceeding 6000 m, but at the same time showed that the characteristic features of the zone are all connected with the fact that it consists almost exclusively of trenches.

The abundant accumulation of sediments in the trenches forms the basis of the enormous dominance of holothurians (elpidiids in particular) and is probably the most important ecological factor in the hadal zone.

A lack of stability and a comparatively low geological age may have led to a low faunal diversity in the trenches, as indicated by the low number of species of holothurians at the hadal stations.

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

The division of the hadal environment into a number of geographically isolated trenches may lead to the formation of polytypic species if an abysso-hadal species becomes extinct at abyssal depths in the intervening regions. An example is provided by *Elpidia glacialis* which, in a number of West Pacific trenches, is represented by endemic subspecies.

As yet, there is no evidence that this divergent evolution has proceeded further to the formation of superspecies. But the fact that the exclusively hadal species of animals are almost without exception endemic to one trench suggests that isolated trench populations have in many cases diverged to species level.

The irregular topography in the trenches may bring about isolation and taxonomic segregation, as evidenced by the pronounced local variation in four species of the Kermadec Trench. The existence in the Kurile-Kamchatka Trench of four closely related species of *Elpidia* raises the question whether such segregation may lead to species formation.

H. Evolutionary aspects

The insignificant role played by immigration from shallower depths in the evolution of the deep-sea holothurians makes this group well suited for a study of the conditions of species formation in the deep sea.

The importance of geographic isolation for species formation has long been recognized for well-investigated groups of terrestrial animals. The deep sea, however, with its uniform and stable environment and its almost complete absence of geographic barriers, seems to offer few possibilities of geographic isolation, apart from the discontinuous environment of the hadal zone.

The distribution and geographic variation of a number of species of holothurians suggest that geographic isolation with a subsequent subspecies and species formation has taken place in an abyssal region along the Pacific coast of Central America and northern South America. Two widely distributed species, *Deima validum* and *Oneirophanta mutabilis,* are in this area represented by geographic subspecies. Two other widely distributed species, *Scotoplanes globosa* and *Molpadia blakei,* are in the same area replaced by the closely related species, *S. clarki* and *M. granulata.*

A clinal variation is present in the deimatid *Orphnurgus glaber,* which ranges from the Bay of Bengal to the Hawaiian Islands.

The deep sea has sometimes been regarded as a refuge for ancient animal groups which are no longer able to stand the competition at shallow depths. This view of a low degree of competition is hardly compatible with the high faunal diversity recently found in abyssal communities.

The existence and dominance of an animal group in the deep sea depend on its ability to compete successfully in this particular environment. The Elasipoda is a pronounced example of a group which owes its dominance to its highly evolved adaptation to life in the deep sea.

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