ANIMAL LIFE FROM A SINGLE ABYSSAL TRAWLING

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INTRODUCTION

In the scientific literature on the deep-sea fauna it has rarely occurred that enumerations of the species and specimens of animals from the single localities have been made or, in other words, that an evaluation of the contents of the single trawlings has been undertaken. The only comprehensive effort along this line was accomplished by MURRAY. In his outstanding account of the results of the Challenger Expedition published in 1895, he listed the names and number of specimens of all species found at each of the stations worked by the Challenger, after the vast majority of animal groups had been worked out by specialists. In his long introduction to the report of the Siboga Expedition, WEBER (1902) presented much valuable information on the contents of many of the abyssal trawlings; this, unfortunately, is somewhat scattered and not easily found in his comprehensive general narrative. The following are listed as examples of later papers giving a preliminary description of the results of distinguished single hauls: Nybelin (1951) on the trawlings of the Swedish Deep-Sea Expedition, BRUUN (1951), dealing with the work of the Galathea in the Philippine Trench,

ZENKEVICH et al. (1955) on the first trawlings by the Russian Vitjaz in the Kurile-Kamtchatka Trench, BRUUN (1957) on the contents of a trawling by the Galathea in the Western Indian Ocean at a depth of 4820 m, SUYEHIRO et al. (1960) on Japanese trawlings in 1958, and WOLFF (1960a) on the contents of each of the known "hauls" (trawlings and bottom samples) at depths exceeding 6000 m (in the hadal zone).

It is generally accepted that animal life decreases quantitatively with increasing depth. The number of species and specimens is generally low in trawls which are brought to the surface after having worked successfully on the abyssal floor at depths exceeding some 2000 m. The contents of the three richest stations (of a total of 138 abyssal bottom trawlings and dredgings) during the *Challenger* Expedition were as follows (Murray 1895):

Station	Locality	Depth	No. of benthic species	No. of specimens
147	S. Indian Ocean			c. 200
146	S. Indian Ocean	2500 m	69	c. 200
237	E. of Japan	3420 m	53	c. 150

In view of this, the results obtained from a single trawling during the Galathea Expedition (St. 716 at 3570 m depth in the East Pacific) were truly remarkable. It is hardly an exaggeration to say that the assemblage of animals from this station is the richest, both qualitatively and quantitatively, that has ever been collected at a single locality in the deep-sea. Qualitatively, the trawling which for the first time brought the ancient mollusc Neopilina to light must in itself be regarded as extraordinary, but, as shown below, several other new forms are also of more than ordinary interest. Quantitatively, it is a unique achievement to obtain from a depth of almost 3600 m 132 different species and about 2100 specimens of benthic metazoans. There are several reasons to account for this high benthic productivity: an area with a large primary production at the surface, excellent conditions for trawling, the fact that the Galathea was the first expedition to use a large trawling gear at great depths, and finally the valuable experiences gained previously - this operation being one of the last to be made during the expedition.

Last year the present author published in Danish an account of the results of this trawling (Wolff 1960b), illustrated with photographs and drawings by the artist Mr. Poul H. Winther. In view of the scarcity of such accounts and the outstanding qualities of this particular trawling, the *Galathea* Committee has found it appropriate to have the paper published in English (in a somewhat altered form) in the *Galathea Report*.

Acknowledgments

Zoologists working on taxonomy will recognize that up to the present only a rather modest number of the animals have been identified to species or described.

It goes without saying that the value of this paper would have been considerably increased if all species had been worked up. It was, however, beyond the scope of the paper to effect more than preliminary identifications of the majority of the species. The following colleagues in the Copenhagen Museum have very kindly helped me with identifying certain animals or with references to literature: KAY PETERSEN (hydroids), JØRGEN KIRKEGAARD (polychaetes), Elise Wesenberg-Lund (gephyreans), JØRGEN KNUDSEN (molluscs), F. JENSENIUS MADSEN (echinoderms), BENT HANSEN (holothurians), and JØRGEN NIELSEN (fishes). Dr. MATHILDE SCHWABL (Berlin), Dr. N. S. JONES (Port Erin), Dr. CLAUDE Lévi (Strasbourg), and Mr. Chas. E. Cutress (Washington) furnished me with preliminary identifications of the animal groups which they are working up (Solenogastres, cumaceans, sponges, and actinians, respectively). Dr. J. H. STOCK (Amsterdam) advised on the walking movement of seaspiders and Dr. J. L. BARNARD (California) supplied information about various amphipods. Finally, Dr. Anton F. Bruun, the leader of the Galathea Expedition, read the manuscript through.

All drawings (except Figs. 10, 14, 15, and 22) were made by Mr. Poul H. Winther and most of the photographs were taken by Mr. H. V. Christensen. The English text was revised by Mrs. M. Goodfellow.

The greater majority of the blocks used for the figures have kindly been placed at our disposal by *Naturens Verden* (Munksgaard, Copenhagen), two of the remainder by *Oikos* (Munksgaard), and one by the Danish Fishery and Sea Investigations, Charlottenlund. This much appreciated help made it possible to include the many illustrations, especially those in colour.

THE TRAWLING

The Galathea was heading south-east along the Pacific coast of Central America. We had reached areas where wind and current cause an upwelling of nutritious water from a depth of a few hundred meters, thus giving rise to a comparatively high production at the surface as well as in the depths. Therefore, there were hopeful expectations of procuring a rich haul.

Throughout the night of the 6th of May 1952 the echo-sounder had indicated a fairly even abyssal plain with rather low, "rolling hills", lying at a depth

of 3500-3600 m. It was agreed to start trawling soon after sunrise, and at 7 a. m. the huge herring otter trawl was made ready. It was of the type used by Danish fishermen. The mouth opening measured 32 m, and the length was 60 m (Pl. VII A). When in action, the mouth of the trawl was kept open by two oblique otter boards, mounted with iron and weighing 150 kg each.

At 7.15 steam was taken off one of the boilers, at 7.45 the trawl and boards were in the water, and the man at the winch began to slowly ease off wire.



Fig. 1. The cod end of the trawl, containing the major part of the catch at St. 716, has just been lifted on board.

(ALEX PETERSEN phot.).

The position was then 9°21′N, 89°12′W, the course 287° (NNW), and the screws were making 126 revolutions per minute. One and a half hours later 4000 m wire had been paid out. By 10.50 a. m. 8000 m were out. This was the length of wire which, according to our calculations, was required for the depth in question if the trawl was to move along the bottom at a rate of 2.3 knots (cf. Kullenberg 1951, 1956).

An angle gauge was attached to the wire astern of the large trawl gallows, and a dynamometre was fixed to the wire above the quarter deck. The inclination of the wire, i.e. the angle between the wire and the surface of the water, was calculated to be 41-43°.¹ This angle would just enable the trawl to reach the bottom with the given length of wire, depth and speed along the bottom. Since the inclination was at first only 30°, the number of revolutions of the screws had to be reduced. Not until 11.45 did the angle reach 41°, and it remained there for slightly less than one hour. Consequently, we presume that the trawl was towed along the bottom for no longer

than 55 minutes, although the interval between the termination of paying out the wire and the commencement of hauling was nearly three hours. The distance trawled was thus a little more than 4 km. The position during the trawling was 9°23′N, 89°32′W, lying about 425 km off the coast of Costa Rica. The direction of the trawling was 287°.

At 13.30 the hauling started. At 16.18 the boards appeared at the surface, and the winch was stopped. Another lengthy interval was required before the trawl bag was safely landed onboard, for the catch was a bulky and heavy one (Fig. 1).

Truly, it was a rich haul. All the zoologists immediately began sorting and pickling the animals obtained (Fig. 2), cleaning the meshes of the net, etc. The work lasted all that evening and the two following days. By then everything had been sorted, labelled and preserved in alcohol or formalin, except the larger fishes measuring more than one meter, which had to be stored in the deep freezer. Preliminary determinations had been made and countings recorded for the journal. Notes had been taken of colours which would eventually fade and sketches prepared, while the more remarkable finds had been photographed and filmed.

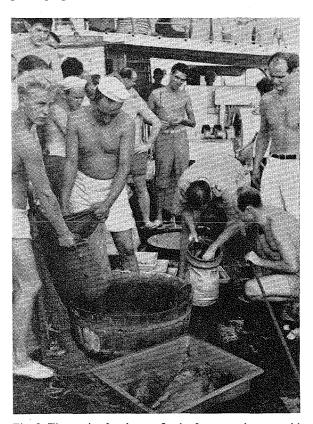


Fig. 2. The sorting has begun. In the foreground a tray with large alepocephalid fishes; behind it the canvas bag.

(ALEX PETERSEN phot.).

Note the misprint in Bruun's explanatory remarks to the List of Stations (1959, p. 21, column 2, line 4 from above): horizontal instead of vertical.

THE ENVIRONMENT

Throughout the trawling at St. 716, the echosounder showed a constant depth of 3570 m. The temperature at the bottom was about 1.9° , i. e. abyssal conditions. The salinity was $34.6^{\circ}/_{00}$, and the oxygen content as high as 2.4 ml/litre at the bottom (Menzies *et al.* 1959). Both the *Galathea* and the *Vema* (see below and p. 135) found the bottom sediments to be a dark greenish, somewhat clayey ooze with many remains of diatoms, radiolarians, and pelagic foraminifers. The *Vema* also

found a geologically-recent (Pleistocene) layer of ash covering much of the area (1. c.). This was 2-15 cm thick and of variable depth in the sediment. An ashfall as extensive as this must have had a marked effect on the fauna even at abyssal depths. The same applies to the strong decrease of temperature which took place in the deep-sea at the onset of the Glacial Age. Thus, an ancient animal like *Neopilina* (see p. 136) was not "just" able to survive to the present time in the constant natural conditions hitherto believed to prevail in the deep-seas. Here, too, upheavals take place that may prove fatal to existing life.

THE ANIMAL ASSEMBLAGE ON PLATE IX

In some of the illustrations it has been endeavoured to show a few of the animals from St. 716 in their natural environment. On the large drawing (Pl. IX) some of the most striking creatures have been especially selected for demonstration. It should be pointed out that depicting this great concentration of animals in one spot was considered necessary for economic reasons, the aim being to show as many locally occurring species as possible. An assemblage of animals to the extent shown would be difficult to envisage – even in this abundant locality. Theoretically – very theoretically – there is, however, a possibility for a "snapshot" like this, since all the animals were actually collected in the same locality.

Neopilina

In spite of their modest size and unimpressive appearance the two cap-shaped molluses in the middle of the plate are, without doubt, the most interesting – and the most famous. The animal was described by Lemche in 1957 under the name *Neopilina galatheae*, as a living representative of the Cambro-Devonian class Monoplacophora. The material comprised ten specimens with soft parts (Fig. 3) and three empty shells, the largest of the former being 37 mm long, 35 mm broad and 13 mm high. A mature male and female were cut in sections and their anatomy described in a large, abundantly illustrated monograph (Lemche & Wingstrand 1959). The fine structure of the shell was studied by Schmidt (1959).

The bearing of *Neopilina* on the systematics of the molluscs was touched upon by LEMCHE & WING-STRAND (1. c.). In addition, several preliminary phylogenetical considerations have been published by LEMCHE (1959 a, 1959 b, 1959 c, 1960). He has, i. a.,

thought it possible to homologize the primitive comb-like gill (ctenidium) with the legs of arthropods, to show that the ventral position of the mouth in *Neopilina* and Polyplacophora (chitons) is similar to that found in trilobites, *Limulus*, primitive crustaceans and polychaete larvae, and to demonstrate that the muscle arrangement points towards a direct derivation of molluses from coelenterates.

The remarkable find of *Neopilina* provided incentive for two American and one Russian research vessel to investigate the type locality of *Neopilina* off Costa Rica in order to procure more material. Only the Lamont Geological Observatory ship (the *Vema*) in 1958, during the course of 11 hauls in the area (with a 1 m dredge – cf. p. 156), found one small specimen at a depth of 3720 m (MENZIES *et al.* 1959).¹

1. Based on the known mouth opening of the trawl or dredge used on the Vema and (probably) the period the trawl remained on the bottom, Menzies et al. (l. c., p. 175) state that each of the eleven Vema hauls in the Costa Rican area covered "an estimated average area of 2000 square meters. This suggests [citation continued] that the animals, if randomly dispersed, occur in the abundance of one for each 22.000 square meters. Doubtless they are not randomly dispersed as was indicated from the "GALATHEA" capture of 10 specimens from one 55 min. cast of the herring otter trawl; however, the average population density must be exceedingly low. The trench monoplacophorans [N. (V.) ewingi] show a significantly higher population density, namely 0.7 for each 1000 square meters or more than 15 times that of Neopilina (sens. str.)." The authors also tabulate the density of each of the other animal groups collected in the Costa Rican area and in the Peru-Chile Trench (Tables 1 and 2).

This is certainly the first time that density has been estimated in this way. It seems premature to do so, unless the authors can satisfactorily explain, a) how the precise moment the trawl reaches the bottom can be determined with this small type of gear (according to our experience this

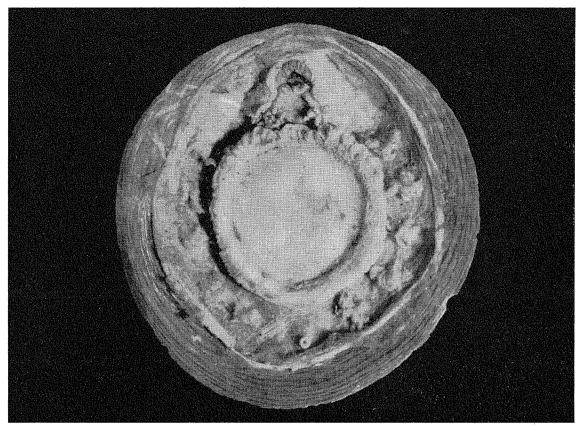


Fig. 3. Ventral view of Neopilina galatheae. On the outside, the continuous pallial fold has been detached from the shell margin as a result of preservation. Anteriorly is the mouth, surrounded by the lips, velum and oral tentacles (homologous with lips and labial palps in bivalves, and the postoral tentacles homologous with the arms in cephalopods). The foot is in the centre, the anus posterior. The metamerism is shown exteriorly by the five pairs of gills, interiorly by ten pairs of nerve connectives, eight pairs of large pedal retractor muscles, six pairs of nephridia, two pairs of gonads, and two pairs of atria.

(M. ØYE phot.).

Later, the Scripps Institution of Oceanography vessel, the *Spencer F. Baird*, collected three more specimens 3000 km further north, off the tip of the southern end of Baja California during the Vermillion Sea Expedition at a depth of 2780-2810 m. A shell fragment was also taken in a Petersen Grab at a depth of 1830 m in a locality just north of the first

happens long after one has stopped paying out wire; b) the exact speed at which the trawl moves along the bottom (the speed at the surface is likely to differ greatly). Only when Kullenberg's calculations for larger trawls (1951) are applied is it possible to provide a rough idea of the said factors in deep-sea trawling (cf. p. 131). The metering devices, designed by R. Bieri and J. Bradshaw (Gunter 1957, Fig. 10) and by R. Riedl (1955, Figs. 1 and 5), or the so-called trawlograph which has been used by Russian oceanographers on sledge (Agassiz) trawls (Zenkevich 1956, Fig. 12, Zenkevich et al. 1959, Fig. 2, and Fig. 4 in this paper), seem to be better methods than that based on Kullenberg's calculations to obtain comparatively reliable data on the area covered during the actual trawling on the bottom.

sample (PARKER, in press). Very recently an Allan Hancock Expedition found 14 very small specimens of a *Neopilina* (1.3-2.4 mm) at 2730-2770 m depth somewhat north of the two latter finds. This is perhaps a third species, having six pairs of gills (like *ewingi* – see below), but differing in shell structure from this species as well as from *galatheae* (MENZIES & ROBINSON 1961).

After the meagre results off Costa Rica in 1958 – as far as *Neopilina* is concerned – the *Vema* continued southwards. Off Peru, at four localities in the upper part of the Peru-Chile Trench (5610-6320 m), the expedition succeeded in obtaining a total of ten specimens of another *Neopilina*, which was described as a new species and subgenus, *Neopilina* (*Vema*) ewingi (Clarke & Menzies 1959).

Neopilina galatheae has six pairs of nephridia but only five pairs of gills (Fig. 3). The five posterior pairs of nephridia open at the base of the gills while

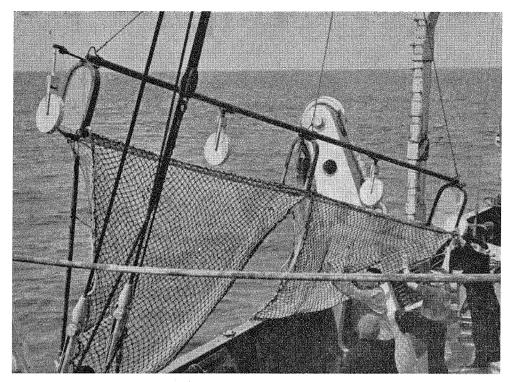


Fig. 4. A 6 m sledge (Agassiz) trawl onboard the Soviet research vessel *Vitjaz*. The trawl is of the same type as that constructed earlier on the *Galathea*. It is furnished with four trawlographs, each consisting of a metal disc with small projections on the edge. The disc rolls along the bottom and a computing apparatus measures the distance trawled. The photograph was kindly placed at my disposal by the Oceanological Institute, Moscow.

(V. Nartsissova phot.).

the renopores of the anterior pair are found in the pallial groove well anterior to the first gill. Thus, a pair of gills was apparently "missing". However, in N. (V.) ewingi a sixth pair of gills is found in connexion with the first nephridia (l. c.).

MENZIES et al. (1959) published photographs of the Peru-Chile Trench floor. Fig. 8C (misprint for 8 D) and Fig. 9 of that paper show what is claimed to be tracks made by two Neopilina ewingi. With the authors' kind permission the original photographs are shown here (Pl. VIII A and B). At the extreme end of the right track is a rather high, compressed object (note its shadow to the right) and behind it (on the other side of the crossing track) is a somewhat similar object, less distinct, but also casting a shadow. In my opinion neither of these two objects can be identified as the upper part of a Neopilina shell as the authors claim. This would appear as a much lower, vaulted "knoll" - cf. Fig. 1 C in CLARKE & MENZIES (1959) and in this paper Fig. D (Pl.VIII) of N. (V.) ewingi and Fig. E of N. galatheae.

It seems more likely that the picture shows a bivalve ploughing its way through the ooze in the

same manner as e. g. Montacuta ferruginosa (personal observations). The tracks are clearly V-shaped and have thus been formed by a compressed, sharp-edged animal. The track left by a Neopilina would be broader and more open. This is extremely evident when the groove-shaped track left by the bivalve Cardium on the soft surface of the wadden sea is compared to the very broad and shallow tracks of the gastropod Littorina (THAMDRUP 1935, Figs. 120 and 124). Moreover, the visible part of the Cardium at the end of the former track (Fig. 120 and Fig. C (Pl.VIII) in this paper) closely resembles the object at the end of the right track in Figs. A and B (Pl.VIII). Finally, the assumption that a bivalve and not *Neopilina* is the animal in question is supported by the fact that while the Vema collected only 3 specimens of Neopilina at this station (150) it took 56 specimens of bivalves. In the total area only 10 Neopilina but no less than 733 bivalves were collected. This would provide a much greater possibility for photographing a moving bivalve, although it is true that some of them may - during their entire lifetime or most of it - remain completely buried in the ooze.

There are apparently two animals at the end of the right track. However, the posterior (lower) object is probably not an animal at all but a small mound which the animal passed close by before reaching the extreme end of the track. A similar, although less high, object can be seen on Figs. A and B, lying close to the track about 20-25 mm behind (under) the first one. The latter object is almost certainly a small mound.¹

MENZIES et al. did not discuss the strange fact that the left track ends blindly. In my opinion the only explanation seems to be that the animal buried itself into the ooze (or, less probable, emerged from it). It is, however, rather remarkable that no trace of a hole or any disturbance of the ooze appears to have been left.

Finally, it is evident that the left track has crossed the right and, consequently, is the most recent. This is surprising in view of the fact that the animal at the end of the right track is so close to it. Again the only possible explanation is presumably, that the visible animal was stationary while another animal, which made the left track, emerged from the bottom, moved behind the first animal and disappeared beyond the range of view before the photograph was taken.²

However all this may be, it is very probable that *Neopilina* actually *does* creep along the bottom, as also shown on Pl. IX. On the anterior part of the shell of one *N. galatheae* small hydroids have been found (possibly *Perigonimus*) which prove that the animal, at most, lives partly buried, but the fact

1. According to Menzies et al. (1. c., p. 178) their submarine photographs covered an area roughly equal to 200 sq. m. in the Peru-Chile Trench locality. Based on the assumption that the two objects under discussion are Neopilina, the authors venture to suggest an, admittedly "very rough", estimate of a density of two Neopilina per each 200 sq. m. and to compare this density to that derived from the trawl catch, the latter representing "around 25 times less density than the photographic density on the bottom". A density estimate derived from such submarine photographs appears to be still more premature to undertake than the above mentioned estimates based on the results of the dredgings.

that the foot is only feebly musculous makes it doubtful whether it moves around very much. It is obviously a deposit feeder. All the intestines were filled with material similar in appearance to the bottom ooze adhering to the outer surfaces. According to Lemche & Wingstrand (1959) this material "includes a high proportion of radiolarians, scattered centric diatoms, etc., mixed up with much undefined detritus matter" (Fig. 5). Similarly, a faecal pellet of N. (V.) ewingi contained "diatom frustules, radiolarian skeletons, pelagic foraminiferal tests and innumerable bacteria-size particles as well as sponge spicules" (Menzies et al. 1959). It seems probable that both the velum and postoral tentacles (Fig. 3) serve as food-collecting organs.

In the current discussion on the antiquity of the deep-sea fauna, Menzies & Imbrie (1958) stated Neopilina to be the only Palaeozoic relict known in the abyssal fauna, while Zenkevich & Birstein (1960) listed it, in conjunction with several others, as an ancient element of the deep-sea. MADSEN (1961b) pointed out that much of the difference of opinion is due to the fact that the two latter authors have attributed animals found below a depth of about 600 m to the abyssal fauna, thereby including not only the abyssal but also most of the bathyal fauna. It is generally accepted that the bathyal region contains a considerably larger number of ancient (i.e. at latest Early Tertiary) species than the truly abyssal region (at depths exceeding about 3000 m). The recent find of *Neopilina* also at bathyal depths (cf. above) may therefore indicate that the Monoplacophora thrived at bathyal rather than at abyssal depths for the greater part of their evolution. This suggestion is in agreement with MADSEN'S (1961b, p. 191) who wrote that "the group may have been already represented in the abyssal deep-sea in the Early Palaeozoic, but it is also conceivable that, when during Devonian times it disappeared from the fossil record, it was still confined to moderate depths, and not until a much later geological period extended its range also to the abyssal zone". Although not generally accepted, there is much evidence of a radical change in temperature and other physical and chemical conditions in the abyssal region towards the end of the Tertiary (cf. MADSEN (1. c., p. 187) and MENZIES et al. 1961). It appears more likely that Neopilina did not descend into abyssal depths until after such changes had taken place, than, alternatively, that it was able to survive there in the period during which these changes occurred.

^{2.} Another of the animals on the photograph (Pl.VIII A) was identified by MENZIES et al. as a "holothurian in upper right corner". This must be a misprint for left corner since the undeterminable object in the right corner is definitely not a holothurian. The many small vertical sticks were termed "worm tubes". These are possibly sea-pens (aff. Virgularia), being certainly too long and stiff for most worm tubes. Two of them have seemingly been lifted up by the holothurian in the upper left corner. They are too long and narrow to be interpreted as papillae of a Scotoplanes (cf. Pl.XB).

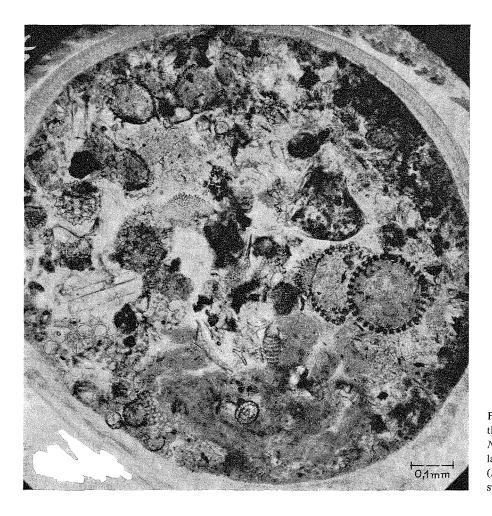


Fig. 5. Cross section through the first intestinal coil of *Neopilina galatheae*. Radiolarians are abundant. (After Lemche & Wingstrand 1959).

Probeebei mirabilis

The orange coloured crustacean on Pl.IX also proved to be of great interest. It is a well-known fact that the hermit crab normally hides its soft abdomen in a gastropod shell which it carries around with it. Owing to this spirally-coiled accomodation, the abdomen has in the course of time attained a wry and asymmetrical shape; the claws have become unequal in size, and certain abdominal legs (pleopods) formerly situated on the right side have completely disappeared. This asymmetry is so genotypically fixed that it inevitably appears in the first postlarval stage independent of whether the snail shell is occupied or not. However, a small, separate family, the Polychelidae – consisting of primarily bathyal species - has preserved the original symmetry of hermit crabs, all abdominal legs are present on both sides, and the abdomen is as symmetrical and armoured as that of a common or of a spiny lobster.

In almost all respects the reddish crustacean from St. 716 is a typical hermit crab: the 2nd and 3rd

pairs of walking legs are long and the 4th and 5th pairs much shorter and of a different shape, the abdomen is asymmetrical, and the abdominal legs absent on the right side. The segments of the abdomen are, however, as hard and calcified as in the Polychelidae. This is, consequently, a species whose ancestors have gone through the entire evolution from the original, symmetrical form, which was freely-roaming, via the stage in gastropod shells where the asymmetrical abdomen, etc. was eventually developed, and finally back to a free mode of life where the abdomen is protected by its own armour but the asymmetry preserved. Only one instance of a similar evolution is known, the robber crab, Birgus latro which lives on dry land. In both cases this secondary calcification of the abdomen must be due to lack of sufficient shell material.

Only one post-larva of this remarkable crustacean has been known previously. It was collected by the American *Arcturus* Expedition at a depth of 1145 m West of the Gulf of Panama and described under the name of *Probeebei mirabilis* by BOONE (1926) who regarded it as a primitive macruran. St. 716 yielded

18 specimens, including adults and several developmental stages. A description of the species and its bearing on phylogeny and evolution has recently been given (Wolff 1961 a, 1961 b).

The body length of the ovigerous female on the plate is 6.5 cm, when measured with the abdomen bent under the body. Situated on the carapace and legs are several small white tubes of a serpulid polychaete worm.

Probeebei is perhaps the most recent and the most highly specialized hermit crab, thereby forming a strong contrast to *Neopilina*. The ancestors of the latter may be traced further back than those of probably any other existing animal. It has remained almost unaltered during the vast span of 350-400 million years.

Neotanais pfaffi

The two chalk white crustaceans in the left bottom corner of Pl. IX are a female and male of tanaids, a group closely related to the isopods. They are c. 20 mm long and were referred to a new species, Neotanais pfaffi (WOLFF 1956a). At St. 716 a total of 41 individuals was collected. Neotanais belongs together with another genus of exclusively hadal occurrence - to a separate, apparently rather primitive family within the tanaids. Apart from a single find in the North Atlantic at about 700 m and at a temperature of some 10°C. (incidentally, a find which is not too reliable) none of the 13 species of this family have ever been taken at depths of less than 2000 m or at temperatures above 3.3°C., and two of the species are even hadal. This is enough to show that Neotanaidae is one of the very few pronounced deep-sea and cold-water families of the animal kingdom (WOLFF 1956c).

Galatheathauma axeli

The large fish Galatheathauma axeli, to the left in Pl. IX, is without doubt the strangest fish taken by the expedition. It obviously belongs to the Pediculati or angler fish, but in length (47 cm) it exceeds almost all other members of the order. The light organ is forked and hangs down like a clapper from the palate *inside* the mouth. The latter is enormous in size and furnished with a terrifying row of long and pointed, slightly curved teeth. There are also smaller teeth around the entrance to the pharynx. The mouth works like a trap when the prey (prob-

ably fish, crustaceans, etc.) is lured too close to it – possibly attracted by the light organ. The eyes are minute and vestigial and are situated close to the corners of the mouth.

There are two factors which seem to indicate that Galatheathauma lives close to the bottom, unlike almost all other deep-sea angler fish; in the first place it has never been caught pelagically—not even during the very extensive work by the Dana Expedition close to this area. Secondly, the mouth is directed downwards which indicates that it attacks from above—unlike the great majority of pelagic Pediculati in which the mouth is directed upwards. However, not until more specimens become available and their stomach contents investigated will the question of the habitat of this unique fish be finally settled.

Bassogigas and the alepocephalid fish

The uppermost of the two fishes (top right) is probably a *Bassogigas digitatus*. It has been taken on four previous occasions, each time in the Eastern Pacific and always at depths between 2200 and 3440 m. Eight specimens were caught at St. 716, three of which may, however, belong to a different species. The specimen shown measures 28 cm, and the beautiful steel grey colour of its head is still preserved. The genus *Bassogigas* contains eight species (GREY 1956) which are all abyssal (1800-4600 m). One of its representatives may descend to the upper part of the hadal zone, the deepest-living fish caught by the *Galathea* being a *Bassogigas* from 7160 m in the Sunda Trench south of Java.

The other fish belongs to the family Alepocephalidae which consists of fairly large deep-sea fishes, in a total of 17 genera with 40 species. Some of these are no doubt pelagic, but others have been taken in bottom trawls only. This fact, as well as certain features in their shape make it highly probable that they are benthic. On the other hand, it is very likely that now and again they may swim away from the bottom - in e. g. a manner similar to that of the cod. St. 716 yielded a total of four giant alepocephalids, 50-66 cm long, with large, broad heads and bulky bodies and with muscles of a rather gelatinous consistency (Figs. 2 and 26). There are two species, one probably belonging to Bathytroctes, of which six, exclusively abyssal species are known (GREY 1956).

Hyalonema and Epizoanthus

To the right and immediately in front of this fish are to be seen two stalked siliceous sponges belonging to the genus *Hyalonema*, which is probably the most common sponge at bathyal and abyssal depths. It contains 95 species which have been referred to 14 subgenera. The present species is *H. bianchoratum* which was previously taken twice – off West Mexico at a depth of 3437 m and off North Peru at 4063 m (WILSON 1904).

The "body" of this species is roundish, of a cotton-like consistency and with distinct openings (oscula) for the outstreaming water. As in other siliceous sponges the spicules are infinitesimal although the long stalk is very conspicuous. It consists of fine, parallel or slightly coiled, siliceous threads, up to 1 m long which are transparent and as sharp as glass splinters.

On several of the stalks abundant growths of colonies of the sea-anemone *Epizoanthus* are present. Such colonies are also frequently seen covering gastropod shells inhabited by deep-sea hermit crabs. These *Hyalonema* stalks often serve as an excellent base for hydroids, the stalked barnacle *Scalpellum* and other sedentary animals which are able, in this way, to raise themselves above the soft bottom.

Umbellula thomsoni

Finally, Pl. IX shows a few pink, flower-like organisms whose fine branches are stirred by the faint bottom current. These are a special kind of sea-pens, almost certainly the species Umbellula thomsoni. The colonies are about 15 cm high and the numerous single individuals (polyps) can be distinguished on the arms. All the colonies of this species and of the two other species from St. 716 (see p. 142) are young ones. This is probably due to the fact that the older colonies, which may reach a length of 2 m, are so firmly planted in the sea bottom that they will bend, but can not be torn away when the trawl passes over them. It is also known that, when alarmed, shallow-water forms may contract violently, whereby all the soft parts suddenly disappear beneath the bottom and only the "empty" stalks remain, thus leaving very little for the trawl to grip. Umbellula thomsoni has frequently been taken in the Atlantic, the Indian, and the Western Pacific Oceans (at depths between 1000 and 5850 m), but not until now in the East Pacific.

The genus *Umbellula* was revised by Broch (1958) who recognized only seven valid species ranging in depth from 77 m (in the Antarctic) to 5860 m.

DEEP-SEA ANIMALS ON STILTS

On Pl. X are grouped together two strange, long-legged forms. A considerable prolongation of legs and sense organs (in crustaceans, especially the antennae) is one of the most characteristic features of deep-sea animals. The stilt-shaped legs have presumably become developed to adapt to the soft bottom, while the prolongation of the antennae is doubtless a result of eternal darkness and consequent blindness.

Colossendeis colossea

Fig. A shows an orange coloured sea-spider or pycnogonid. The *Galathea* collection of this extraordinary group was worked up by Louis Fage (1956a, 1956b) who referred this individual to the species *Colossendeis colossea*, i. e. "the gigantic giant". It is indeed a giant among sea-spiders, the majority of which grow no bigger than the size of a normal hand (many being much smaller). This particular specimen measures more than half a meter from the tip of one of its walking legs to the far end of the opposite leg.

The sea-spiders form a group which is fairly poor in species and their systematic position within the Arthropoda is still uncertain. The legs are almost always greatly prolonged and are attached to a body ridiculously minute in comparison. Therefore, there appears to be reason enough for the intestine sending blind sacs far out into the legs. The abdomen is reduced to a very small tap. A long proboscis is present on the head and is extremely mobile at the base. Interiorly, it is provided with teeth and a complicated sieving apparatus which rejects coarser particles. The long-legged forms always have a greatly prolonged proboscis - perhaps analogous with the long neck of the giraffe. In front of the four pairs of walking legs, which are of equal length, this species has a pair of palps which - at least in littoral species - are used for seizing and holding the prey. Next is a pair of so-called ovigers on which the male carries the eggs in a ball-shaped lump. On the inner side of their distal segments these legs are provided with comb-shaped spines whose function it is to clean and rid the other legs of mud, etc.; this is performed by movements from the proximal towards the distal end of the legs, as shown in the drawing.

Certain difficulties were encountered in reproducing the exact manner in which the animal walks along the bottom. Prell (1910) and Helfer & Schlottke (1935) have published descriptions of the slowly advancing walk and swimming movements of closely related forms. On the basis of these descriptions and advice given by the Dutch specialist Dr. J. H. Stock, we have tried to reconstruct the animal's walk. Actually, this corresponds closely to the method of swimming – in slow-motion. The articulations of the legs are built in such a way that the legs themselves can only move in the vertical plane. Furthermore, the pycnogonids do not walk on the tips of their claws but keep them rather somewhat bent towards the direction of the following joint.

An excellent photo (from a depth of 1800 m) of a large *Colossendeis*, measuring 70 cm, was published by OWEN (1958).

With regard to food, littoral forms show a preference for hydroids and sea-anemones. On almost all occasions the Norwegian *Michael Sars* Expedition collected hydroids together with sea-spiders in the same deep-sea trawling, and frequently also antipatharian corals, sea-pens and sea-anemones (Murray & Hjort 1912). This may indicate that seaspiders share the same choice of food in the deep-sea and that "our" *Colossendeis* could fill all of its many blind sacs by sucking on the hydroids and antipatharians, mentioned on p. 141, or the seapens and sea-anemones, shown on pl. IX.

Colossendeis colossea is an example of the rather few deep-sea species among the sea-spiders which are known from all oceans except the high-arctic ones. Like a considerable number of other species of sea-spiders it has a wide vertical distribution (from 865-4140 m). It is, however, limited to bathyal and abyssal depths, as are nearly all the other species of the genus.

Limopsis compressus and Stephanoscyphus simplex

The partly buried bivalve (Pl. X A) is *Limopsis* compressus which is about 4 cm long. It was originally taken by the *Albatross* in 1891 at eight localities in the Gulf of Panama, at depths between 1950 and 4100 m (DALL 1908)¹ and not seen again until

the Galathea collected numerous specimens in the same area – e. g. at St. 716 twenty individuals. Limopsis is primarily a deep-sea genus which includes almost a score of species, all with the outer horny layer (the periostracum) prolonged into a hair-like fringe along the edge of the shell. The possible function of this fringe is unknown.

Attached to the shell of Limopsis compressus are some old tubes of the same species of serpulid worms as those which have settled on the hermit crab (p. 137). On the right side of the shell is a single tube of the polyp Stephanoscyphus simplex. This tube is unbranched, measures up to 2 cm in length, is ringed and fairly soft, and has interior thickenings. At the base there is a small disc. Kramp (1959) worked up the large Galathea collection of this species from a total of 29 localities. This is an impressive number, considering that the species was only recorded from eight other localities by all previous deep-sea expeditions. It is distributed in all three world oceans at depths between 450-7000 m. By far the majority of the finds are abyssal, and consequently, from areas with temperatures below 4°C. The few localities (e. g. off the Philippines) where it occurs at temperatures up to about 10°C. all seem to be characterized by a very rich fauna. It is very likely that the abundance of food is a strong factor in making it possible for a primarily abyssal species like Stephanoscyphus to thrive here; the higher concentration of food thus compensates for the increase in metabolism which is a consequence of the higher temperature.

The actual type of medusa produced from this polyp is still in some doubt. Kramp (1. c.) found very young medusae in the tube of one individual which can, with some hesitation, be referred to the genus Nausithoë. It is known that this genus represents the medusa of one or two other species of Stephanoscyphus. Three bathypelagic species of Nausithoë exist, and some time in the future one of them will certainly prove to be the sexual generation of the asexual polyp Stephanoscyphus simplex.

Munnopsis longiremis

The two crustaceans on Fig. B. (Pl. X) are isopods, belonging to the species *Munnopsis longiremis*. Of this species only one specimen has previously been taken (at a depth of 1485 m off the Galapagos Islands by the *Albatross*), whereas we obtained 37 individuals at St. 716. *Munnopsis longiremis* belongs to a family with two genera, one

The American Albatross is the only other research vessel which worked in the deep-sea of this area prior to the Galathea; most of its work took place around the turn of the century.

of which has three purely pelagic species, while all ten species of the other genus appear to be bottom forms (WOLFF, in press). The species are i. a. characterized by their enormously prolonged antennae and 3rd and 4th pairs of legs. The body length is less than 20 mm.

A study of the intestines of seven specimens of *M. longiremis* from St. 716 – and of several other *Galathea* isopods – has shown that the deep-sea forms are primarily deposit feeders, utilizing the organic matters in the bottom sediments. In all seven specimens of *longiremis* I found many diatoms, radiolarians and sponge spicules, a few polychaete bristles in some, and several shells of pelagic foraminifers in another. They are probably also occasional predators or scavengers, since one contained fragments of an asellote isopod and another, fragments of a benthic copepod.

The movements of these animals are very interesting and were studied on a Nordic species, M. typica, by SARS (1899) and HULT (1941). Since typica is a closely related species with a virtually identical shape, I have ventured to assume that the same characteristics are true of longiremis. The walking movement is slow and tottering and may be taken in all directions, forwards, backwards or sideways. Now and then the animal stops to pick up small particles from the bottom, using the first and, in particular, the second pair of walking legs. The particles are brought to the mouth, but apparently no actual feeding takes place in this way. If the animal is disturbed in some way or other the body is pressed close to the bottom. But if seriously alarmed, the oar-shaped posterior legs (5th-7th pairs) make violent, simultaneous strokes, causing the animal to dart backwards and upwards, away from the bottom. Meanwhile the antennae and the four elongated legs remain close together and are drawn after the body (as illustrated by the swimming animal which, accordingly, is moving towards the left in Fig. B). When the animal ceases to swim the antennae and legs are spread apart, and like a parachute it sinks again towards the bottom, in much the same manner as a swimming sea-spider. It is not unlikely that it will land upside down, but a forward or a backward somersault turns it around again – successfully preventing its long appendages from becoming entangled.

Scotoplanes n. sp.

The animal in the foreground of Fig. B is a representative of the most abundant deep-sea group of animals - at least as far as weight is concerned, i. e. the sea-cucumbers or holothurians, relatives of the starfish, brittle-stars and sea-urchins. The present species is identical with one taken by the Albatross at two localities off Peru (at 4050 and 5200 m depth). CLARK (1920) referred the Albatross specimens to Scotoplanes murrayi, collected by the Challenger in the Antarctic Indian Ocean (2300 m). In his monograph on the Galathea holothurians BENT HANSEN has, however, the intention of describing the Pacific form as a new species. The Challenger collected one specimen, the Albatross four, and the Galathea fiftyfour. Scotoplanes is a pronounced deep-sea genus, even counting two hadal species, one in the Kermadec Trench (6180-6770 m) and one in the Philippine Trench (9820-10.000 m), so far the deepest record for identified species of holothurians (B. HANSEN 1956).

The holothurian is here drawn visibly on the bottom, not buried in the ooze. This was done purposely owing to the existence of a deep-sea photograph (LAUGHTON 1959, Fig. 11), showing a species of the closely related genus *Peniagone* crawling free of the bottom.

This species of *Scotoplanes* may vary in size from 2 to 8 cm. The mouth is surrounded by a ring of tentacles which help to collect the bottom sediments, the sea-cucumbers being typical mud-swallowers. As well as a double row of tube feet there are four long papillae on the dorsal side. The skin contains a large number of minute spicules, and as in most other deep-sea holothurians, it is very delicate and transparent.

THE REMAINING ANIMALS

Sponges

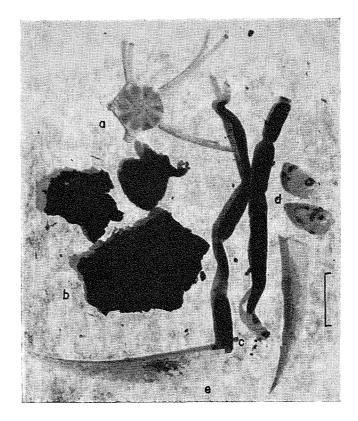
In addition to the *Hyalonema* shown on Pl. IX, St. 716 yielded two other species of this abundant genus. One is, according to Dr. CLAUDE LÉVI, a new species of the genus *Asbestopluma* which has a bipolar and abyssal distribution. The sponge is globular

in shape and raised from the bottom by means of a stalk. The other is the second known record of *Cladorhiza linearis* which was first taken by the *Challenger* in 1875 at a depth of 4362 m in the Central South Pacific (RIDLEY & DENDY 1887).

Although the protozoans from St. 716 are not

Fig. 6. Various animals from *Vema* stations off Costa Rica. a, an ophiolepid, probably either *Ophiura irrorata* or *Ophiosphalma glabrum*; b, the large, flat foraminifer *Stannophyllum zonarium*; c, tubes of a maldanid polychaete; d, the holothurian *Sphaerothuria bitentaculata*; e, the scaphopod *Dentalium megathyris*. The identifications are made by comparing them with specimens from the *Galathea* trawling. The scale is 2 cm long.

(After Menzies et al. 1959).



under consideration in this paper, there are worth-while reasons for mentioning one foraminifer which occurred at this locality in large quantities. Its shape is flat and mat-like, the consistency much like that of felt and the colour very dark green. It is badly broken but there are specimens as large as 10-15 cm. It was preliminarily referred to the sponges in Copenhagen and sent to Professor Lévi with the sponge collection. The *Vema* also obtained specimens in this area and likewise regarded them as sponges (MENZIES *et al.* 1959); some fragments are shown on Fig. 6 b.

This peculiar group was first described by HAE-CKEL (1889) who worked on the *Challenger* material. He established no less than 26 very arbitrary "species" and 11 "genera" which he referred to the horn sponges (Keratosa). Goës (1892) studied material from the Albatross and found the animals to be Foraminifera. Goës' species was later shown to be identical with HAECKEL's Stannophyllum zonarium and according to Dr. AKSEL NØRVANG of the Copenhagen Museum, the Galathea specimens may also belong to this species. It is probable that HAE-CKEL's eight species of the two genera Psammophyllum and Stannophyllum can all be referred to S. zonarium which has thus a wide distribution (Pacific and Indian Oceans) and occurs only at depths between 3000 and 5300 m.

Coelenterates

Some of the coelenterates were mentioned above, namely the scyphozoan Stephanoscyphus (p. 139) and the hydroid on the Neopilina shell; this hydroid also occurred on some of the sea-stars from this station (see p. 152). In addition, there were three small colonies of a Sertularia species, only a few cm high, on which a few individuals of the genera Lafoea and Campanularia were growing. More conspicuous are eight beautifully feathered colonies of an antipatharian coral of the genus Bathypathes, each about 25 cm high. The stem of the colony is attached to a worm tube, and the numerous single polyps are situated in ranks along the fine, dark brown branches.

In addition to the zoantharians on the *Hyalonema* stalks (see p. 138), seven species of actiniarians were taken at St. 716. Mr. CHAS. E. CUTRESS has kindly provided me with preliminary identifications.

Twenty-six specimens, up to 5 cm in length, are referred to the genus *Edwardsia*. They closely resemble *E. intermedia*, one specimen of which was taken by the *Albatross* in 1887-88 off the southern coast of Chile from 223 m (McMurrich 1893).

A single specimen of *Bolocera pannosa* occurred in the haul. This species was previously collected once (also by the *Albatross*) from off Southern Cali-



Fig. 7. A specimen of the sea-anemone *Chondrophellia coronata* from the North Atlantic. 2×nat. size. (After Gravier 1922).

fornia at a depth of 757 m. The *Bolocera* are large, many-tentacled sea-anemones. The tentacles, usually long and robust, possess circular muscles at their bases. Through the action of these muscles *Bolocera* easily shed their tentacles when disturbed.

Actinoscyphia plebeia is represented by six specimens. The species was previously known from a single specimen, taken by the Albatross off Central Chile at a depth of 1238 m. The broad oral disc of this sea-anemone bears two cycles of tentacles at its periphery. These tentacles (especially the outer ones) are conspicuously thickened on the aboral sides of their bases.

Thirteen specimens belong to the East Pacific and Atlantic species *Chondrophellia coronata* (Fig. 7), which has a known bathymetric range of 600 to 3570 m.

The genus Amphianthus is represented by 41 specimens which closely resemble A. lactea, also described by MCMURRICH (1893) from a depth of 821 m off Southern Chile. The Galathea specimens were on shells of living scaphopods while those collected by the Albatross were on dead corals, but amphianthids show little or no host preference.

Finally, there is one specimen which is a new species, perhaps referable to *Telmatactis*, and three specimens which are probably a new species of the genus *Kadosactis*, hitherto known only from the North Atlantic.

Young specimens of *Umbellula* were mentioned above (p. 138). Two other species of sea-pens were represented by about a dozen young colonies, each 10-30 cm high and of a white-yellowish colour. The species belong to the genera *Pennatula* and *Funiculina* which include a great number of littoral species, while about 25 species live on the continental slope and at abyssal depths.

Worms

Dominating animals on soft bottom at all depths are the bristle-worms or polychaetes; these were so frequent at St. 716 that in spite of their moderate size they could be measured in litres: $^{1}/_{2}$ 1 living worms and 2 1 empty tubes.

By far the most common was one very big and one smaller species of maldanids (almost without doubt the genus Maldane) which live in heavy tubes of black ooze (Figs. 6c and 8, Nos. 7-10). Five or six species could be referred to Aphroditidae and Eunicidae which, likewise, are tube-dwelling. Among the former were a dozen large Macellicephala which have their huge probosces everted (Fig. 8, 5-6). This genus has no less than five species in the hadal zone, four of which were even taken exclusively at depths exceeding 6700 m, one being the deepest known polychaete, procured from a depth of 10.210 m in the Philippine Trench (KIRKEGAARD 1956a). A single specimen of the eunicid Lumbriconereis was also found at St. 716; this genus is also known hadally. Another eunicid worm was represented merely by several empty tubes (Fig. 8, 1-4); these were tough and semi-transparent and without exception, were found twisted around the spines of sea-urchins (cf. p. 153).

One short and thick specimen of *Travisia* was present (Fig. 8, 12), probably the species *profundi* which is the only deep-sea species of this genus (1000-7300 m); its distribution is extremely scattered (Bering Sea, W. and E. Pacific, E. Atlantic). Of the family Flabelligeridae a large and very hairy species was found. In addition to a few representatives of several more families, there were finally, two species of serpulids; one being the small species mentioned above, found on the shell of *Limopsis* and on the hermit crab, the other a larger species found growing on a piece of cinder from a ship. Fig. 9 shows that, for reasons unknown, the serpulid in the middle has left its safe substratum, the tube being raised almost vertically – like a snake about to attack.

The sipunculids form a group poor in species, ten of which are, however, found at depths exceeding 3000 m, two of these even penetrating a little into the hadal zone (Murina 1957). Five specimens of the deep-sea genus *Golfingia* were represented at St. 716. Also found was one priapulid; this is the second specimen from that area of *Priapulus abyssorum* (Fig. 10), described by Menzies (1959) on one specimen taken by the *Vema* at 5680 m about 200 km north of St. 716. The priapulids are likewise poor

Fig. 8. A few of the larger polychaetes from St. 716. 1-4, empty tubes of an eunicid, twisted around echinoid spines; 5-6, proboscis and complete specimen of *Macellice-phala* sp.; 7-10, two species of maldanids, partly or entirely drawn out of the black mud tubes; 11, small ampharetid; 12, *Travisia* sp. Measurement in cm. (H. V. C. phot.).



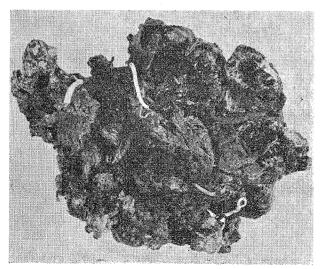


Fig. 9. Piece of cinder with three white serpulid tubes, other polychaete tubes and one *Stephanoscyphus simplex*. $^3/_4$ nat. size.

(H. V. C. phot.).

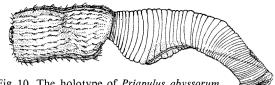


Fig. 10. The holotype of *Priapulus abyssorum* from 5680 m off Central America. $\frac{1}{3}$ nat. size. (After Menzies 1959).

in species and until this species became known the group was recorded down to a depth of some 500 m only. The species is important as these two records prove tropical submergence of *Priapulus*, a genus which was hitherto regarded as a classical case of bipolar distribution (l. c.).

Finally, mention should be made of a single specimen of a leech, found clinging to a fish of the genus *Bassozetus*. The 3570 m at St. 716 (and 3830 m at St. 607 in the Tasman Sea where another leech was found) are by far the greatest depths from where leeches have hitherto been recorded.

Crustaceans

The number of crustacean species found at St. 716 is no less than a total of 32. The smallest of these are three benthic copepods belonging to the large group of harpacticoids. There are 32 specimens of stalked barnacles of the genus Scalpellum, characterized by having both a short and a thick stalk and many plates covering the "head" (capitulum). The genus comprises an enormous number of species (approximately 175), 40 of which are found deeper than 2000 m, although only two seem to reach just into the hadal zone.

Another group of Cirripedia are the ascothoracids which live parasitically on, or more often in-

side, anthozoans, sea-anemones or echinoderms. The body is enclosed in a mantle; in most species the body segmentation has been lost, and the legs also are unsegmented or have entirely vanished. The mouthparts are stinging-sucking. On the dorsal side of a sea-star (Eremicaster gracilis, see Fig. 23) F. J. Madsen discovered two tiny holes leading in to one or two ascothoracids. It is most likely that they are a species of the genus Myriocladus, which lives in sea-stars of this family. Another ascothoracid from an anthozoan host is known from a depth of 4200 m (Krüger 1940).

The cumaceans are merely represented by a fragment of one specimen (Fig. 11). The length of the beatifully sculptured carapace is approximately 5 mm, which makes it one of the largest cumaceans known. Unfortunately, most of the slender pleon is missing. However, it is without doubt a new species, probably of the deep-sea genus *Makrokylindrus*, which i. a. comprises the only known hadal cumacean.

In addition to *Neotanais pfaffi* (p. 137), St. 716 yielded another new species of the same genus, *N. armiger* (WOLFF 1956a)¹ and there are still five other species of tanaids which have not yet been studied.

The isopods are certainly one of the dominating deep-sea animal groups. The biggest species from St. 716 is a true giant among isopods, 6 cm long; it is surpassed only by a few species (especially *Bathynomus giganteus*) and is the largest of the asellotes. The three specimens are not only representatives of a new species but also of a new genus and have been named *Paropsurus giganteus* (WOLFF, in

 The two tanaids shown on Fig. 7 C in Menzies et al. (1959) are almost certainly Neotanais armiger (left) and pfaffi (right).

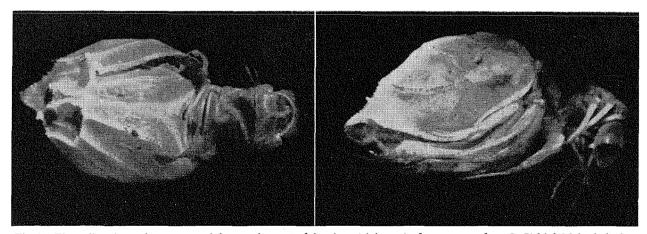


Fig. 11. The well sculptured carapace and the anterior part of the pleon (abdomen) of a cumacean from St. 716 (cf. *Makrokylindrus* n. sp.). $10 \times$ nat. size. (H. V. C. phot.).

press). As in the genus *Bathyopsurus*, which was first taken by the Swedish Deep-Sea Expedition in 1948, the posterior body segments and the abdomen are greatly swollen. The integument is transparent and very slightly calcified, almost parchment-like. As well as a large amount of unidentifiable detritus, the gut contained a great many diatom tests. In addition to St. 716 in the East Pacific, the *Galathea* also took this species in the Tasman Sea, in the diametrically opposite end of the huge Pacific Ocean only a few benthic deep-sea isopods are so widely distributed.

The stately, almost 30 mm long isopod Storthyngura pulchra (Fig. 12) was originally described by H. J. Hansen (1897) who gave it the very appropriate species name. It is indeed a splendid animal, chalkwhite and provided with elegant spines. It is seldom that an isopod is brought up from the deep-sea with such well preserved legs but, unfortunately, the second pair of antennae have as usual been broken off. HAN-SEN's material was taken by the Albatross in two localities in the Gulf of Panama (2500-2700 m) from where the Galathea also procured a single female (3000-3200 m), in addition to the three males from St. 716. Another subspecies of Storthyngura pulchra was described by BENEDICT (in RICHARDSON 1901) under the name Eurycope caribbea and was taken by the Albatross at 1260 m off the West Indies, while a third subspecies is being described on Galathea material from 6700 m in the Kermadec Trench N.E. of New Zealand (Wolff, in press). The genus Storthyngura is no doubt the most pronounced abyssal-hadal genus within the isopods; it comprises 30 species and subspecies, all of which - apart from one antarctic species taken between 400 and 750 m - have been collected at depths exceeding 1260 m and always at temperatures ranging between -1.9 and +4.9 °C. No less than nine species are wholly or partly hadal, and the deepest known species descends to 8430 m in the Kurile-Kamtchatka Trench (BIRSTEIN 1957).

St. 716 yielded two new species of the curious isopod genus *Ischnomesus* which has a long and narrow, stick-like body. One has been named in order to match the beautiful rosy to very faint light green tinge of the calcified integument, which is ordinarily pure white or yellowish. The other species is represented only by the posterior part of the body and pleon of one individual, but the pleotelson is so characteristically pear-shaped and flattened that it was found justifiable to give the species a name despite the head and anterior part still being unknown (WOLFF, in press). Like *Storthyngura*, *Ischnomesus*

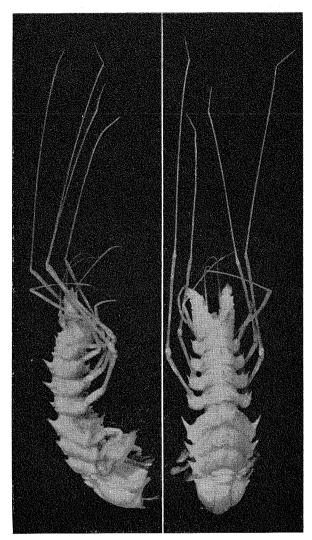


Fig. 12. The magnificent, 30 mm long isopod Storthyngura pulchra. Hardly 2×nat. size.

(H.V. C. phot.).

is a distinct deep-sea genus: apart from one nordic species which goes up into the littoral zone and two bathyally occurring species, the remaining eighteen are restricted to abyssal depths, three even penetrating into the hadal zone (Wolff 1956b; Menzies, in press). One more asellote isopod, *Munnopsis longiremis*, was mentioned above (p. 139).

Five specimens of the large isopod genus Arcturus (perhaps representing two species) were caught. Like so many other deep-sea isopods, these Arcturus are provided with an abundance of spines (Fig. 13), and in particular, the front pair of walking legs are furnished with very long setae, probably serving to prevent the animal from sinking into the soft bottom. The specimen shown measures 30 mm.

As with the isopods, the amphipods also are among the prevailing groups in the abyssal zone.



Fig. 13. A spiny isopod of the genus Arcturus. $3 \times nat$. size. (H. V. C. phot.).

The finest amphipod from the expedition is the magnificent, elegantly keeled *Parargissa galatheae*, recently described by BARNARD (1961). The nominate species which is shown on Fig. 14 was taken in the S.W. Indian Ocean off Durban at 4360 m while the single specimen from St. 716 is regarded as a separate subspecies, *P. g. americana*; it is 42 mm long.

Since the other species of the family Hyperiopsidae, to which it belongs, are pelagic, BARNARD (l. c., p. 56) presumes that this is also true of *Parargissa*

galatheae. However, in the stomach of the nominate species Barnard found "slender flakes of material which might be bits of epidermis or comminuted muscle strands, a few falcate flakes, some larger bulky brown particles resembling woody debris, and a very few small hooks, perhaps chitinous parts of polychaetes". This almost exactly corresponds to what I myself have found in the intestine of a very large isopod, Bathyopsurus nybelini, of which several specimens have been studied, partly from the Puerto-Rico Trench at 5850 m (Swedish Deep-Sea Expedi-

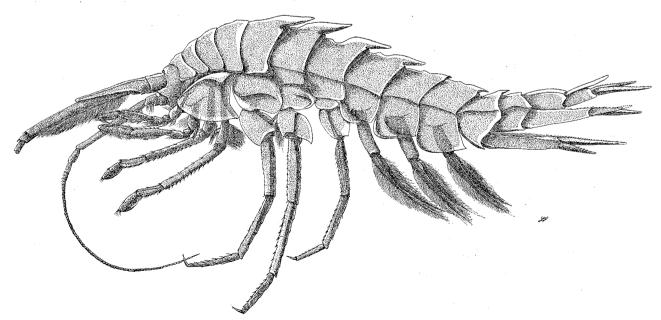


Fig. 14. The splendid, 50 mm long amphipod *Parargissa galatheae*. (After Barnard 1961).

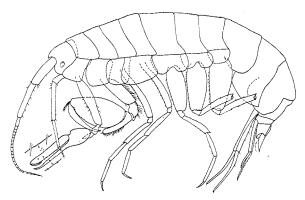


Fig. 15. The amphipod Leucothoe panpulco from St. 716. $8 \times \text{nat. size.}$ (After Barnard 1961).

tion) and partly from the Tasman Sea at 4400 m (Galathea). Besides pieces of epidermis with spicules, several muscle fragments, remains of what seems to be an amphipod, and an enormous collection of bits of wood (some with Campanularia-like hydroids) there were a few diatom tests, radiolarians and sponge spicules which clearly show that Bathyopsurus – like Paropsurus (cf. above) – is benthic. I therefore suggest that this is also the case with Parargissa galatheae.¹

Of the two other previously known species of *Parargissa*, one was taken abysso- or hadopelagically in the Kurile-Kamtchatka Trench (at depths between 4190 and 8050 m) and the other was caught – probably bathypelagically – at the Azores (depth to the bottom: 1920 m).

There are seven amphipods of a new species, *Haploops lodo*, which are 7-8 mm long and blind. The species of this genus live in extremely long tubes of mud which project a little over the surface of the bottom. *H. tubicola*, a littoral and bathyal species which is especially common in the eastern Kattegat in North Europe, lies on its back on top of the tube, holding on to the rim with the middle pairs of legs (ENEQUIST 1949, Fig. 63). In this way the pleopods are free and can be used for providing a slight current while the long, setiferous antennae capture the food – which consists of tripton and microorganisms. It is believed that other species obtain their food in the same manner.

The genus *Haploops* contains 12-13 species which range from sublittoral down to 3570 m, *H. lodo* from St. 716 being the deepest record so far. The genus is primarily bathyal in distribution.

A third new species, Leucothoe panpulco (Fig. 15), is 9 mm long. Although it is probably not quite blind like the former two, the eyes are poorly developed. There are 21 species in this genus, but only four apart from the present are bathyal or abyssal.

Three or four pale pink specimens of *Rachotropis* were too fragmentary to permit a description. This large genus contains several abyssal species and one hadal representative from 7160 m in the Sunda Trench. The last pair of legs of this species were extremely elongated (DAHL 1959).

Finally, two fragments can be referred to the genus *Epimeria* which contains 19 species. Two new species from the *Galathea* are abyssal and one new species from the *Vitjaz* was taken in a vertical haul from 8000-0 m. All the remainder are bathyal or may occur in shallow water in polar regions.

At least nine species of benthic decapod crustaceans were collected at St. 716. Among the Natantia or true shrimps there are at least two bottom-living species. One is represented by ten beautiful scarlet crangonids and by three specimens of the genus *Hymenopenaeus*. The latter have extremely long, stalked legs – presumably again, an adaptation to the soft bottom. The legs are also provided with a tuft of fine setae at the base of the distal joints. It is impossible to decide whether some of the ten other species of shrimps were taken pelagically while the trawl was on its way up, or at the bottom; we have reason to presume that a couple of the large, 25 cm long penaeid species spend at least part of their life at the bottom.

The most striking reptant decapod is, of course, the hermit crab *Probeebei* (p. 136). There are two species of Galatheidae of the genus Munidopsis. As their eyes are vestigial they are, without doubt, blind, but in compensation the antennae are strongly developed. Munidopsis comprises more than 100 species, but in spite of several vigorous attempts, no natural division of the genus has so far been brought about. These various species are found exclusively in the bathyal and abyssal zones. The only exception is one species which, living at a depth of only a few meters, has become adapted to life in the dark, subterranean caves in a salt lake on Lanzarote - one of the Canary Islands. The lake is in direct connection with the sea and its local crustacean is as pale and blind as its deep-sea relatives. - The decapods differ from all other important groups of marine animals in having apparently a sharp lower limit at comparatively moderate depths (a good 5000 m), probably due to the fact that almost all decapods are

Unfortunately, the specimen from St. 716 lacked all the internal parts of the body, thus preventing a study of its stomach contents.

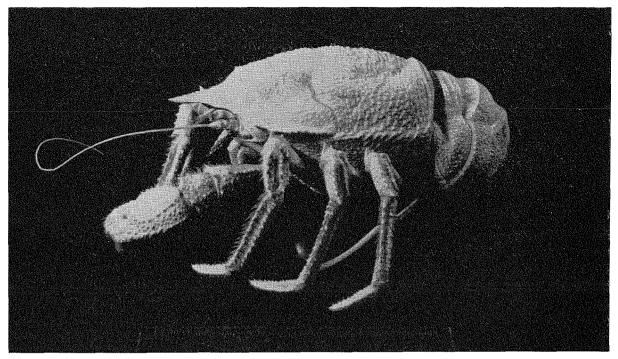


Fig. 16. An almost 20 cm long, new species of the anomuran genus *Munidopsis*. (H. V. C. phot.).

predators (or scavengers) and thus less adapted to life at the greatest depths. At least a dozen species of *Munidopsis* occur deeper than 3000 m, and four even deeper than 4000 m. Consequently, this genus includes more abyssal species than any other genus of Decapoda.

One of our two *Munidopsis* species is available in five specimens and seems to be closely related to *M. antonii*. This is presumably cosmopolitan, having previously been reported from such scattered areas as Australia, Chile and the Azores at depths between 2500 and close to 4000 m. When freshly caught, the specimens were white with orange eggs and yellow eye rudiments; the length is 10 cm. I have not been able to identify the other, which is most probably a new species. This is represented by one splendid individual (Fig. 16) measuring barely 20 cm and differing from nearly all other species by its broad and flattened carapace.

The most exciting group of decapods from greater depths are the Eryonidae. The first representatives of this family became known about a century ago as fossils; they date back as far as the Triassic, having their main occurrence in Jurassic. The fossil eryonids were shallow water forms with large, well developed eyes. When the *Challenger* Expedition in the 1870's found living relatives of these fossils in the deep-sea much attention was focused on the

event, confirming as it did the popular theory that the really ancient forms and "missing links" have been preserved in the deep-sea right up to the present time. As far as the abyssal zone is concerned, this has proved to be without foundation, perhaps with the exception of *Neopilina*, one genus of Eryonidae, and a few other examples.

This abyssal genus of Eryonidae is *Willemoësia* which occurs between 2500 and 4400 m. From St. 716 there are eight individuals (Fig. 17), the longest being about 13 cm. Among the species of this genus our eight specimens seem to be most closely related to *W. leptodactyla* and, in particular, to a few individuals from 2500 m off Chile. However, a careful revision of the entire genus is badly needed before a safe decision can be reached.

Characteristic of these lobster-like creatures is the flattened carapace and also the exceptionally meagre chelipeds. In addition, each of the succeeding four pairs of legs are provided with a set of claws and all that remain of the eyes are useless rudiments. The integument is soft and flexible, being less calcified than that of other reptant decapods.

Below in Fig. 17 are two larvae which, as an exception, are not from St. 716 but were taken at St. 726 in the Gulf of Panama (3270-3670 m), where we obtained eleven adult specimens of the same species and, in addition, four larvae. Such

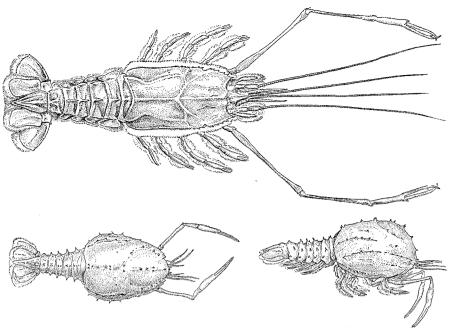


Fig. 17. The eryonid *Willemoësia*; above, the adult and below, two *Eryoneichus* larvae. Nat. size. (After "The Galathea Deep Sea Expedition 1950-1952").

larvae have been known for some time previously and are all referred to the genus Eryoneichus. However, their correct relationship was for a considerable time subject to discussion i. a. due to the largest specimens found having, apparently, fully developed external sexual organs. No specimens of Eryoneichus have ever been found carrying eggs, however, nor are there any known post-larvae which could justly be considered juvenile forms of the adult eryonids. There is no doubt, therefore, that Eryoneichus larvae are developmental stages of Willemoësia, or of Stereomastis or Polycheles - the two other genera of the family. Nevertheless, despite Bernard's great work (1953) on the Eryoneichus of the Danish Dana Expedition only three "species" of Eryoneichus can safely be referred to an adult species, none of them being a Willemoësia. Accordingly, it is very fortunate that larvae and adults were taken here in the same haul; a preliminary study seems to show that morphologically they are in fine agreement.

Finally, from St. 716 there are three small, roundish crabs, only 10 mm broad. Their claws are weak while their two hindmost pairs of legs are short, hooked at the tip and twisted backwards and upwards to carry a sponge (or more rarely a bivalve shell) above the carapace, serving as a shelter while the crab is walking about.

I have been unable to determine these crabs; they almost certainly belong to a new species which, strangely enough, must be referred to the genus *Ethusa* – of which the twenty known species occur from quite shallow water down to 1900 m. The surprising thing is that they do *not* belong to the closely related genus *Ethusina* which is the most pronounced bathyal-abyssal genus of crabs (with eight species from 500-4300 m). Only about 125 of a total of about 3500 crab species go deeper than some 200 m, and a correspondingly low number of species occur in shallow water in boreal and arctic areas: consequently, the crabs are almost exclusively a warmwater group.

Pycnogonids

The sea-spiders were dealt with when discussing *Colossendeis colossea* (p. 138). Another two species of this genus are present, one being represented by four specimens of *C. cucurbita*. This species owes its name to the cucumber-shaped proboscis and may measure up to 33 cm from the tip of one leg to the end of the opposite. The species was previously taken

^{1.} Above (p. 139) i. a. Stephanoscyphus was mentioned as an example of the abundant collections of benthic deep-sea animals procured by the Galathea. Even so, this wealth of material is easily surpassed by the enormous Dana collections of pelagic forms, particularly in comparison with all previous and subsequent activities in this environment. This can be illustrated by an obvious example: Before the Dana Expedition a total of 57 specimens of Eryoneichus were known, distributed on 13 species, whereas the Dana collected 255 specimens, representing 34 species.

south of Australia, at the Galapagos Islands and off the Azores at depths from 3300 m to 4150 m. The Galathea collected the four specimens from St. 716 at 3570 m and five more in the Kermadec Trench and the Tasman Sea at 2640 and 4400 m – i. e. a purely abyssal species with a very wide distribution.

The other is *C. macerrima*, represented by 15 specimens at St.716. It is likewise to be found in all oceans, but stands temperatures exceeding 10°C., since in the Indo-Malayan area it goes up to about 500 m depth. Apart from St. 716, the *Galathea* took specimens at 3400 m in the Mozambique Channel and at 3300-3700 m in the Gulf of Panama, all these records being deeper than any known previously (FAGE 1956b).

Molluscs

St. 716 is also rich in molluscs, having yielded a total of 14 species. Of the primitive scaphopods or tusk shells, 50-60 individuals of *Dentalium megathyris* are present (Fig. 6e), known from a dozen earlier finds, all at great depths (1450-4100 m) along the entire Pacific coast of America.

We may assume that this large species (up to 7 cm long) is also buried in an oblique position similar to the shallow water forms (only the pointed tip of the shell with a hole for the respiration water being visible above the bottom), and that it also feeds on foraminifers which are caught by a large number of thin, sticky tentacles, situated on the head and swollen at the tips.

The haul included many gastropods, amongst them one large *Tractolira sparta* which has previ-

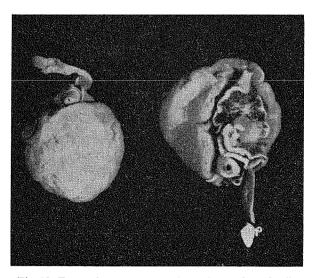


Fig. 18. Two unknown gastropods, perhaps of the family Lamellariidae. 1.3×nat. size. (H. V. C. phot.).

ously been taken in the Gulf of Panama between 3000 and 4100 m (Dall 1908). It is the only species within the genus, is 7 cm long and resembles a slender red whelk. Two small individuals of the closely related genus *Fusus* have not yet been determined to species, neither has a small, 2 mm long *Cocculina*. All the species of this genus occur in fairly deep water and are considered to be rather primitive. The shell is cap-shaped, and it was first taken for a juvenile *Neopilina*; in all probability it is a new species.

The deep-sea genus *Pleurotomella* is represented by a single specimen which may be *agonia*, previously taken in the East Pacific by the *Albatross*. In addition, eleven *Stilifer*-like small snails were found. The species of this genus are ecto-parasites on various kinds of echinoderms, boring by means of the proboscis through the skin of the host. It is quite likely that the eleven *Stilifer* were living on some of the many sea-stars from this haul. Although it is not identical with it, the species closely resembles an undescribed, hadal *Stilifer* which was taken by the *Galathea* at a depth of 8300 m in the Kermadec Trench.

There are two further gastropods, purple in colour and almost ball-shaped (Fig. 18). Their systematic position is uncertain. They may belong to the family Lamellariidae which are definitely prosobranchs, but whose shell, nevertheless, is partly or wholly reduced. Or perhaps they are something quite new and still more exciting.

Apart from the above mentioned Limopsis (p. 139) four more bivalve species were found, at least two of which are new. One is a beautiful, approximately 5 mm long, species of the deep-sea genus Dacrydium (Fig. 19) which is related to the common mussel. Two minute bivalves (1 mm) can be referred to Kelliella, a genus of which the Galathea obtained two additional hadal species, from the Kermadec and Sunda Trenches, respectively. Another deep-sea genus, Verticordia, is represented by four specimens which are 5-6 mm long. Finally, there are two large individuals of Cuspidaria both 40 mm long (Fig. 20), belonging to a small group of bivalves, remarkable in being predatory. While all other bivalves feed on plankton organisms or very fine organic material, the species of Cuspidaria are unique in having a muscular septum. Its rhythmic movements draw as well as water, food (crustaceans and polychaetes) into the mantle cavity. From here, palps forward the prey into the big mouth whereupon it continues into the roomy, muscular stomach.

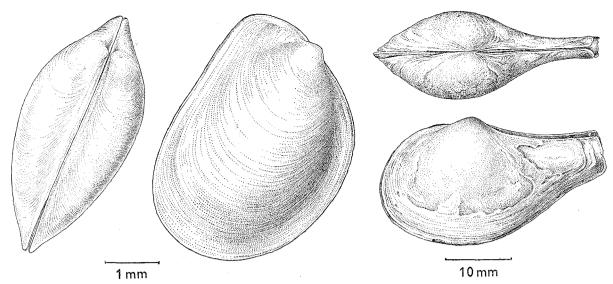


Fig. 19. A handsome new species of the mytilid *Dacrydium*. $12 \times \text{nat. size.}$ (P. H. Winther del.).

Fig. 20. A new species of the carnivorous bivalve *Cuspidaria*. 1,5 × nat. size. (P. H. Winther del.).

Among the molluscs is a group of worm-like animals, Solenogastres or worm molluscs, which is poor in species. The shell is missing, but, as in gastropods, there is a radula. At St. 716 15 specimens of *Chaetoderma* were collected. This genus comprises about 30 species, most being bathyal and only one previously recorded from the abyssal zone. The specimens probably belong to *Chaetoderma californicum* which was previously known in one specimen at 1100-1200 m off Southern California (HEATH 1911).

Echinoderms

This group is extremely abundant in the deep-sea, in particular the holothurians or sea-cucumbers. At St. 716 these are represented by no less than 14 species with 512 individuals!

The holothurian order Elasipoda is the highest systematic taxon of marine animals almost exclusively restricted to the abyssal zone. The above mentioned *Scotoplanes* (p. 140) and five other species from St. 716 belong to this order. Dorsally, many elasipods have one or more particularly thinskinned papillae, which, since no member of the group has water lungs, have been interpreted as respiratory organs. The species *Psychropotes longicauda* has an especially impressive papilla which is almost like a tail (see Fig. 21 which illustrates its suggested movements along the bottom). From St. 716 are four specimens, the largest having a body length of 21 cm. The distribution of this species is typically cosmopolitan, as many individuals pre-

viously regarded as being different species from different oceans have since proved to pertain to this species; the depth range is 2200 m to almost 5000 m.

Further, there are 29 Oneirophanta mutabilis, provided with numerous, long dorsal papillae. This is one of the most common holothurians and is also distributed in all three oceans. It was hitherto known from a depth of 1800-5300 m; the Galathea caught specimens at seven stations, i. a. in the Kermadec Trench at 5900 m. A new species of Peniagone is represented by 41 specimens, and there are two species of Benthodytes (typica and incerta). The former of these is a cosmopolitan and both are restricted to the abyssal zone. Both Peniagone and Benthodytes have a representative in the hadal zone, the former in the Kermadec Trench, the latter in the Banda Trench (B. HANSEN 1956).

Among the other orders of holothurians there are 51 specimens of *Synallactes aenigma*. It was taken once by the *Albatross* in the vicinity of this area and was not known elsewhere. The large, cucumbershaped *Pseudostichopus mollis* has – as the name indicates – no spicules; it is represented by about 100 specimens. A single *Paroriza* is a new species. The two latter genera both have a hadal species (the Banda Trench and the Kermadec Trench, respectively).

The ninety Staurocucumis abyssorum (about 10 cm long) are also cucumber-shaped. Their tentacles are branched like a tree, and they feed on plankton. A closely related species is the almost spherical,

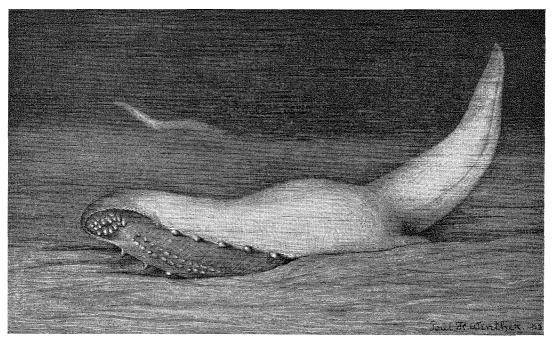


Fig. 21. The holothurian *Psychropotes longicauda* ploughing its way through the surface of the ooze, with the "tail" raised high. About ¹/₂ nat. size.

(After "The Galathea Deep Sea Expedition 1950-1952").

spined Sphaerothuria bitentaculata (Fig. 22) which is also a cosmopolitan. The same applies to Molpadia musculus of which 51 specimens were collected, whilst another equally numerous species (granulata) of the same genus, seems to be limited to the East Pacific. Finally, there is the extremely common Protankyra brychia which lives at depths between 900 and 5200 m and was taken at numerous Galathea stations. We have vivid memories of this small creature – the tough brown body has an extraordinary ability to get entangled in the meshes of the net and often it might take hours to disengage the hundreds of specimens.

The crinoids or sea-lilies do not take long to survey. All that is found are fragments of three

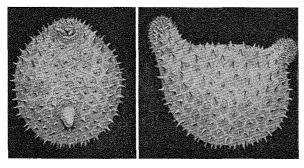


Fig. 22. The curious, almost spherical holothurian *Sphaerothuria bitentaculata* from above and from the side. 2.5 × nat. size. (After Ludwig 1894).

small stalked individuals of 5-10 cm length, belonging to *Bathycrinus*, which is the only abyssal genus.

There are, however, 210 specimens of asteroids or sea-stars, composed of seven or eight species. Half of them belong to *Dytaster gilberti*, which may reach a size of 25 cm, and apart from having a splendid orange colour, resembles the common *Astropecten*. Unlike the following species it takes its food from the surface of the bottom. It is limited to the Eastern Pacific between 3200 and 4300 m.

The 86 Eremicaster gracilis only grow to a size of 11 cm in diameter and are greyish in colour. They are deposit feeders and presumably bury themselves in the bottom. As in other species of the family, the central part of their dorsal side may be raised in the shape of a cone (Fig. 23), in young individuals even in a pointed tip. This cone is probably of great importance to the respiration as it keeps a passage open through which water may be exchanged from the narrow cavity surrounding the buried animal. The specimen in Fig. 23 contains one or two parasitic ascothoracids (p. 144). Around the mouth, or in the furrows of a few other specimens were some very minute hydroids, all of which were about 1 mm high and provided with only three tentacles. They may be of the same species as those on the shell of Neopilina. Eremicaster gracilis is typically abyssal,

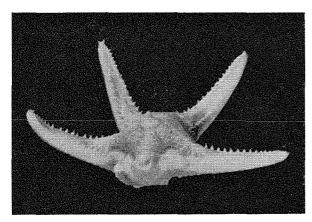


Fig. 23. On the dorsal side of the deposit feeding sea-star *Eremicaster gracilis* a cone is visible in the centre; this probably contributes towards providing a water current which enables the buried animal to breathe. This specimen maintains one or two parasitical ascothoracids. Nat. size.

(H. V. C. phot.).

the 18 finds having been made between depths of 2609 and 5200 m and at temperatures of 1.3° to 2.6° C. Besides the 18 finds along the entire American west coast it is also recorded from the recent Russian deep-sea explorations near Kamtchatka (MADSEN 1961a, Fig. 39).

A preliminary identification has referred one pillow-shaped, violet sea-star with a size of 15 cm to the genus Hymenaster. Another specimen of 13 cm may be "Mediaster" elegans which is known from the Gulf of Panama (1800-3300 m) but is somewhat divergent; the quotation marks indicate that the species elegans does not belong to the genus Mediaster (F. J. MADSEN, verbal communication). A couple of small, whitish, much damaged sea-stars should perhaps be referred to Pteraster, and finally, there are seven multi-branched brisingids which are likely to be of the genus Freyella and are represented by 2-3 species. One of the four specimens of a beautiful 12-armed species has miraculously been preserved with most of its arms (Fig. 24), as has, to a certain extent, a 6-armed specimen. Moreover, there are two central discs, one 8-armed and one 13-armed – plus a great many loose arms!

Five species of ophiuroids or brittle-stars are present in more than 300 specimens. Three species belong to the family Ophiolepidae which lack spines, are strongly calcified, and take their food on the surface of the bottom. Of *Ophiura irrorata* (Fig. 6a) there are no less than 162 specimens, a fact indicating that this species – like its nordic relatives – may be found in great abundance over limited areas, forming a whole layer of animals. It is a cosmopol-

itan and known from 125-3570 m. A similar distribution, although with a somewhat deeper occurrence, has *Ophiernus vallincola*, of which there are twenty specimens, while only eight *Ophiosphalma glabrum* (Fig. 6a) were found. The latter is limited to the Eastern Pacific between depths of 1600 and 5200 m.

The genus Amphiura is represented by about 100 specimens of a species which is almost certainly A. serpentina. It is also restricted to the Eastern Pacific (about 800-2000 m) and is a frail, thin-armed creature which lives buried in the bottom. Much more sturdy is Ophiacantha cosmica, whose arms are covered with a large number of spines. It is to be found in all seas and at depths between 640 and 4840 m. Not only the spines, but also the very flexible arms enable the animal to cling to the residences preferred: sponges, sea-pens, water-logged remains of wood, pieces of lava and other rock, etc.

Three species of echinoids or sea-urchins were taken at St. 716. There were no less than 126 Aporocidaris milleri with shell diameters ranging from 2 to 35 mm and spines with a maximum length of 60 mm. They were often overgrown with the twisted tubes of a polychaete (Fig. 8, 1-4). In this way the worm is kept free of the sediments, since this sea-urchin crawls on the bottom surface with its spines slightly raised. It was previously taken in the tropical East Pacific between 3000 and 3900 m depth.

Of the extremely thin-shelled, violet, irregular *Urechinus loveni*, the macerated remains of a couple of fairly large specimens are present. This species has practically the same regional and vertical distribution as the former sea-urchin. Finally, there are two greyish specimens of the irregular species *Aëropsis fulva*, shaped like a large date. It occurs in the Pacific between 1500 and 5200 m. Like *Urechinus* it no doubt lives buried in the ooze,

Ascidians

A total of 41 species of ascidians or sea-squirts go deeper than 3000 m; of these, the *Galathea* secured two at St. 716. One, *Dicarpa simplex* (Fig. 25), was represented by eight well preserved specimens which are about 5 cm long. The body is raised from the bottom by means of a stalk which is safely anchored with fine suckers.

The presence of a stalk in glass-sponges, sea-pens, sea-lilies, some ascidians, etc. is generally regarded as an adaptation for lifting the animals above an

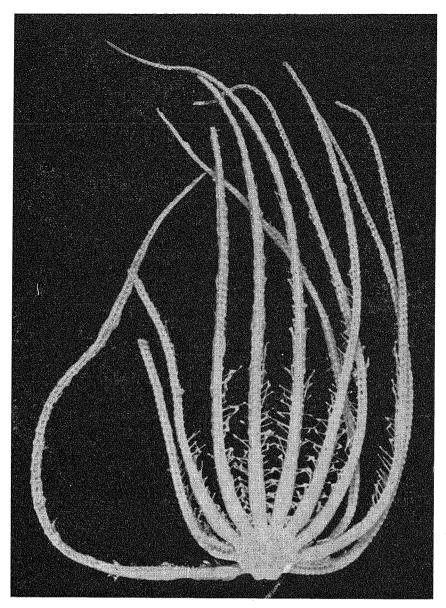


Fig. 24. A well preserved specimen of the 12-armed brisingid *Freyella*. Nat. size. (H.V. C. phot.).

upper, semi-liquid layer of ooze. However, deep-sea photographs indicate a fairly firm surface in many places; MADSEN (1961b, p. 201) suggests that the stalk may rather, perhaps be advantageous in raising sessile animals above an oxygen-poor water layer close to the bottom.

Dicarpa simplex was first taken in 1948 by the Swedish Deep-Sea Expedition at 4600 m depth in the western Atlantic. As it was collected by the Galathea both in the Kermadec Trench (N. E. of New Zealand at 2470 m) and in the eastern Pacific, it soon proved to be cosmopolitan (MILLAR 1959). The other species was found to be too fragmentary to allow identification.

Fishes

Only one of the fish species from St. 716 (Galatheathauma) has been worked up so far (cf. p. 137).

According to the latest statement (NYBELIN 1957), there are altogether 69 species of bottom fish from a total of 137 localities deeper than 3000 m. To this should be added the fish known from the greatest depths, *Careproctus amblystomopsis*, taken by the Russian *Vitjaz* Expeditions at 7200 m in the Kurile-Kamtchatka Trench and at 6160 and 7590 m in the Japan Trench (Andriashev 1955; Rass 1958).

The fish family richest in deep-sea species is the Brotulidae. Most of the species seem to have a

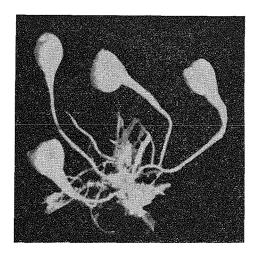


Fig. 25. Some specimens of the stalked ascidian *Diparca simplex*. Nat. size. (After MILLAR 1959).

rather restricted distribution both regionally and vertically. The majority are bathyal and abyssal, and among the limited number occurring at lesser depths several are cave forms or species living buried. Their shape is always longish, with a relatively large head, the body becoming prolonged into a long and narrow, pointed tail; consequently, they are not good swimmers. Most of them are pale brownish or colourless, though not infrequently they are blackish or are of a dark violet colour on the head and gill operculum. Many have vestigial eyes. Besides Bassogigas mentioned on p. 137, the following closely related genera were represented at St. 716: Bassozetus with 26 individuals up to 30 cm long; only one of the seven species of the genus is bathyal, the others are abyssal, and one lives as deep as 5600 m. Further, there were five individuals of *Porogadus* which has four bathyal and seven abyssal species, and fifteen Mixonus, a genus whose three species are abyssal (Grey 1956).

Another very important deep-sea fish family is Macrouridae. They have almost the same body shape as the brotulids, but in actual fact, there is no close relationship between them. The biggest fish caught at St. 716 belongs to this family. It is a species of *Nematonurus*, about 86 cm long (Fig. 26); there were also two somewhat smaller specimens. *Nematonurus* comprises one cosmopolitan species (280-4600 m), one species from the Eastern Pacific (2500-4000 m), and one antarctic species (2800-3250 m).

The four specimens of Alepocephalidae were mentioned above (p. 137).

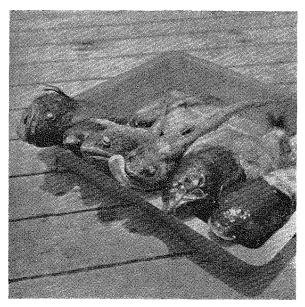


Fig. 26. From left to right: A macrourid (Nematonurus), 86 cm long; an alepocephalid fish; two more Nematonurus; two more alepocephalids. The reduction in pressure has forced the stomach out through the mouth of the fish in the middle.

(Mogens Høyer phot.).

THE DOMINATING ANIMAL GROUPS

In table 1 the number of species and individuals¹ of the various animal groups from St. 716 have been compared. Moreover, it was found practicable to include in Table 1 the number of individuals obtained from a total of 11 trawlings carried out by the *Vema* between 3290 and 3700 m in the immediate vicinity of St. 716 (MENZIES *et al.* 1959, Table 1 and MENZIES *et al.* 1961, Table 1). Unfortunately, no information about the number of species is available.

 When estimating the number of individuals each colony of colonial animals has been counted as one individual only. The amazing difference in numbers of individuals of the various groups captured by the two expeditions must, without doubt, partly be ascribed to the type of gear applied. As mentioned above (p. 130), the *Galathea* used a large herring otter trawl. The size of the meshes varied from 80 mm at the head to 14 mm at the cod end. Nevertheless, a fairly high number of small and very small animals (5-1 mm) was obtained, due to a 25 litre canvas bag being placed at the cod end of the trawl which helped to bring up large or smaller quantities of bottom se-

Table 1. The number of species and specimens of various groups of benthic animals from *Galathea* St. 716, the number of specimens of the same groups from *Vema* 15, Sts. 128-129 and 131-139, and the relative order of group abundance.

		Galathea St. 71 (3570 m)	Vema Sts. 128-129, 131-139 (3290-3700 m)		
Animal groups	No. of species	No. of specimens	Relative order of abundance (1-10)	No. of specimens	Relative order of abundance (1-10)
Porifera	3	c. 41		21	
Coelenterata	16	c. 137		141	
Hydroidea	3	4		5	
Scyphozoa (Stephanoscyphus)	1	13		101	6
Alcyonaria	1	8		15	
Pennatularia	3	17		0	
Coral	0	0		3	
Actiniaria	8	95	6	17	
"Vermes"	c. 23	c. 317		1142	
Aschelminthes	0	0		52	10
Polychaeta	c. 20	c. 310	3	1090	1
Hirudinea	1	1		0	
"Gephyrea"	2	6		0	
Crustacea	c. 32	c. 208		742	
Copepoda	1	3		6	
Ostracoda	0	0		15	
Cirripedia	2	32		1	
Nebaliacea	0	0		8	
Cumacea	1	1		41	
Tanaidacea	7	60	8	221	4
Isopoda	7	50	10	198	5
Amphipoda	5	12	10	250	3
Decapoda	c. 9	c. 50	10	230	3
Pycnogonida	3	18	10	1	
Mollusca	14	132		539	
	1	132		1	
Monoplacophora (Neopilina)	1			80	0
Solenogastres	1	15	0		8
Scaphopoda	6	55	9	33	
Gastropoda		18		51	•
Bivalvia	5	34		374	2
Brachiopoda	0	0		1	-
Bryozoa	0	0		89	7
Echinoderma	30	1171	-	104	
Holothurioidea	14	512	1	25	
Crinoidea	1	3		2	
Asteroidea	7	210	4	7	•
Ophiuroidea	5	315	2	67	9
Echinoidea	3	131	5	3	
Pogonophora	0	0		3	
Ascidiacea	2	10	_	16	
Pisces	9	66	7	0	
Total	c. 132	c. 2100		2799	
Average per trawling	c. 132	c. 2100		256	

diments (Fig. 2). Careful washing through sieves with a mesh diameter of 1 mm brought the tiny creatures to light. The *Vema*, however, used a very small dredge which could be towed by a hydrographic wire. The opening was only 1 m wide and 10 cm high; the bag was 3 m long and made of

nylon with a mesh diameter as low as 0.5 mm. The sorting of the material, which usually consisted of about a quart of sediment plus animals, was performed under a binocular microscope.

Due to the small size of the gear it is obvious that the *Vema* could not capture many, if any, of the larger, faster or firmly anchored benthic animals like sea-pens, sea-spiders, fish and above all, echinoderms. It is equally certain that the number of minute forms is much too small in the *Galathea* trawl; this is true of all the groups of smaller crustaceans (especially amphipods), and of gastropods and bivalves.

All things considered, it cannot be denied that a close study of Table 1 gives rise to no little surprise. Why did the Vema take so many of the sedentary polyp Stephanoscyphus, but only a single specimen of the equally sedentary, stalked barnacle (Scalpellum) while the Galathea took 32 of the latter? Why should St. 716 be especially poor in amphipods which are otherwise - also in other Galathea trawlings - amongst the most frequently occurring abyssal animals? Most of the echinoderms from St. 716 are fairly large specimens (5-15 cm); yet we obtained many small, juvenile stages of the various echinoderm groups too. Considering the fact that more than half of the animals taken at St. 716 are echinoderms (only the number of polychaete worms is equal to the average number of the groups seacucumbers, brittle-stars, sea-stars and sea-urchins), it is very surprising that they play such an unimportant role in the Vema hauls.

The total absence of certain forms is also striking. Why did the *Vema* take no gephyreans, while other partly or completely buried animals like polychaetes, cumaceans, solenogastres and bivalves are well represented? Where are the flatworms, ostracods, bryozoans, and pogonophores in the *Galathea* collection? As to the two former groups, they may be so small in size that they passed right through

the sieve. Concerning the bryozoans obtained by the *Vema*, it has not been stated whether they were growing in colonies on a substratum or whether they occurred more or less singly; in the latter event they are likely to be very small forms. But the pogonophores live in tubes which are of a considerable length and easy to recognize. *Vema*'s three pogonophores may be identical either with a species taken by the *Vitjaz* off the west coast of North America and recently described by Ivanov (1961), having a tube 30-45 cm long, or with one of the two species taken by the *Galathea* in the Gulf of Panama; one had a tube 15 cm long while the other a tube 3-7 cm long (KIRKEGAARD 1956b).

As an explanation it might be assumed that the animals are not randomly dispersed. It is known that this is true of certain animals like cumaceans and ophiuroids, but in this case it surely cannot be of importance. The table in Menzies et al. (1959) not only gives the total number of individuals of the various animal groups, but also the number for each of the eleven hauls. A comparison shows that in all the more abundantly occurring groups the number of individuals varies amazingly little from haul to haul.

Whatever may be the reasons for the marked disagreement in the relative number of individuals it is very clearly shown that one cannot afford to draw too far-reaching conclusions from a single or a few hauls (or bottom samples) at a given locality – however rich in species and individuals they may be. Even in relatively well-explored areas of the deepsea we may come across similarly surprising facts. Our knowledge of the fauna of the abyssal depths is still exceedingly poor.

GENERAL DISTRIBUTION

Of the 132 species occurring at St.716, a total of 65 have, up to the present, been identified with sufficient certainty to be considered in a survey of the general distribution of the species found at this station. Sixteen of these 65 species were described recently or are under description (1 sponge, 2 sea-anemones, 8 crustaceans, 3 molluscs, and 2 holothurians), but it is as yet too early to state whether 10 of these new species were taken exclusively at St. 716 or whether they also occur at other *Galathea* stations. These 10 species have, therefore, not been included in the present survey. The remaining 6 new species (which are all crustaceans) are known from St.716 only and are entered in Table 2. It should

be noted that for several of the remaining 49 species in the table it is as yet not known whether they have been taken at *Galathea* stations other than St.716. For all species, the find at St.716 has been included in Table 2.

Regional distribution

Of the 55 species in the table, no less than 30 species and 2 subspecies are, according to our present knowledge, restricted to the East Pacific Ocean, and two more species (*Pseudostichopus mollis* and *Aëropsis fulva*), are almost exclusively known from this part of the Pacific. Even if 20 of these 30 species are

Table 2. Regional and bathymetrical distribution of identified species from St.716. In most cases the total number of finds is given. The identification of the species marked (*) is not quite certain. In species marked (°) all *Galathea* finds are included. Records of subspecies not found in the East Pacific are in paranthesis.

Species		R	Bathymetrical distribution					
	East Pacific	West Pacific	Atlantic Ocean	Indian Ocean	South Polar Sea	Bathyal	Abyssal	Hadal
Porifera								
Hyalonema bianchoratum	3	_	***	_	-	****	3	
Cladorhiza linearis	2	****		-	_		2	-
Coelenterata								
°Stephanoscyphus simplex	3	18	8	11	1	12	25	4
*Edwardsia intermedia	2		_	_	_	1	1	_
Bolocera pannosa	2	_				1	1	
Actinoscyphia plebeia	2	-~		_	_	1	1	_
Condrophellia coronata	2		8	_		7	3	
*Amphianthus lactea	2	400	_	_	_	i	1	_
Umbellula thomsoni	1	2	12	4	_	2	17	
Vermes"	1	des.	12	4		4	17	_
	2	4	1			1	2	2
*Travisia profundi	. 2	4		_	_	1	3 2	3
°Priapulus abyssorum	. 4	-	-	_	acros .	_	2	
Crustacea	2						2	
°Neotanais armiger	2	-			_	_	2	_
°Neotanais pfaffi	1	-	_	_	_	-	1	-
°Ischnomesus roseus	2		_	_	. mare	-	2	
°Ischnomesus planus	1		_		-		1	-
°Paropsurus giganteus	1	1	-	-	-	-	2	· <u>-</u>
°Storthyngura pulchra	4	(1)	(1)	_		(1)	4	(1)
°Munnopsis longiremis	2	_	_	_	-	1	1	-
°Parargissa galatheae	1	-		(1)		at and	2	_
°Haploops lodo	1	_		_	_	_	1	_
°Leucothoe panpulco	1	-			****		1	_
°Probeebei mirabilis	2	_	-	-		1	1	_
Pycnogonida								
°Colossendeis colossea	×	×	×	×	?	×	×	_
°Colossendeis cucurbita	2	3	2				7	_
°Colossendeis macerrima	×	×	×	×	?	×	×	_
	.^	^	?	^	•	^	^	_
Mollusca	4					1	2	
°Neopilina galatheae		_			_	1	3	
Dentalium megathyris	13		_		~	4	9	_
Tractolira sparta	5		_	_	_	-	5	-
*Pleurotomella agonia	3	_	-	_		2	1	_
Limopsis compressus	9	-	_	_	-		9	-
*Chaetoderma californicum	2	-		_	-	1	1	
Echinoderma								
°Oneirophanta mutabilis	12	5	5	5	2	1	28	-
°Benthodytes typica	2	6	19	12	_	2	35	2
°Benthodytes incerta	3		-	_	_ '	-	3	_
°Psychropotes longicauda	2	2	-		3	_	7	***
°Synallactes aenigma	6	1	~	_	_	-	7	_
°Pseudostichopus mollis	23	· <u>-</u>		1	3	17	10	
°Staurocucumis abyssorum	24	3	4	1	4	5	31	
°Sphaerothuria bitentaculata	14	20	5	16	_	36	19	_
°Molpadia musculus	×	×	×	×	_	×	×	_
°Molpadia granulata	4		_	_		_	4	_
	5	5	16	4	_	3	27	_
°Protankyra brychia		<i>3</i>	-	~		- -	c. 16	-
°Dytaster gilberti	c. 16		_	_	_			_
°Eremicaster gracilis	18	4	-	***	_	_	22	-
*"Mediaster" elegans	3 .	_			_	1	2	-
Ophiura irrorata	several	some	several	several	some	c. 6	c. 20	
Ophiernus vallincola	c. 6	c. 5	c. 10	-		8	c. 13	-

Total number of finds ¹	c. 295	c.83+1	c. 101+1	c.61+1	13	c. 130+1	c. 441	9+1
°Galatheathauma axeli	1	_		-			1	
Pisces								
°Dicarpa simplex	1	1	1		****	-	3	***
Ascidiacea								
Aëropsis fulva	c. 10	1	-		-	1	c. 10	
Urechinus loveni	c. 10	_	-	-		-	c. 10	
Aporocidaris milleri	6	_		-		_	6	_
Ophiacantha cosmica	c. 6	c. 2	c. 10	c. 7		1	c. 24	
*Amphiura serpentina	c. 9	-	-	_	_	c. 8	1	
Ophiosphalma glabrum	c. 35	-		and a		5	c. 30	

^{1.} Exclusive of four cosmopolitan species in the regional distribution and of three in the bathymetrical.

known from only three localities or fewer, it is, nevertheless, a remarkably high number and is in strong opposition to that claimed by EKMAN (1953, p. 292). This author could find no indication of a special fauna element in the deeper part of the East Pacific corresponding to that existing in the littoral and sublittoral zone. Moreover, it seems likely that most of the 10 new species, mentioned above and not included in the table, will also prove to be restricted to the East Pacific Ocean.

EKMAN used the 1000 m line as the limit between the bathyal and abyssal faunas, and according to this definition practically all 30 species are exclusively abyssal. If the limit is placed at the more generally accepted depth of 2000 m, 11 of the 20 East Pacific species known from at most three finds are abyssal, while the remaining 9 are both bathyal and abyssal; of the 10 species from more than three finds, six are abyssal, a further three are abyssal but with a few finds from bathyal depths, while one (Amphiura serpentina, the identification of which is not quite certain), is almost exclusively bathyal.

The, apparently considerable, number of endemic abyssal species in the East Pacific, (and to a much minor extent the Central, Pacific which is, however, very poorly known) supports the suggestion put forward by Madsen (1961b, p. 210) of a special East (and Central) Pacific fauna element.

The number of cosmopolitan species is also considerable. Of the 55 species considered, 12 occur in all three oceans and at least three of these also in the South Polar Sea. Moreover, *Psychropotes longicauda* has been recorded from the Pacific Ocean and the South Polar Sea south of the Indian and Atlantic Oceans. According to Mr. Bent Hansen (verbal communication), his unpublished data show that this species is also typically cosmopolitan. When the

Indian Ocean becomes better known the four Pacific-Atlantic species (*Travisia profundi, Colossendeis cucurbita, Ophiernus vallincola,* and *Dicarpa simplex*) will probably prove to be cosmopolitan too.

Bathymetrical distribution

Of the 55 species, no less than 24 are exclusively abyssal, having been taken only between depths of 2000 to 6000 m and below 4°C. Ten of these 24 species have been recorded from at least four localities.

Three species have a wide bathymetrical distribution, ranging from bathyal to hadal depths but are primarily abyssal (one even with separate subspecies in the hadal and the bathyal zones). A fourth species with a similarly wide vertical distribution, has been found only once in the bathyal zone.

Of the 23 bathyal-abyssal species, 10 are so far known from only 1-4 finds each, while the remaining 13 have been taken 9-55 times each. Eight of the latter species are primarily abyssal, more than 75 per cent of the finds having been made at depths greater than 2000 m. The average abyssal percentage of these eight species taken together is even as high as 89 and, in addition, many of the finds from depths of less than 2000 m were made at temperatures below 4°C.

Thus, a total of 36 of the 55 species are almost exclusively abyssal and 22 of them have been recorded from at least four localities.

Finally, three species (Chondrophellia coronata, Pseudostichopus mollis, and Sphaerothuria bitentaculata) are primarily bathyal, having been taken about twice as many times in this zone as in the abyssal. One species (Amphiura serpentina) is, as mentioned above, almost exclusively bathyal; the identification of this species is, however, somewhat doubtful.

SUMMARY

- 1. Apart from John Murray's comprehensive lists of the names of all species and of the number of specimens collected at each of the *Challenger* Expedition stations (1895), accounts of the animal assemblage found in abyssal trawlings of other deepsea expeditions are very few and far between. The present paper deals with the species dredged at *Galathea* St. 716 at a depth of 3570 m in the East Pacific off Costa Rica. This extremely rich trawl yielded no less than 132 different species and about 2100 specimens of benthic metazoans. The trawling operation is described in detail and information on the environment provided.
- 2. A description of all the more noteworthy species is given. Facts or suggestions on the biology or behaviour of several of them are discussed, sometimes by referring to what is already known about related shallow water species. The regional and bathymetrical distribution of species previously described from other sources is recorded, as is the majority of the genera represented at St.716. The tracks shown on a deep-sea photograph, published by Menzies et al. (1959) and identified as Neopilina tracks, are discussed and the argument put forward that they might instead originate from bivalves. The estimates on population density, based on trawlings and deep-sea photographs (1. c.) are discussed and criticized. In view of a recent bathyal find of Neopilina it is suggested that it may have descended into the abyssal zone fairly recently. It is shown that the amphipod Parargissa galatheae must be considered benthic due to the stomach content being composed of i. a. woody debris.
- 3. A comparison between the number of species and individuals of various animal groups at St. 716 is presented in Table 1, which also gives the number of individuals obtained from a total of 11 trawlings carried out by the *Vema* Expedition in the same area. Primarily due to differences in the size of gear

used by the Galathea and the Vema (a large herring otter trawl and a 1 m dredge with a very fine meshed bag, respectively), a marked difference in the abundance of the various animal groups was found. The dominating groups at St. 716, as far as the number of individuals is concerned, are holothurians, ophiuroids, polychaetes, asteroids, and echinoids while in the Vema trawlings polychaetes, bivalves, amphipods, tanaids, and isopods proved to predominate. There were also, however, several inconsistencies which can hardly be ascribed to the different collecting techniques. Nor can they, in this case, be satisfactorily explained by the animals in question having a patchy distribution, since the contents of the eleven Vema trawlings are remarkably uniform. The obvious disagreement in the relative number of individuals obtained by the two expeditions suggests that one should not draw too far-reaching conclusions from a single or a few hauls in the deep-sea.

4. The general distribution of 55 identified species is given in Table 2. No less than 30 species and 2 subspecies are restricted to the East Pacific (10 of the species and 1 subspecies are known from at least four localities); two more commonly recorded species are almost exclusively from the East Pacific. More than half of the East Pacific species are restricted to the abyssal zone. Thirteen species are cosmopolitan and another four, which have not yet been taken in the Indian Ocean, will probably also prove to be distributed in all three oceans.

Of the 55 species, 24 are exclusively abyssal (from depths exceeding 2000 m and temperatures below 4° C.), and 10 of these are recorded from at least four localities. Three of the four species with a wide bathymetrical distribution from the bathyal to the hadal zone are primarily abyssal, and this is also the case with eight of the more commonly found bathyal-abyssal species. Only four species are primarily bathyal.

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