ON THE ZOOGEOGRAPHY AND ORIGIN OF THE ABYSSAL FAUNA IN VIEW OF THE KNOWLEDGE OF THE PORCELLANASTERIDAE

By F. JENSENIUS MADSEN

Zoological Museum, Copenhagen

CONTENTS

Ι.	Introductory remarks	178
II.	Historical steps in the exploration of the deep-sea fauna $\ldots \ldots \ldots \ldots \ldots$	179
III.	The delimitation of the abyssal region	180
IV.	The bathymetrical range of the Porcellanasteridae	180
v.	The mode of life of the Porcellanasteridae	181
VI.	The geological age of the Porcellanasteridae	183
VII.	The interrelationships of the porcellanasterid genera	184
VIII.	The geological age of the deep-sea	185
IX.	Life conditions in the ancient and in the recent deep-sea	186
X.	The theoretical composition of the deep-sea fauna	188
XI.	The geological age of the recent deep-sea fauna	188
	1. The alleged antiquity	188
	2. The Mesozoic and Early Caenozoic elements	191
	3. The Late Caenozoic elements	195
XII.	The factors deciding the vertical zonation of the deep-sea fauna	197
XIII.	Some characteristics of deep-sea animals	200
XIV.	The horizontal distribution of the abyssal fauna	203
	1. The cosmopolitanism	203
	2. Some cosmopolitan species	205
	3. EKMAN's considerations on a possible cosmopolitanism of the abyssal fauna	206
	4. The main subdivision of the lower abyssal fauna	207
	5. The "guests" in the abyssal region	208
	6. Commentary on N.G. VINOGRADOVA's view on the abyssal zoogeography	209
	7. Possible explanations for an Atlanto-Indian and a Pacific (East Pacific) abyssal	
	fauna element respectively	210
	8. The alleged endemism in the trench faunas	212
	9. The distribution of the abyssal fauna in relation to the condition of the bottom	212
	10. The possible fluctuations in the abyssal populations	214
XV.	Summary	215
XVI.	References	216

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12

I. INTRODUCTORY REMARKS

In his preliminary account of the Challenger Deepsea Exploring Expedition WYVILLE THOMSON (1877 II p. 328) noted that: "some of the most interesting of the problems which are now before us (after the establishment of the fact that the distribution of living beings has no depth-limit) have reference to the nature and distribution of the deep-sea fauna, and to its relations with the fauna of shallower water, and with the faunæ of past periods in the earth's history." But he thereafter emphasized that: "This is however precisely the class of questions which we are as yet least prepared to enter into, for everything depends upon the careful study and the critical determination of the animal forms which have been procured."

In the following years the results of these studies were published in the scientific report of fifty quarto volumes which provides a permanent record of the Challenger Expedition, and is the starting point for all subsequent taxonomic work on deep-sea animals. Eventually then in 1895 the knowledge collected here, was made use of by MURRAY for a general discussion on the problems of the origin and zoogeography of the fauna of the deep-sea.

The origin of the deep-sea fauna, and the zoogeography of the deep-sea, have, on the whole, been favoured subjects of discussion ever since the existence of a deep-sea life was recognized, and strongly divergent notions have been presented. To some degree, however, apparent incompatibilities may be due to different uses of terminology. Moreover, the problem of the origin of the deep-sea fauna is complicated by this fauna being a mixture of different elements. Further, as regards the zoogeography of the deep-sea, the pattern of distribution may differ in elements of different geological age and perhaps also in different animal groups. A main reason for the difficulties in reaching definite conclusions regarding the problems of the deep-sea fauna, has also been the still insufficient knowledge. More exhaustive collecting is necessary and much more taxonomic work still to be accomplished before a really satisfactory concept of the problems of the deep-sea fauna can be had.

The investigations of the Galathea Expedition Round the World aimed, i.a., at giving us the first knowledge of the fauna of the extreme deep-sea; and it was due to this expedition that we have the ultimate proof of the existence of animal life at all depths. Another remarkable result was the discovery of the Palaeozoic relict, *Neopilina*. However, in the long run the reputation of the Galathea Expedition, as was the case with the Challenger Expedition, will rest on the detailed taxonomic reports on the entire collections, the pains' taking and timeconsuming working up of which is now in progress.

The Galathea collections are, from a zoogeographic point of view, of considerable interest, as they offer the taxonomist the rare opportunity of a simultaneous study of materials from widely separated localities. Most other deep-sea expeditions since the Challenger, have collected in more or less limited areas and apparently their collections have sometimes been worked up without much attention being paid to the fauna of other areas. Thus, the taxonomic revision of the deep-sea sea-stars, the Porcellanasteridae, now undertaken on the basis of the Galathea material (see the preceding paper in this report), showed that at most 25 species could be recognized at present, although no less than 57 nominal species have been previously described. Similarly, BROCH recognized only 7 valid species among 39 nominal ones when in 1958 he revised the deep-sea pennatularian genus Umbellula. The trend is evident, and at least some increase in the number of synonyms must be expected as a result of taxonomic revisions on comprehensive materials of many other deep-sea groups.

The Porcellanasteridae, which constitute a characteristic element in the abyssal deep-sea fauna, were obtained in a fair percentage of all the dredgings hitherto made in the abyssal depths (e.g. in about one-third of the Galathea dredgings in depths exceeding 2000 m) and at present are among the best known exclusively deep-sea animals as regards taxonomy and distribution (cf. the accompanying table p. 182). It has been found worth-while therefore, on the basis of this knowledge, to review some of the theories set forth on the origin of the abyssal fauna, and on the zoogeography of the abyssal region.

In some earlier papers (cf. p. 204) the writer took up the view that there is a large cosmopolitan element in the abyssal benthic fauna, a view which is corroborated by the now known distribution of the Porcellanasteridae. Further, the amount of evidence now available on the Porcellanasteridae supports the assumption that the recent abyssal fauna in the main is younger than the bathyal and sublittoral faunas.

Even before the investigation of the deep-sea began, many authors had speculated on the possibility of life and the conditions of life in the great depths. Some curious theories were advanced but also some shrewd guesses made. It is not always possible therefore, to state with any certainty who was the first to express this or that idea. In addition, several authors have been known to arrive independently at the same conclusions.

The most valuable of the earlier surveys on the deep-sea fauna is undoubtedly the paper 'On Deep-Sea Dredging and Life in the Deep-Sea', read in 1880 by MOSELEY, one of the Challenger scientists. This paper is quoted more or less directly by most later authors dealing with the subject, and will frequently be referred to in the following pages. Another very important paper on the subject is MUR-RAY's summary of the scientific results of the Challenger Expedition already mentioned.

II. HISTORICAL STEPS IN THE EXPLORATION OF THE DEEP-SEA FAUNA

The deep-sea was the last of the larger life spheres of the earth to be explored. Up to about 1860 it was generally thought to be lifeless, and this assumption seemed to be confirmed by the researches undertaken by FORBES in the Aegean Sea; the distribution of the animals there (due to the peculiar hydrographic conditions) leading him to the conjecture (1843) that a "zero of animal life would probably be found somewhere about 300 fathoms". It is true that as early as 1819 JOHN Ross had reported animals obtained from depths down to about 1900 m in Baffin's Bay. This, and other reports of animals brought up with the sounding lines, was overlooked however, or even discredited; it being assumed that the line had coiled up on the bottom or that the animals had been captured while floating near the surface.

WALLICH, who in 1860, in the North Atlantic, had obtained brittle-stars from a depth of 1260 fms (2300 m), published in 1862 a detailed discussion on the possibility of a deep-sea fauna. He stated that the pressure of the vast depths could not preclude the existence of animal life and inferred that, "the deep-sea has its own special fauna, and that it has always had it in the ages past". The final and irrefutable proof of the existence of a deep-sea fauna was, however, the find in 1860 of sessile animals (cf. MILNE-EDWARDS 1861) on a Mediterranean telegraph cable taken up for repair from a depth of about 2000 m.

Animals were collected in abundance in the great depths during the subsequent British explorations

of the North Atlantic. Therefore WYVILLE THOMson (in 1873, p. 31) concluded: "if there be nothing in the conditions of a depth of 2500 fms (4500 m) to prevent the full development of a varied fauna, it is impossible to suppose that even an additional thousand fms would make any great difference". The famous Challenger Expedition 1872-76 brought back rich collections of animals from all oceans and from depths down to 5490 m. A long series of other deep-sea expeditions with more limited scope followed. Prince ALBERT of MONACO's expedition on the Princesse Alice in 1901 made a successful haul (yielding e.g. a porcellanasterid) at a depth of 6035 m, and up to recent years this was the acknowledged depth record for marine life; (the dredging of a siliceous sponge at a depth of 7600 m by the U.S.Albatross in 1899 (A.AGASSIZ 1902 p. 77) usually being overlooked).

It was generally held, however, that the greatest and hitherto unexplored depths would also have a fauna, until some experiments on the resistance of various animals and of cellular tissue to high pressure (FONTAINE 1930) led to the assumption that the increased pressure might be prohibitive to the presence of life at depths below about 7000 m (cf. p. 199). Therefore, although the Swedish Deep-Sea Expedition in 1948 brought up animals from a depth of almost 8000 m, it was only when the Galathea Expedition in 1951 collected animals at a depth exceeding 10.000 m, that the existence of an animal life at all depths in the ocean was conclusively established.

III. THE DELIMITATION OF THE ABYSSAL REGION

The concept of the 'abyssal region' was originally synonymous with the entire deep-sea, i.e. the ocean deep beyond the shelf (and beyond the reach of fishermen), thus, any depth exceeding about 200-400 m. When the explorations of these depths began, it soon became evident however (cf. e. g. E. PER-RIER 1899 p. 340), that two main faunistic regions might be distinguished: 1) a lower zone with a sparse and uniform fauna and a very low temperature (to which zone alone the term abyssal is now restricted), and 2) an upper transitional zone (now called the bathyal, or sometimes, the archibenthal zone) with a richer and more varied fauna, and, except for the polar regions, with relatively high temperatures.

The boundary between the abyssal and the bathyal zones can roughly be placed at a depth of about 2000 m, but is set by different authors at 1000 m, 1000 fms, 2000 m, 1500 fms, and 3000 m respectively. These discrepancies, as noted by BRUUN (1957), are partly due to the different position of the 4° C isotherm in different regions; (a temperature of about 4° C being the highest temperature at which the endemic elements in the abyssal fauna are found (cf. p. 198)). – The upper limit of the bathyal zone, or the deep-sea as a whole, similarly depends (as already noted by the Challenger scientists) on the hydrographic conditions in each area. Thus, a deep-sea fauna may be found in the Arctic at depths of perhaps only 30 m, while in western subtropical regions it may not be found until a depth of about 800 m (cf. p. 198). That the temperature adapted for a deep-sea fauna comes nearer to the surface in the tropics than in the temperate zones was pointed out e.g. by A. AGASSIZ in 1888 (p. 164).

The extreme deep-sea (the trenches and deeps), is now considered to constitute a special faunistic region – the hadal (or ultra-abyssal) zone. The upper boundary of this zone (and lower boundary of the abyssal zone) is set at a depth of 6-7000 m.

IV. THE BATHYMETRICAL RANGE OF THE PORCELLANASTERIDAE

All the major marine invertebrate groups have representatives at all depths. Thus the echinoderms (cf. e.g. WOLFF 1960) are represented down to the deepest known depths by the holothurioids and the crinoids (deposit- and suspension-feeders), whereas the ophiuroids are as yet only known to occur down to about 8000 m, the echinoids to about 7250 m, and the asteroids to about 7600 m. Within the Asteroidea, three families, viz. the Pterasteridae, the Brisingidae, and the Porcellanasteridae, reach into the hadal depths. Of these, the Porcellanasteridae are remarkable in being exclusively confined to

the deep-sea (no porcellanasterid has hitherto been found at depths of less than about 900 m), and in having their main distribution in the truly abyssal zone, i.e. below a depth of about 2500 m.

Six of the genera of Porcellanasteridae, Hyphalaster, Abyssaster, Thoracaster, Styracaster, Eremicaster, and Porcellanaster (in all comprising about 20 species), live in the abyssal depths, and only a few of them, Porcellanaster and Eremicaster, occur also at depths less than about 2500 m, viz. 1200 and 1600 m respectively. (Another species of Eremicaster reaches down into the hadal zone, to a depth of



Fig. 1. The vertical distribution of the species of Porcellanasteridae in relation to that of the Asteroidea as a whole.

about 7200 m¹). The three remaining genera, *Sidonaster, Benthogenia,* and *Lysaster*, which are all monotypic, seem to be exclusively bathyal, being known only from depths between 900 and 2300 m.

The porcellanasterid genera which occur in the

1. Dr. G. M. BELYAEV has kindly informed the writer that a specimen of *Porcellanaster* was collected at 7584-7616 m in the northern part of the Mariana Trench, during the recent Russian explorations of the Pacific deep-sea.

V. THE MODE OF LIFE OF THE PORCELLANASTERIDAE

A century ago WALLICH noted, in his classical discussion on the presence of animal life at great depths in the ocean, that the deep-sea would be "for ever closed to human gaze". And although the first deepsea explorers may have visualized it, they could never have seriously considered the possibility of photographing the deep-sea floor, televising the activity there, or of sending a man-manned ship down to the greatest of all depths. These now realized possibilities will eventually give us a reliable knowledge of the life-phenomena in the deep-sea. At present, however, we can still only speculate (albeit with a reasonable degree of certainty) about the mode of life led by the animals there.

The porcellanasterid sea-stars, to judge from their morphological characters and by comparison with knowledge of the mode of life of a related form such as the arctic Ctenodiscus, must spend most of their life buried in the soft muddy deep-sea bottom. A very characteristic morphological feature is the so-called cribriform organs (bands of closeset perpendicular cilia-covered folds of skin, or rows of papillae, supported by microscopic 'spines') which are situated on the marginal plates in the arm angles, around the vertical sutures. By means of their ciliary action these organs must serve in producing a circulation of fresh water around the seastars in their burrows; a canal being kept open to the surface (to judge from the condition in Astropecten) by distention of the usually more or less distinct central dorsal prominence (apical appendage or apical cone).

Like so many other deep-sea animals the porcellanasterids are mud-swallowers or mud-eaters; and abyssal zone, are known solely from temperatures below about 4°C, and thus seem to be decidedly stenothermal. The bathyal *Sidonaster* seems to be rather eurythermal as it has been found to live at temperatures ranging from 1.8° to 11.3° C. *Benthogenia*, which is known from two localities only, has been found at 9.7° and 11.5° C; and *Lysaster*, known from a single find only, probably lived at a temperature between 6° and 8°C.

presumably they are able, by means of the water currents created by the cribriform organs, to secure and draw down the surface material (which is comparatively rich in organic matter) in order that it may be caught in the mucus secretion and then led to the mouth by the podia. The stomach is a large undivided cavity which fills out almost the entire disk; this latter becoming greatly inflated when the stomach is well filled with bottom material. There is no intestine and anus; thus, after the organic matter has been utilized, the stomach content has to be emptied out through the mouth opening. This can be greatly expanded, and it would seem that the porcellanasterids besides being deposit-feeders, may be scavengers and facultative predators.

The gonads are small, even when ripe, consisting merely of a few branched tubules, not much longer than the height of the marginal plates where they are closely juxtaposed. The ripe eggs measure 0.5-0.6 mm in diameter which confirms an expected non-pelagic development. Individuals with ripe gonads have been found with the stomach well filled, which would indicate that the reproductive phase is not accompanied by any pause in feeding activity. The available samples of populations further include individuals with unripe gonads besides those with ripe ones, agreeing with the assumption of a sporadical reproduction within the populations.

A commensal hydroid has been found living on *Eremicaster*, and is usually attached to the ventral side of the sea-star, especially in the region around the mouth. The porcellanasterids are also fairly frequently infested with dendrogate ascothoracids, and with myzostomes.

	Number of finds in								Total	Number of finds in							
	Atlantic	Indian	Malayan	Pacific Ocean		Temperatures recorded in C ^o	Bathymetrical range	number of	00 m	и 00 н	00 H	90 11 11	00 H	00 H	00 m 00	00 H	
	Ocean Ocean		n region	West	miđ	East	-		records	900 -100	-20	-30(300-400	-500	500	600 -70(-800
Hyphalaster hyalinus					1		1.7°	5030 m	1						1		
Hyphalaster inermis	20	8		3	1		1.1°-3.9°	2278-5413 m	32			7	11	9	5		
Hyphalaster giganteus		1						ab. 3850 m	1				1				
Hyphalaster scotiae	(1)							2580 m	1			1					
Lysaster lorioli		1					ab. 6°-8°	≧ 1000 m	1		1						
Benthogenia cribellosa			1				9.7°-11.5°	905-925 m	1	2							
Abyssaster tara		7		1			1.1°-1.8°	3200-6280 m	8				6	1		1	
Abyssaster diadematus						1	1.8°	3950 m	1				1				
Abyssaster planus		(1)					0°	3566 m	1				1				
Thoracaster cylindratus	6	8		1		5	$1.3^{\circ} 2.8^{\circ}$	2600-ab. 5000 m	20			. 3	5	12			
Styracaster horridus	9	4		2			$1.1^{\circ} 2.4^{\circ}$	4040-5610 m	15					9	6		
Styracaster caroli		6					$1.7^{\circ} 2^{\circ}$	2600-4820 m	6			3	2	1			
Styracaster elongatus	5	2						3310-4870 m	7				3	4			
Styracaster chuni	4			2			1.1°-3.9°	2550-ab. 4550 m	6			3	1	2			
Styracaster paucispinus						1	1.8°	4335 m	1					1			
Styracaster robustus	(1)							3846 m	1				1				
Styracaster armatus		3		1			1.3°-1.9°	3365-4350 m	4				3	1			
Styracaster spinosus	5							2995-4360 m	5			1	2	2			
Styracaster clavipes		1					1.7°	3197 m	1				1				
Styracaster monacanthus						1	1.9°	4143 m	1					1			
Porcellanaster cæruleus	69	8	3	3		3	1.1°-4.2°	1158-6035 m	86*		15	17	6	4	1	1	
Eremicaster crassus		4			1		$1.2^{\circ}-1.8^{\circ}$	3390-4271 m	5				4	1			
Eremicaster gracilis				5		18	1.3°-2.6°	2690-5204 m	23			3	9	8	3		
Eremicaster pacificus				[1]		14	1.6°-2.9°	1571-4088 m	15**		4	5	4	1			
Eremicaster vicinus	1	1		3		2	1.3°-2.4°	5204-ab. 7200 m	7						3	3	1
Sidonaster vaneyi		11	6				1.8°-11.3°	1147-ab. 2300 m	17		13	3					-

Table 1. Survey of the geographical and bathymetrical distribution of the Porcellanasteridae.

* The survey of the bathymetrical distribution of *Porcellanaster cæruleus* considers only 44 finds; exact information of the 42 finds made by the Albatross 1883-84 in the N.W. Atlantic, in depths of 1657-3520 m, not being available.

** The depth of one find is unknown.

0 The finds in question were made in the Antarctic region.

[] The find was made in the Bering Sea.

VI. THE GEOLOGICAL AGE OF THE PORCELLANASTERIDAE

When summarizing his considerations on the Porcellanasteridae SLADEN (1889 p. 126) noted that in some respects they "appear to present a more archaic character than the Archasteridae", but that this seemed to him to be "dependent on striking features of structural detail rather than on general fascies". He further noted that the apparently archaic fascies was "largely due to the remarkable degree in which the Porcellanasteridae present permanently characters which are regarded, in the majority of forms at least, as essentially embryonic". Probably SLADEN had in mind the large terminal ossicles, the large marginal plates, and perhaps also the apical appendage.

FISHER in his Monograph of the Asteroidea of the North Pacific (1911-30) grouped the families, as closely as a linear arrangement would permit, in what seemed to him the most natural order. The Porcellanasteridae he placed first however, not because they were conclusively considered the most primitive, but (1911 p. 4) in order "to avoid sandwiching them between the Astropectinidae and some other family, and because they stand apart from the other Phanerozonia". (FISHER recognizes within the Asteroidea the three main groups: the Phanerozonia, the Spinulosa, and the Forcipulata). In 1928 he called the Porcellanasteridae "archaic though highly specialized".

It is the typical phanerozoniate sea-stars, such as *Astropecten* and allies, which FISHER and several other authorities on sea-stars (e.g. SLADEN, LUDWIG, DÖDERLEIN, KOEHLER, MORTENSEN, and SPENCER) regard as being the most primitive of the recent forms. However, other authorities (e.g. E. PERRIER, GEMMILL, and MACBRIDE) consider these sea-stars highly specialized, and regard the Spinulosa as the most primitive.

MACBRIDE (1923), when criticizing the concept of the primitiveness of the Astropectinidae, says somewhat sarcastically that the systematists holding this view are "– for the most part – students of the external features of preserved specimens only". He notes that "what these specialists are impressed by is the 'phanerozoniate' character of the Astropectinidae, that is the edging of the arms with a series of broad plates termed the 'marginals'"; and then goes on to critizise this view, claiming that the apparent marginals of the ancient starfish "are not homologous with the marginals of the modern Paxillosa (i.e. *Astropecten* and allies) at all but are the adambulacrals". – The writer should like to point out, however, that although this argument was allowed to stand, it does not hold. True enough, in some types of Palaeozoic sea-stars (e.g. the Ordovician *Cnemidactis*) the adambulacral ossicles are very large and appear along the sides of the arms as a series of inferomarginals, but in other Palaeozoic sea-stars (e.g. the Ordovician *Hudsonaster*) the adambulacral skeleton only bounds the furrows, whereas the arms are armed laterally with genuine marginal plates. Thus, MACBRIDE's criticism cannot refute the concept of the phanerozoniate sea-stars being the most archaic type.

It appears however, taking everything into consideration, that the question of which recent group of sea-stars is the most primitive in existence, is an unanswerable one. The knowledge of the earliest types of sea-stars does not seem to offer any clue to the interrelationships of the later ones. The early Palaeozoic star-shaped echinoderms, which are placed in the classes Asteroidea and Ophiuroidea, are actually so different from the modern types, that it has even not always been immediately evident to which of the two classes, certain of the Palaeozoic forms belonged. Palaeozoologists therefore also generally place the Asteroidea and the Ophiuroidea in a common supergroup, the Stelleroidea. In some modern works (e.g. HYMAN 1955) it is maintained, however, that the Ophiuroidea are more closely related to the Echinoidea than to the Asteroidea. This view is based, among other things, upon the similarity in the general appearance of the larvae of the Ophiuroidea and the Echinoidea, and upon the occurrence of the same type of sterols in some biochemically tested ophiuroids and echinoids, and a different type in the asteroids (cf. BERGMANN 1949). However, the palaeozoological and morphological evidence (cf. SPENCER 1914-40) supports equally well the concept of a closer relationship between the Asteroidea and the Ophiuroidea than between the Ophiuroidea and the Echinoidea. But taken together these three groups stand apart from the other recent echinoderms, the Holothurioidea and the Crinoidea.

The possession of the so-called cribriform organs makes the Porcellanasteridae a highly specialized group among the paxillose phanerozoniate seastars. The group is also in some other characters distinct from its nearest relatives within the Phanerozonia, i.e. the Goniopectinidae and the Astropectinidae. It seems justified, therefore, to consider the Porcellanasteridae as a special suborder, the Cribellosa, as did FISHER in 1911.

In the writer's opinion the Porcellanasteridae may be roughly estimated to have split off from the common astropectinid stock in Late Mesozoic, if one judges from the rate of evolution ascertained through fossil evidence in some other groups (e.g. in the echinoids which are so well known through TH. MORTENSEN's monograph, 1928-51). A support of this assumption may also be the fact that the geological age of the recent non-endemic abyssal fauna elements, to judge from the Palaeontological evidence, is similarly Late Mesozoic (at the earliest).

The marginal plates of the Porcellanasteridae have the cribriform organs typically developed on more or less marked depressions which show distinctly on the plates when the papillae in the organs are removed. Possible fossilized marginal plates of porcellanasterid sea-stars, should therefore, be very easy to recognize. No fossil porcellanasterids are known however, and though one cannot rely on negative palaeontological evidence, this nevertheless may be mentioned as a fact consistent with the exclusive deep-sea occurrence of the group (the origin of all fossil marine faunas being shallow water or moderate depths at most). The absence of fossil porcellanasterids supports the assumption that the group has evolved within the deep-sea, i.e. that the complicated cribriform organs were not acquired by their astropectinid-like ancestors until after they had become deep-sea dwellers (see further p. 200).

Because of their embryonic characters the writer suggests that the evolution of the Porcellanasteridae has been brought about by the phenomenon which GARSTANG (1922) designated as paedomorphosis (i. e. by a delayed morphological development along with a gradually accelerated sexual maturing, or in other words with embryonic characters moved into the fullgrown stage).

VII. THE INTERRELATIONSHIPS OF THE PORCELLANASTERID GENERA

The nearest relatives of the Porcellanasteridae are the Goniopectinidae and the Astropectinidae, and it is probable that these three groups have arisen from a common astropectinid-like stock. Astropectinid-like sea-stars are known from the Jurassic, and true astropectinids from the Cretaceous (cf. e. g. DURHAM & ROBERTS 1948) while the goniopectinids, like the porcellanasterids, are without fossil records. The recent astropectinids have a world-wide range and also include several abyssal forms, but otherwise have their chief development in the tropical sublittoral and bathyal regions. The Goniopectinidae show close similarities to the Porcellanasteridae and may have split off from the common astropectinid stock along with this group. However, they are less specialized and are entirely confined to the sublittoral and bathyal depths.

The porcellanasterid genera may roughly be divided into two groups (fig. 2):

1) A larger and somewhat heterogeneous group comprising the most primitive genera, *Lysaster* and *Benthogenia*, as well as *Hyphalaster* and *Thoracaster* (a simple adambulacral armature and in general many cribriform organs) plus the more specialized and thus phylogenetically younger *Styracaster* and *Abyssaster* (smaller number of cribriform organs, possibly a more specialized oral and adambulacral armature, and, in the case of *Styracaster*, a specialized arm-armature). 2) A homogeneous group of probably young phylogeny (with few cribriform organs and a more or less specialized oral and adambulacral armature) comprising *Sidonaster*, *Eremicaster*, and *Porcellanaster*. (The forms in this group may have evolved from primitive porcellanasterids by a further paedomorphosis (cf. above)).

Two primitive members of the first group, Lysaster and Benthogenia, are confined to the bathyal zone, being known from depths of 900-1000 m. Hyphalaster and Thoracaster have a known range of 2275 to 5410 m, and of 2600 to 5000 m, respectively. Styracaster ranges from 2550 to 5610 m, and Abyssaster from 3200 to 6280 m. The four latter genera are thus confined to the truly abyssal zone.

One of the genera in the second group, *Sidonaster*, is exclusively bathyal, ranging from 1150 to 2300 m. The other two, *Porcellanaster* and *Eremicaster*, have the widest bathymetrical range of all the porcellanasterid genera, viz. 1160 to 6035 m, and 1570 to about 7200 m, respectively. Thus, it is the presumably younger types of porcellanasterids which have penetrated into the greatest depths.

The two supposedly most primitive genera of the Porcellanasteridae, *Lysaster* and *Benthogenia*, belong to the bathyal zone in the tropical Indo-Malayan region, where on the whole the greatest number of genera occur. Thus this region might be considered the center of creation of the Porcellan-



asteridae, as has also been the assumption with regard to several other animal groups. However, as will be touched upon in the following (p. 211) this

reasoning is probably not sound, the faunal richness rather being due to the fact that the ecological conditions during the Tertiary and Quaternary periods have remained more stable in the Indo-Malayan region than in most other regions of the ocean.

The older types of abyssal porcellanasterid genera, *Thoracaster* and *Hyphalaster*, comprise only

VIII. THE GEOLOGICAL AGE OF THE DEEP-SEA

Some of the first deep-sea biogeographers, e.g. WY-VILLE THOMSON and MURRAY, were of the opinion that a continuous deep ocean had existed since early Palaeozoic times. Other authors, however, have expressed quite different opinions as to the age of the oceans. Some have even considered that they were formed as late as Jurassic times, and others have considered the Pacific an ancient and permanent feature of the earth's crust, while they assigned a youthful development to the Indian and Atlantic oceans. The prevailing opinion now seems to be that of the permanency of the oceans.

The land and ocean masses, according to such theories as those set forth by VENING-MEINETZ (1944), and HILLS (1947) (see KUENEN 1950), were in the main already formed when the crust of the earth hardened (the present distribution of the land

masses being remarkably similar to the distribution which is arrived at on purely theoretical grounds when considering the action of convection currents on the masses of a cooling earth). The great oceans according to these theories thus constitute a primitive feature of the earth's crust and may never have been subject to any drastic changes, but only to changes connected with the elevation or subsidence of continental marginal areas, isthmian links and island festoons.

one and a few (3) species respectively, and both

Thoracaster cylindratus and Hyphalaster inermis,

which are abundant in individuals, show rather fixed taxonomical characters. A younger type, such

as *Styracaster*, is split up into a fairly large number of species (10). *Eremicaster*, another young type, is

split up in two or three species showing evidence of

somewhat unstable taxonomical characters. Porcel-

lanaster, probably the youngest abyssal generic

type, is monotypic but polymorphic.

"It is important to note," says KUENEN (1950 p. 130) when summarizing his considerations on the geological history of the oceans, "that, since as far back as the Cambrian, at least, the upper surface of the continents has been close to sea level, just at it is at present, being sometimes partly flooded, sometimes laid almost dry."

IX. LIFE CONDITIONS IN THE ANCIENT AND IN THE RECENT DEEP-SEA

Life in the deep-sea, because of the absence of sunlight, is totally dependent upon the supply of organic matter from land and from the upper lighted water layers. In the first case the organic matter is washed out into the sea by the rain water (together with enormous quantities of inorganic material), or carried out over the sea by the wind; and the landderived material which is deposited on the bottom near land (the terrigeneous deposits) then may be transported far into the ocean by mud flows or turbidity currents. In the second case the organic matter is basically produced through the photosynthesis of the phytoplancton, and then transferred to the deep-sea via the dead remains of the pelagic plants and animals sinking, or by animals actively descending.

Essentially the deep-sea is, and has always been, a very calm milieu. Very small particles, inorganic and organic, may settle on the bottom, and this is consequently covered with a very soft substratum. (However, on the bottom far from land (with eupelagic deposits) in the areas with a low productivity in the upper water layers, the intensity of sedimentation may be only 0-0.4 cm per 1000 years (cf. ARRHENIUS 1950 p. 86).)

The biomass (i.e. the quantity of substance in live organisms, or total standing crop, in grams per square meter) is extremely small in the deep-sea in comparison with that in the shallow coastal areas. Near the shore, in depths of 50 m e.g., the biomass may exceed 1000 gr/m² (cf. BARNARD 1959), and 500 gr/m² is a common figure in richer sublittoralupper bathyal areas. With increasing distance from land and with increasing depth the biomass diminishes rapidly, however. In the abyssal depths (>3000)m) in Antarctic and sub-Antarctic regions, and in the offshore regions of the boreal Pacific e.g., the biomass is of a magnitude of $0.8-0.5 \text{ gr/m}^2$. In the tropical open oceans (on the eupelagic deposits) it is on average 0.08 gr/m² in the Pacific and 0.03 gr/m² in the Indian Ocean (cf. BELYAEV 1959), and in the trenches far from land it is still smaller (e.g. in the Tonga Trench, in 10.500 m, only 0.001 gr/m² (cf. BIRSTEIN 1959)).

In accordance with their opinion that there had been a continuous deep ocean from Silurian times to the present day, WYVILLE THOMSON and others also assumed that there had always been an abyssal life. Since, however, the deep-sea dredgings of the Challenger, contrary to anticipations, did not bring up representatives of a decidedly ancient fauna, MOSELEY (1880), A. AGASSIZ (1888), and MURRAY (1895), advanced the view that the deep-sea had been uninhabitable to a higher life during the whole or most of the Palaeozoic era, and that its fauna dated back no further than the Cretaceous.

MOSELEY (1880 p. 591) offered as a rather vague explanation of a lifeless Palaezoic deep-sea that it had been overcharged with various gases, salts and mud, whereas MURRAY (1895 p. 1439) suggested that it had been anaerobic because a vertical circulation between the deep waters and the oxygenated surface waters was prevented by the conditions of the temperatures, which he assumed were fairly high and universally uniform. – According to this latter assumption a deep-sea life did not become possible until Late Mesozoic, when the poles began to cool off, and cold, dense and oxygenated waters descended to the greater depths.

Oxygen can be added to the ocean only in the upper water layers, by the absorption of air and the photosynthesis of plants. Thus the deep-sea region is entirely dependent on the continuous supply of oxygenated water-masses for its content of oxygen.

Some recent water-masses have been estimated, on the basis of measurements of the C14 activity, to be almost 2000 years old (cf. SUESS et al. 1959), and if they remain stagnant they will eventually become anaerobic. It is possible, therefore, that there have been large stagnant and anaerobic water-masses in the depths during earlier geological periods. On the other hand this can surely never have been a universal feature, since at least some vertical circulation must have been maintained through those differences of the surface waters of the high and low latitudes which, however slight, must have existed at all times on account of the different solar radiation. - In the recent oceanic bottom waters the amount of oxygen is on an average 5-6 cc/l in the Atlantic, and somewhat less, e.g. 3.5 cc/l, in the Pacific (cf. e.g. RICHARDS 1957).

One of the primary characteristics of the recent abyssal deep-sea is its constant and very low temperatures (0-2°C), which are conditioned by the extremely cool water-masses sinking down in the polar regions and from there streaming over the bottom towards the equator. This characteristic was probably acquired in fairly recent geological times, since during the Mesozoic and earlier Tertiary the abyssal waters must have been warmer; the temperatures at the poles being higher than now, and the vertical circulation more effective on account of the relatively higher density of the polar surface waters when not diluted by melting glaciers (SIMPSON 1940). – At present the time required for the surface waters to reach, from e.g. the Antarctic to the equator along the bottom, may be from 10 to 30 years (cf. DIETRICH 1957 p. 395).

It is the very similar Triassic and Jurassic marine shallow water faunas, including coral reefs, known from high as well as from low latitudes (cf. e.g. NEAVERSON 1955, MÜLLER 1959), which imply that the ocean temperatures during earlier Mesozoic periods were fairly equable all over the globe, or at least, rather high in the higher latitudes of the northern hemisphere. (This is on the assumption that the ecology and tolerances of temperatures of the coral reefs have not changed essentially from then until now.) The disappearance of the coral reefs in the higher latitudes during Late Mesozoic then denotes the commencement of the general cooling of the polar regions which eventually led to the glaciations and to the formation of the marked hydroclimatic zones.

The temperatures in the abyssal deep-sea during the Early Tertiary, on the basis of these considerations, were assumed (e.g. by MURRAY 1895 p. 1456) to have been markedly higher than now, probably about 10°C. Apparently a final proof of this assumption was the palaeotemperatures estimated by EMI-LIANI & EDWARDS (1953) and EMILIANI (1954) by the method of oxygen isotopic analysis on bottom foraminifera from deep-sea cores from depths of about 4000 m in the eastern tropical Pacific, viz. about 10.4°C in Middle Oligocene, 7°C in Lower Miocene, and 2.2°C in uppermost Pliocene; while the bottom temperature in the region in Recent is a little less than 2°C.

Recently, however, BIRSTEIN (1959) and ZENKE-VITCH & BIRSTEIN (1960 p. 13) noted that the palaeotemperatures determined may not refer to the abyssal but to the bathyal and sublittoral zones, since the foraminifera (in the Middle Oligocene sample, *Cassidulina spinifera*, and in the Lower Middle Miocene sample, *Gyroidina zelandica* and *Laticarinina bullbrooki*) might have been shelf species, of which the empty shells were secondarily shifted to a greater depth.

It is true that for this reason the quoted palaeotemperatures do not offer the ultimate proof of a higher temperature in Early Tertiary. On the other hand the assumption of a higher abyssal temperature at that time appears well-founded alone from the presence of coral reef faunas in the higher latitudes. The foraminifera in question may well also have lived in the abyssal depths as originally assumed. (A recent species of *Gyroidina*, *G. soldanii*, is recorded as having a bathymetrical range of about 40 to 4350 m, being abundant at the greater depth, which will indicate that this was also its habitat, and a recent species of *Laticarinina*, *L. pauperata*, is recorded as having a range of about 300 to 3980 m, being abundant e.g. at a depth of 1650 m (CUSH-MAN 1931).)

ZENKEVITCH & BIRSTEIN apparently assume that the abyssal temperatures have been continuously low far back in the history of the oceans. At least they (p. 13) consider BRUUN (1956) to be in error when he infers that "the relatively sudden onset of the glacial age and its cooling of oceanic deep water must have been catastrophic for the abyssal and hadal faunas", and "only the relatively eurythermic and eurybathic species could survive". They also note (p. 13) that another fact disproving the probability of sharp temperature changes in abyssal waters, is the undoubtedly long existence of several ancient species in these waters, e.g. Neopilina. As shall be discussed in a following paragraph (cf. p. 191) it is by no means certain, however, that Neopilina has lived continuously in the abyssal deep-sea from Cambro-Silurian times.

(A decrease in abyssal temperatures of a magnitude of 8° C since the Middle Oligocene, about 35 million years ago, means a yearly decrease of an average of $0.23 \cdot 10^{-6^{\circ}}$ C only; and therefore the assumed extinction of the greater part of the possibly earlier existing Palaeozoic and Early Mesozoic abyssal fauna will have been a gradually proceeding phenomenon during the whole of the Tertiary period rather than a relatively sudden mass-mortality at the initiation of the glacial epoch).

The reasons for the undoubtedly well established general climatic change in the later geological history of the earth are obscure, but must be correlated with a change in cloud amounts, precipitation, forces of wind, and oceanic currents; perhaps ultimately depending on a change in the solar radiation. A possible shifting of the position of the poles may also have played a role.

The amount of water in the oceans has most probably been about the same since Early Palaeozoic as it is to-day, and it is probable also that the chemical composition of the oceans has been fairly stable throughout the fossil record (see e.g. PEARSE & GUNTER 1957 p.133). – In the recent deep-sea, the salinity is on an average 34.8%, and varies only about $\pm 0.2\%$.

A more detailed review of the life conditions in the deep-sea would not be appropriate here. Refer-

X. THE THEORETICAL COMPOSITION OF THE DEEP-SEA FAUNA

The first life in the sea must have evolved in the lighted regions, and a floating or swimming life may have existed all over the oceans in the upper waters while a higher bottom life was still restricted to the shallow coastal waters (life in the dark deepsea not being possible until a source of food was created by organic matters produced in the lighted regions sinking to the depths). Bacterians, able to live under possible anaerobic conditions, must have been the first kind of life in the deep-sea. Occasional wanderers from the upper pelagic fauna must have continually strayed into the dark deeper waters, and eventually it has become possible for pelagic scavengers and predators to live there permanently. Ultimately then, the higher bottom fauna spread outwards from the coastal regions, descending further and further out onto the ocean floor. The exact kind of animals first to settle in the deep-sea, and when this ocurred, is a question which will always remain unanswered. It would seem, however, that some reasonable theories on the origin of the recent abyssal deep-sea fauna can be deduced.

Theoretically the recent deep-sea fauna (since an ocean with great depths must have existed since Praecambrian times), could be composed by elements of Palaeozoic and Mesozoic geological age as well as those of a Caenozoic age. These elements could either have originated in the shallow waters and thereafter merely have extended their range to the depths, or they could, after having become deep-sea dwellers, have been so strongly modified that they can now be regarded as having evolved (as

taxons of higher rank than genera), within the deepsea itself.

ence is given to e.g. the summaries presented by

EKMAN (1953a), FAGE (1953), and BRUUN (1957).

The possible influence exerted on the distribution

of the benthic fauna by the various ecological fea-

tures in the deep-sea will be discussed in more de-

tail, however, in chapters XII-XIV.

The following brief discussion will center on three main categories of faunistic elements in the abyssal region:

1) The possible Palaeozoic element, which should comprise animal types which, almost unchanged during the course of their evolution, have lived in the sea since Palaeozoic times, without having been influenced by variations in such ecological factors as depths and temperatures.

2) The Mesozoic and Early Caenozoic elements, which will include animal types which have not been modified to any marked degree after having extended their range to the deep-sea, as well as such types which by radical modifying of older (Palaeozoic or Mesozoic) deep-sea forms have evolved into forms which are now endemic in the deep-sea. (If their shallow-water relatives have become extinct, the forms of the former category will be relicts in the deep-sea, but they will appear endemic if the shallow-water forms in question have left no fossil record).

3) The Late Caenozoic elements, in which the taxons of family or higher rank will all be immigrants simply because the time lapse within the period is presumably too short for more than the evolution of genera or species. – The time of the immigration into the abyssal region, and also to some extent the place of origin, may be discussed on a firmer basis regarding this category than is possible with regard to the geologically older categories.

XI. THE GEOLOGICAL AGE OF THE RECENT DEEP-SEA FAUNA

1. The alleged antiquity

(Including a discussion of the view held by ZENKEVITCH & BIRSTEIN 1960)

Early in the history of the deep-sea exploration it was generally expected that the great depths would prove to be inhabited by a fauna corresponding to that known from Early Tertiary deposits, an expectation inspired by the finds of various forms related to or reminiscent of forms known previously as fossils from the Tertiary and Cretaceous periods. (The most celebrated of these is the minute sea-lily *Rhizocrinus lofotensis* which was described by M. SARS in 1864; others include various echinoids and molluscs.)

However, the assumption of the deep-sea fauna

being essentially archaic became untenable from the results of the Challenger investigations. It is true that WYVILLE THOMSON in 1877 (p. 353) stated, "the abyssal fauna is certainly more nearly related than the fauna of the shallower water to the fauna of the tertiary and secondary periods, although this relation is not so close as we were first inclined to expect". It must be borne in mind, however, that what WYVILLE THOMSON understood by the "abyssal fauna" was the entire deep-sea fauna, including that of the more moderate depths (the bathyal fauna) which harbours, as is to be discussed in the following, a larger percentage of ancient forms than that of the greater depths. Furthermore, the rarity and novelty of the deep-sea forms led them to be erroneously endowed with too great an importance as indicators of antiquity, in comparison with the commonly occurrent and familiar littoral forms such as Lingula and Limulus.

The first clear denial of the concept of the true deep-sea fauna being an archaic relict fauna, was given in 1880 by MOSELEY who pointed out (p. 571) that: "Contrary to anticipation, the deep-sea fauna is mainly composed of more or less modern shallowwater genera and their allies. The fish of the deepsea comprise amongst them no Dipnoi, no Ganoids, and no Lampreys ... There are no Trilobites in the deep-sea, and no Graptolites, no Bellemnites. All the most ancient forms which now survive occur in shallow water. Lingula, most ancient of all, is abundant in two or three feet of water ... Trigonia and Limulus survive in shallow water, and so do Amphioxus and Cestracion ..." MoseLey further pointed out: "scarcely a single animal ... of firstrate zoological importance was obtained in great depths", which, he emphasized, "is a most extraordinary fact, for in our deep-sea dredgings we have explored for the first time nearly three-quarters of the earth's surface".

Yet the fauna of the deep-sea, despite its not being fundamentally different from that of the shallowwater, was revealed by the Challenger Expedition to comprise a number of peculiar families and also higher taxonomic categories. The most sensational perhaps was the discovery (WILLEMOES-SUHM 1873) of the occurrence in the deep-sea of decapod crustaceans belonging to a group, the Eryonidea, which was known from Jurassic deposits, but considered extinct since that time. (A recent representative of the same group was described in 1862 by HELLER, but no mention of its fossil relationships was then made).

The Challenger Expedition was also responsible for showing the importance in the deep-sea fauna of the group of holothurians now known as the order of Elasipoda. This expedition also brought to light the first representatives of the Porcellanasteridae, the only family in the suborder Cribellosa within the Asteroidea. It was left to the Galathea Expedition, however, to collect (at a depth of 3570 m off the Mexican west coast) the first abyssal animal of really "first-rate zoological importance", viz. the mollusc Neopilina, described by LEMCHE in 1957 and found to be a living representative of the order Tryblidiacea in the class Monoplacophora, a group dating back to Cambrian and hitherto supposed to have become extinct already fairly early in Palaeozoic (Late Devonian).

The colloquium On the Distribution and Origin of the Deep-Sea Bottom Fauna held in 1953, led to conclusions (cf. SPÄRCK 1953) closely agreeing with those drawn by MOSELEY (op. cit.), viz. that the deep-sea fauna could not be considered to be of any special age, that it certainly included some few archaic (i.e. Mesozoic) forms, but in the main was composed of representatives of shallow-water groups which penetrate into the great depths, and that such a penetration is still in process.

An attempt to give a numerical expression of the relative geological age of the recent marine fauna in various zones of depth, was made by MENZIES & IMBRIE in 1958. They surveyed a number of invertebrate groups where sufficient information was available and found the generic composition of the fauna to be as follows: 1) in depths exceeding 3000 m (the abyssal fauna), about 86 % Tertiary, 14 % Mesozoic, and no Palaeozoic types, 2) in depths between 200 and 2000 m (the bathyal fauna), 62 % Tertiary, 37 % Mesozoic, and 1 % Palaeozoic types, 3) in the intertidal depths, 66 % Tertiary, 30 % Mesozoic, and 4 % Palaeozoic types. Molluscs were not among the groups considered, but Neopilina was noted as the only Palaeozoic relict known in the abyssal fauna. (As shall be touched upon in the following, also some other invertebrates of Palaeozoic relationships occur in the abyssal deep-sea, but none of these are peculiar to the region).

The benthic foraminifera were found by MEN-ZIES & IMBRIE to show a higher percentage of genera extending from Palaeozoic to Recent than any of the surveyed invertebrate groups, and also the highest abyssal Palaeozoic generic representation. Since, however, cases of convergency may be more difficult to detect in the foraminifera than in the invertebrates, foraminiferan phylogenetical taxonomy may be less reliable. All the same it seems most likely that foraminifera were rather the earlier colonizers of the deep-sea than was higher life, and also better survived the changes in deep-sea temperatures since Palaeozoic. When A. AGASSIZ (1888 p. 157) supported the opinion that the first benthic invertebrate inhabitants of the deep-sea dated back no further than the Cretaceous, he also noted: "Of course, there must have been pelagic animals, and foraminiferans may have lived at great depths in the track of the currents."

Russian scientists, working with the rich material collected during the recent Russian deep-sea explorations, seem to have adopted the assumption that the deep-sea fauna on the whole has a general antiquity. It is not a Palaeozoic but a Mesozoic origin which they attribute to the abyssal fauna however, and this is also usually understood as being the whole fauna below a depth of about 600 m. Thus ZENKEVITCH in 1959 lists a number of echinoid families, "well known from Upper Cretaceous deposits and formerly thought to be extinct", as being ancient inhabitants of the abyssal zone (i.e. the depths below 600 m).

All the same, the differently expressed opinions of the age of the deep-sea fauna, by, on the one side ZENKEVITCH & BIRSTEIN and on the other e.g. BRUUN (1956) and MENZIES & IMBRIE (op. cit.), does not merely rest on the different use of terminology but has a background too in somewhat different interpretations of the facts known. ZENKEVITCH & BIRSTEIN (1960 p. 10) state that "the percentage of primitive archaic forms in the abyssal fauna is far higher than in the fauna of the shelf, thus providing evidence of the greater antiquity of the abyssal fauna". They note further (p. 14) that the groups discussed by MENZIES & IMBRIE include only 11 % of all species encountered below 3000 m, and that the extent of the conclusions drawn by these authors (viz. the concept of a relatively young abyssal fauna) to the whole abyssal fauna "is unlikely to be correct when they are based on so small a fraction".

It is true that since adequate palaeontological data are lacking with regard to a considerable part of the deep-sea fauna, MENZIES & IMBRIE were unable to discuss its palaeontological relationships in great detail. But the results they arrived at are closely parallel with the general impression of the age/depth distribution of the marine fauna which MOSELEY held (cf. above). As will be discussed in the following, also various other considerations can but lead one to the assumption that in the main the recent abyssal deep-sea fauna is of no great age, and that at least, the concept of it being essentially archaic is erroneous.

ZENKEVITCH & BIRSTEIN (p. 16) claim that "when we determine the geological age of the genera and families which today live at a given depth we are certainly not determining their actual age, but are merely establishing to which shallow-water fauna of particular periods they are related". The writer fails to understand, however, why this should not be a fairly reliable estimate of the (maximal) geological age of the deep-sea forms.

In theory, a taxon of e.g. family rank could have evolved in the abyssal deep-sea, and thereafter extended its range of distribution upwards, in competition with the bathyal and sublittoral faunas. But this course of events, if ever having taken place at all, will be the exception and the reverse the rule. ZENKEVITCH & BIRSTEIN also note (p. 12) that in their opinion "no formation of major taxonomic units occurred under abyssal conditions: there was simply an adaptive radiation into species and genera".

This view is also held by the writer (on the condition that 'abyssal' is taken in the restricted sense, meaning depths exceeding about 2000 m, and that allowance is made for possible exceptions with regard to taxons of family rank, among which e.g. the actiniarian group, the Galatheanthemidae, may be a case). In the writer's opinion the quoted view will certainly mean, however, that the geological age ascertained through fossil evidence on former shallow-water relatives of any one recent abyssal deepsea group (if the fossil record is not too incomplete) will at the same time be the maximal age of the group in the abyssal deep-sea.

ZENKEVITCH & BIRSTEIN further state (p. 16) that "The earlier the migration (into the deep-sea) the less likely that the affinity can be traced between a recent deep-water group and a shallow-water group of the past ...", and that the assumption "concerning the higher proportion of ancient elements in the fauna of the shelf as compared with the abyssal depths can be easily explained by the obvious fact that it is not the fauna of the abyssal waters but the fauna of the shelf that has been preserved in fossil condition".

(The taxons of higher rank which are more or less exclusively confined to the recent deep-sea are few. There are e.g. within the molluscs, the Monoplacophora (cf. below), within the crustacea, the Neotanaidae and the Eryonidea (cf. p. 194), and within the echinoderms, the Porcellanasteridae and the Elasipoda).

ZENKEVITCH & BIRSTEIN (1960 p. 12) now consider that "those higher taxonomic units, mainly, or entirely confined to great oceanic depths, should be most correctly regarded as relicts which in former times lived under the favourable conditions of the shallow seas and were displaced by relatively young and more progressive groups". The writer is unable to agree completely with this conclusion however (see also p. 197).

Thus, the two characteristic deep-sea groups among the echinoderms, the Porcellanasteridae and the Elasipoda, which ZENKEVITCH & BIRSTEIN list as ancient relicts in the deep-sea, are in the writer's opinion, examples of higher taxons which have evolved in the upper deep-sea, in the region of the mud-line (cf. p. 200) at the end of the Mesozoic era, and first extended their range to the abyssal zone during Tertiary. The Porcellanasteridae are regarded (cf. chapter VI) not as archaic, but rather as paedomorphic paxillose phanerozoniate sea-stars of a comparatively young phylogenetical origin (cf. pp. 184, 194); and a similar point of view may be adopted for the Elasipoda (cf. p. 194). Both groups are without fossil records.

Peculiarly enough, ZENKEVITCH & BIRSTEIN (p. 12) when giving their opinion on the taxonomic groups confined to the deep-sea conclude: "Whether their descent into great depths and disappearance from shallow waters occurred during the Palaeozoic, Mesozoic, or Cenozoic, is a matter of secondary importance". This question in the writer's opinion is on the contrary a very important one, although in general difficult, if not impossible to answer.

Take e.g. Neopilina (inclusive of Vema), the only Palaeozoic relict so far recorded from the abyssal fauna. This mollusc, known in Recent solely from depths between 3000 and 6000 m in the eastern tropical Pacific, belongs to a group, the Tryblidiacea, known from Cambro-Silurian deposits, but without fossil records since that time. 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. - If it was at all possible, it would certainly be of great interest to ascertain during exactly which geological period the form became abyssal.

If the invasion of the abyssal deep-sea by the a-n cestors of its recent fauna has taken place almost exclusively since Mesozoic (and many considerations lead to this conclusion), then the abyssal fauna must be considered relatively young (in comparison with the bathyal and the littoral warm-water fauna), no matter which types of animals are now dominant in the region.

ZENKEVITCH & BIRSTEIN (p.12) conclude: "We can, however, be sure that the great oceanic depths play the part of refuges for relatively primitive relict groups which in their struggle for existence had to desert the more favourable conditions of life in the shallow waters." As already stated the writer considers this point of view unwarranted. Those groups which during evolution became adapted to the life on a soft bottom, such as the Porcellanasteridae and the Elasipoda, and are now abundantly represented, by species and individuals, in the abyssal deep-sea, are conquerors of this habitat rather than refugees into it.

When discussing the young elements in the deepsea fauna, ZENKEVITCH & BIRSTEIN (p. 20) refer to a characteristic difference in the pattern of vertical distribution between these "secondary deep-water forms" and what they consider "the ancient deepwater forms": "In most secondary deep-water animals the number of species regularly and rapidly decreases with increasing depth, whereas in the ancient deep-sea animals the number of species tend to increase with depth and begin to diminish only with the passage to the lower abyssal and the ultraabyssal waters". In the writer's opinion this fact is correlated not merely with possibly a different geological age, but equally as much with the fact that the "ancient deep-water forms" are those forms especially adapted for a deep-sea life, being pronouncedly soft-bottom dwellers. (They have evolved in the region of the mud-line (see p. 200) and have spread from there over the deep-sea bottom and into the greater depths with similar ecological conditions, but were prevented in spreading upwards into the shallower water on account of the greater competition from other animals there (cf. p. 200) and the more unstable ecological conditions).

2. The Mesozoic and Early Caenozoic elements

The following review of some of the characteristic abyssal animal forms together with information of their known geological age (according to MÜLLER 1957-60, Treatise of Invertebrate Paleontology 195359, and Traité de Paléontologie 1952-53) will show that a late Mesozoic origin (i.e. a continuous history in the deep-sea since that time) is in general the earliest possibility indicated. There do occur in the abyssal region, it is true, various animal types which show a Palaeozoic relationship, belonging as they do to orders which are known from the Palaeozoic. The families in question, however, cannot usually be traced further back than the Mesozoic. It should be borne in mind too that the immigration of the various groups into the abyssal deep-sea may well have taken place late in their geological history (see also p. 191).

The abyssal poriferans belong to orders which date back to Cambrian. The Hexactinellida e.g. constitutes a very characteristic element in the recent deep-sea fauna; and members of this group, which flourished already in Devonian, are often quoted as examples of a survival of Palaeozoic types in the deep-sea. None of the families to which the recent genera belong, are, however, known from further back than Cretaceous.

The order of Scleractinia (= Madreporaria) is known from Triassic, and the characteristic solitary deep-sea corals belong to suborders which are known from Late Jurassic. The oldest known recent genera, *Deltocyathus* and *Stephanocyathus* (syn. *Stephanotrochus*), date from Eocene.

The order of Octocorallia is mainly represented in the deep-sea by groups without fossil records. The Primnoellidae, which comprises the deepest occurring species of gorgonarians, is known from Cretaceous. The genus *Primnoella*, to which the few abyssal species belong, has its main distribution in shallow water however, and moreover, the abyssal forms are dwarfed (MADSEN 1956*a*). It may he ustifiable therefore to consider the invasion of the deep-sea habitat a late event in the history of the family.

The subphylum the Pycnogonida is known from late Devonian, but the order of Pantopoda, to which the abyssal families belong, is without fossil record.

The subphylum Crustacea, which is one of the dominant groups in the abyssal depths, dates back to Cambrian, and e.g. the order of Decapoda, to which the Eryonidea referred to above belong, is known from Devonian. The Eryonidea themselves are known from Upper Jurassic and seem to have become extinct in the shallow depths during Cretaceous, at least they are without fossil records since that time. Thus this group is a Mesozoic relict in the deep-sea (i.e. the bathyal zone, cf. pp. 194, 197). Two other groups of decapods with representatives in the abyssal region, the Galatheidae and the Homolodromidae, are known from as far back as the Jurassic.

In the Brachiopoda the two cosmopolitan abyssal species (cf. p. 206) belong to orders dating back to Ordovician and Devonian. The genera, however, are known only from Recent.

The Bivalvia are represented in the abyssal region by species of e.g. the families Nuculidae and Ledidae of the taxodonte order Nuculacea, which is known already from Silurian. These bivalves are abundant, however, in the Arctic sublittoral and also in shallow water in temperate regions. Therefore, the extension of their distribution to the deepsea may well be a comparatively late geological event. The Cuspidaridae of the heterodonte order Poromyacea, is another group of bivalves with several abyssal representatives. It is known from Triassic and is also represented in the sublittoral of colder regions.

In the phylum Mollusca belongs further the only really archaic form known from the abyssal zone, viz. *Neopilina* (inclusive of *Vema*) of the order Tryblidiacea and class Monoplacophora (cf. p. 189).

The stalked crinoids constitute a very characteristic element in the deep-sea, and are often considered the indication of an ancient origin of its fauna. The recent forms are thus generally referred to as the last and feeble survivors of a once flourishing type of animal. Stalked crinoids existed already in Ordovician, and an abundance of species are known from all later periods. However, all the Palaeozoic orders seem to have become extinct during Late Palaeozoic and Early Mesozoic, and the single recent order, the Articulata, can be traced back only to Triassic.

The majority of the recent stalked crinoids, and e.g. all the larger forms, are primarily bathyal in their distribution, thus requiring temperatures higher than 4°C. The family Hyocrinidae, which is known from Quaternary, comprises 5 recent genera. It has a bathymetrical range of between 700 and 4640 m, with the least specialized (and thus oldest) genus, *Calamochrinus*, confined to the depths between 700 and 1400 m (GISLÉN 1953).

The stalked crinoids which occur in the abyssal depths are all small and dwarfed in comparison with the bathyal forms. Stalked crinoids do not now occur in really shallow water, where, however, unstalked free-living forms also of the order of Articulata, are abundant.

Crinoids are probably on the whole as common

in the recent oceans as ever they were in the ancient ones, and in some areas this also applies to the stalked type. Some very large recent stalked species form veritable forests in depths of a little more than a hundred meters in both the West Indian and East Indian regions, and other species occur in vast numbers in other areas. Prior to the Challenger Expedition only a few recent specimens were known however, and these could consequently be considered the last rare survivors of a once flourishing group. Although long ago proved untenable, this view on the stalked crinoids is still manifest in handbooks and textbooks. - That the stalked type of crinoid is such an extremely common fossil is explained by its exceptional suitability for fossilation; both on account of its solid calcareous skeleton and by the fact that its habitat is in calm waters where sedimentation may quickly cover its dead remains.

The Echinoidea is another group of echinoderms with characteristic representatives in the deep-sea and with a fairly well-known geological history. The most ancient of the recent groups is the order Cidaroidea, which dates back to Carboniferous. The order comprises (according to MORTENSEN 1928) 10 recent genera with a total of about 80 species, the majority of which live at depths between about 100 and 1000 m. Thirteen species occur between 1000 and 2000 m; while only 4 occur between 2000 and 3000 m and 3 between 3000 and 4000 m. The small number of species of cidaroids occurring in the abyssal region compared to the abundance of species in the upper bathyal and sublittoral depths, may well be an indication that the immigration of the group into the abyssal zone is a rather late event in its geological history. (But of course this conclusion may be objected to on the grounds that the more varied ecological conditions in the moderate depths are more apt to lead to speciation than the stabler ecological conditions in the deep-sea).

The only order of echinoids which descends into the hadal zone, the Spatangoida, is a young type dating back only to Cretaceous.

A few of the examples given in the preceding illustrate how, within the various groups, it is often the youngest forms which have descended furthest down in the deep-sea. It should be noted also that the two abysso-hadal isopod genera, *Eurycope* and *Storthyngura*, often quoted as being examples of primitive types surviving in the great depths, may (as stated by WOLFF in 1959b) be in reality the most highly developed types within the asellote crustaceans.

Further, it will appear from this brief survey of some of those characteristic deep-sea animals whose geological history is more or less known, that only a few of the recent abyssal animal forms belong to families which can be traced as far back as the Middle or Late Mesozoic eras. Families of Mesozoic origin play, contrariwise, a fairly important role in the recent bathyal and littoral faunas (cf. p. 189); and those Mesozoic forms which now live in the abyssal region and have bathyal and sublittoral relatives, may well be only Tertiary immigrants in the region. The general absence of definitely archaic animals in the abyssal region may be an indication that the recent abyssal fauna as a whole dates back no further than Late Mesozoic at the earliest. The same age therefore, may be attributed to the endemic abyssal families and orders: a Late Mesozoic origin also being assumed, from another point of view, with regard to the Porcellanasteridae (cf. p. 184).

Within the echinoderms there are besides the Porcellanasteridae (cf. pp. 184, 194) some other groups of higher taxons, characteristic of the bathyal and abyssal depths, which, since they are without known fossil representatives, similarly may be assumed to have evolved within the deep-sea itself (in Late Mesozoic, as discussed above). These are e.g. the asteroid family (or order) the Brisingidae, the echinoid family the Pourtalesiidae, and the holothurioid order the Elasipoda.

Some Middle-Cambrian fossils were, it is true, originally described as elpidiid holothurioids (= Elasipoda), but as discussed by the writer in 1956 and 1957, they were without doubt wrongly interpreted. The supposed occurrence of elasipods in the Middle-Cambrian shallow sea, was otherwise one of the main bases for the assumption by A. H. CLARK in 1913 (in a discussion of the fossil marine faunas in relation to the recent deep-sea fauna) that progressive distance from land in the Palaeozoic sea would be the biological equivalent to progressive increase in depth in the recent deep-sea. (The further from land the less the inorganic material in the water and the fewer the plankton organisms, resulting in less and less favourable biological conditions).

The order of Elasipoda is often, like the Porcellanasteridae, considered to be an archaic group, but, as in the latter group, the apparent archaic character is rather embryonic. The spicules of the Elasipoda frequently resemble developmental stages of spicules in other holothurian orders, and the stone canal opens on the body surface, while in the adult specimens of the other holothurian orders the connection with the surface is usually lost. The writer thus presumes that also the evolution of the Elasipoda was correlated with the phenomenon of paedomorphosis.

The reasons for the smaller percentage of animals of Mesozoic types in the abyssal rather than in the bathyal and littoral regions, and the general absence in the abyssal region of Palaeozoic animal types, may be sought for in the geological history of the oceans and found in changing conditions of environment; the most important being the change in temperatures which have taken place in the deepsea during the Mesozoic and Caenozoic eras.

The existing deep-sea fauna must have been subjected to a very selective influence when, at the end of the Mesozoic era, the general cooling of the regions of higher latitudes commenced, and when during Late Tertiary and Early Quaternary colder water slowly filled the deeper parts of the ocean basins (cf. p. 187). Those stenothermic types which were adapted to temperatures of about 10° C or more (and were unable to acclimatize themselves to the changing conditions of environment) have accordingly been eliminated in the abyssal region.

This assumption offers a reasonable explanation for the insignificant role played by Palaeozoic types of animals in the recent abyssal fauna, since naturally it might be expected that these older types would be the most affected by the deterioration of climate; presumably being more conservative in their demands on the ecological conditions than the younger types. With the exception of the remarkable case of Neopilina it also seems that most of the "living fossils" are now confined to the shallower water of the warmer regions of the sea, where they live at temperatures approximately corresponding to those at which their ancestors may have lived in ancient times. (A possible Early Palaeozoic deepsea fauna will have been subject to a similar destructive influence by the climatic changes connected with the Permian glaciations).

Forms belonging to a possible older Mesozoic fauna element in the abyssal region may, similarly, have been largely destroyed by the progressive decrease in temperature there during the Tertiary. It would seem that Mesozoic types had a better chance of survival in the bathyal region where the temperatures range up to about 10°C, corresponding to the supposedly almost universal deep-sea temperature in the Late Mesozoic and Farly Tertiary periods. Such Mesozoic types of animals, and also of course Palaeozoic ones, which now live in the abyssal region with the very low temperatures $(0^{\circ}-4^{\circ}C)$ may very possibly be the descendants of bathyal survivors which did not until Tertiary extend their range downwards, gradually replacing the dying out older abyssal fauna.

The case of the Porcellanasteridae may be quoted as a typical example of this course of events. In all probability this group evolved from astropectinidlike ancestors, which, in Jurassic and Cretaceous times, migrated from the sublittoral region of the Tethys Sea (cf. pp. 184, 200) to the bathyal depths, where the most primitive porcellanasterid genera still occur. From there the Porcellanasteridae then, during Early Tertiary, commenced an invasion into the abyssal region where most of the (from an evolutionary point of view) more advanced genera are now to be found. To judge from the distribution of *Eremicaster* and *Porcellanaster* (cf. p. 212), this invasion into the greatest depths is still going on.

In this connection attention may also be called to the case of the Eryonidea. This order of decapod crustacea, which, as mentioned, dates back to Jurassic, is still represented in Recent by a Jurassic family, the Polychelidae, and includes three other families, the Tetrachelidae, the Coleiidae, and the Eryonidae s.str., known from Triassic-Cretaceous deposits (cf. BALLS 1957 p. 1563 ff.). The members of the Polychelidae are blind, deposit-feeding forms with feeble mouth parts, whereas the other forms had well developed eyes and stronger mouth parts, and were no doubt predatory. Thus the deep-sea dwelling recent Eryonidea are the direct descendants (cf. also p. 196) of those Late Mesozoic sublittoralbathyal forms which, as deposit-feeders, were especially suited for a deep-sea life and could persist in the bathyal depths, while their predatory sublittoral relatives were exterminated in their habitat (at the beginning of the Tertiary or earlier).

The Eryonidea comprises two recent genera: *Polycheles* (with 20-30 species) and *Willemoesia* (with half a dozen species). The bathymetrical range is from about 200 m to 4400 m. *Polycheles* is exclusively bathyal, *Willemoesia* abyssal, but only three species are recorded from below 3000 m, and only one from below 4000 m. Thus the Eryonidea are bathyal-upper abyssal in their distribution (they have also pelagic larvae), and while they are of a Late Mesozoic origin in the bathyal zone, their immigration to the abyssal zone may be a much later event in their geological history. Deep-sea groups of more comprehensive taxonomic categories such as the Porcellanasteridae (= suborder Cribellosa) and the Elasipoda within the echinoderms, and the Neotanaidae within the crustacea are rather few. On the other hand a considerable number of genera, and of course species of diverse other groups, are endemic in the abyssal region. Thus, to judge from the surveys published in the Reports of the Swedish Deep-Sea Expedition and from other surveys compiled by the writer, about half of the species hitherto recorded from depths exceeding 3000 m seem to be exclusively confined to these depths.

3. The Late Caenozoic elements

In the preceding chapters two types of elements in the abyssal fauna were discussed: 1) the possible Palaeozoic element, which was found to be insignificant, and 2) the endemic element of higher taxonomic categories which must be considered geologically to date from Mesozoic, but which at the same time may not have extended their range from the bathyal to the abyssal region until during Tertiary.

There yet remains to be discussed the non-endemic abyssal fauna element of taxons higher than genera. Reference has been made to some of those groups which already in Mesozoic times must have lived in the bathyal region, i.e. the geologically old groups which have an extensive deep-sea distribution (some of them now more or less rare, perhaps even extinct in the sublittoral region), and which probably had begun the immigration into the abyssal region fairly early in Tertiary. Amongst these are the recent Hexactinellida, crinoids (order Articulata), Cidaroidea, and Eryonidea.

Other groups which, since their recent shallowwater relatives live in the tropical sublittoral, may have extended their range to the abyssal region fairly early during Tertiary (before the fall in the abyssal temperature had begun to tell) are e.g. the Gorgonaria, the Astropectinidae, most decapod crustaceans, and the Macrouridae.

(The endemic deep-sea groups, and the other groups of a long-standing occurrence in the deepsea are often called primary deep-sea forms, while the younger deep-sea groups, with close shallowwater relatives, are called secondary deep-sea forms (see also p. 208)).

A Late Tertiary invasion of the deep-sea may be assumed to have taken place with regard to those groups which are extensively distributed in the abyssal zone, and have their shallow-water relatives in the colder regions. A Late Quaternary (postglacial) invasion, however, must have taken place regarding those species which have their main distribution in the cold polar shallow-water and from there, being eurybathic, extend into the neighbouring deep-sea with identical temperature conditions. (The latter species, to a considerable extent, may be only guests in the region).

The polar element in the deep-sea fauna is very prominent. Early in the history of the exploration of the deep-sea, when it was discovered that many of the animals inhabiting the North Atlantic depths were identical with forms known previously from the polar shallow water regions, it was accordingly assumed that the deep-sea had been colonized by a mainly Arctic (and Antarctic) fauna (WALLICH 1862, LOVÉN 1863 e.g.).

The recent abyssal fauna includes, on the whole, a very large number of diverse species which have their main distribution in neighbouring bathyal depths, and are either in the course of extending their range permanently to the abyssal zone or are only more or less accidental inhabitants (guests) there (cf. p. 208).

The larger percentage of Tertiary animal types in the abyssal rather than in the bathyal fauna (cf. p.189) must be an indication, as already noted (see p.193), that the colonization of the abyssal depths by their recent fauna has been a markedly later event than the colonization of the bathyal zone. On the whole it would seem that the larger the depth the younger the inhabitants, from a geological point of view. Documentation in support of this assumption is given e.g. in the bathymetrical distribution of the various genera of Porcellanasteridae (cf. p. 184). Attention may also be called to the fact that while the liparid fishes, a group without special adaptations for a deep-sea life and with many representatives in shallower water of colder regions, are found down to depths of more than 7500 m, the endemic families of oceanic deep-sea fishes, with light and tactile organs, have hitherto only been found down to depths of about 5500 m (cf. RASS 1959).

The relation between the recent abyssal fauna and the polar shallow-water faunas which are subjected to similar conditions of temperature, should be discussed in more detail.

In the high latitudes in Late Mesozoic times, when the deterioration of climate began and the Jurassic coral reefs and their associated faunas disappeared, the relatively few eurythermic species which survived, and the already cold-adapted ones from the highest latitudes (cf. below), could increase their number of individuals considerably, in accordance with the general rule (perceived by MöBIUS as early as 1877) that the biomass which may be supported in a given habitat will be present, irrespective of the ratio between species and individuals.

The fauna elements which due to the lowered temperatures became extinct in the high latitudes evidently were (as was similarly assumed to be the case in the deep-sea) the oldest, i.e. most of the Palaeozoic and a major part of the Mesozoic types. At least none of the so-called "living fossils" such as *Lingula* and the others listed p. 189 occur in the higher latitudes.

The gradual cooling during Tertiary must have set in initially in the higher latitudes where the water must always have been somewhat cooler than in the rest of the ocean. The first relatively coldadapted forms must have evolved here and those which were eurybathic were then able to spread to the deep-sea along with the gradual lowering of temperatures there, and replace those older forms which eventually became extinct. Examples of such Tertiary invaders of the deep-sea may possibly be the bivalve groups Nuculacea and Poromyacea (Cuspidaridae) and among fish, the Liparidae. Mostly however, it is not higher taxons but only genera and species which belong in this category.

Still later, when the extensive glaciations set in, the northern waters became extremely cold. Presumably a number of species were eliminated there for this reason, whereas they survived in deep-sea regions with suitable temperatures. Although it is difficult to give definite examples, any species or genus peculiar to the oceanic deep-sea and belonging to families with a wide distribution in the shallower waters of the temperate regions, could belong in this category.

The Antarctic region has had fairly stable climatic conditions throughout the Caenozoic and far back in the Tertiary period when the cold climate developed (cf. PRIESTLEY & WRIGHT 1928). The benthic shallow-water (sublittoral and upper bathyal) fauna here is also richer in species and genera than that of the Arctic, and, as suggested by WYVILLE THOMSON (1877), a fair portion of the bathyal deep-sea fauna may have been derived from the Antarctic fauna.

It may be noted that just as polar species may extend into the deep-sea, the reverse can also occur, and truly deep-sea species reach up into comparatively shallow water in the higher latitudes when temperature and other conditions permit (cf. p. 200). WYVILLE THOMSON (1873 p. 44) mentioned this possibility, and MOSELEY (1880 p. 546) considered it an established fact. The distribution of the deepsea holothurian *Elpidia glacialis* is a fine example of the phenomenon.

As soon as the first accurate knowledge of the oceanic deep-sea fauna was obtained, it was recognized that this fauna must have derived from that of the shallower water by continuous downwards and seawards migrations of diverse animal forms. Thus MURRAY (1895 p. 1436) noted that the relatively large number of genera in the deep-sea in proportion to the number of species "could be accounted for by such migrations having taken place at many different periods of time and from many different parts of the world" and (p. 1454) "There are many indications that the migration into the deep-sea has taken place continuously since Mesozoic times, and is even now going on".

As discussed in the preceding pages, it is possible in some cases to estimate roughly the geological period when the colonizing of the deep-sea by certain groups of animals took place. In some few cases it may even be possible to establish the time of immigration fairly exactly also for those immigrations which took place before the time of the Caenozoic glaciations.

Thus, by correlating the fossil records of some groups of recent deep-sea crustaceans with the palaeographic character of the ocean, i.e. whether in a period of transgression or regression, BEURLEN (1931) considered it possible to establish the time of their invasion into the deep-sea. BEURLEN refers 1) to the Eryonidea (cf. pp. 192, 194), known as fossils from Late Jurassic, a period of transgression, until Early Cretaceous, when a regression set in, and to the Homolodromidae which, he states, behave in a similar way; 2) to the Dynomenidae and Homolidae, known as fossils from Middle Cretaceous, a period of transgression, and according to him, disappearing from the fossil record in Late Cretaceous when a regression began; 3) to the Geryonidae and Carcinoplacidae, known as fossils from Early Tertiary, a period of transgression, but, again according to him, disappearing as fossils with the beginning of the transgression in Oligocene.

BEURLEN now concludes that the immigration into the deep-sea by the groups in question has

taken place simultaneously with their disappearance from the fossil record. During the periods of transgression, the extension of the shallow sea (the shelf sea) is greatly enlarged, with the result that many diverse groups flourish. When regression sets in and the area of the shelf sea gradually becomes diminished, the result is a greatly increased competition between the various groups: to some of them this means, considers BEURLEN, the choice between extinction or escape into a new and different habitat.

On three occasions since Jurassic, notes BEURLEN, an immigration of decapod crustaceans into the deep-sea took place. Further, he points out that together with these three invasions into the deepsea, a fourth is now in progress, induced by the regression during Diluvium and Recent, and exemplified by the bathymetrical distribution of the Maiidae and Leucosiidae.

BEURLEN's reflections on the immigration into the deep-sea by these crustacean groups are most interesting. Nevertheless, his conclusions that: it is only under compulsion of actual geographical developments that the animals penetrate into the inhospitable deep-sea region, in order to take refuge, may not be the correct presentation of the course of events.

Those groups of deep-sea animals which were formerly represented in the shallow depths but which are now extinct there, are, it is true, commonly described (cf. p. 191) as having withdrawn to and taken refuge in the deep-sea after having been forced away from the ecologically more unstable shallow-water regions by more vigorous competitors. It is hardly feasible, however, that an animal group on the verge of extinction in one habitat, would be able to extend its range to a new one with different ecological conditions. The conquering of a new habitat undoubtedly requires vigorous and adaptable immigrants. (A different phenomenon altogether is the spreading to another zone of depth along with an extension or displacement of watermasses offering suitable ecological conditions, e.g. accounting for the submergence of shallow-water polar animals into the deep-sea).

With regard to the fossil records of the decapod groups examined by BEURLEN, these must be most complete from periods of transgression, since most known fossil marine faunas naturally date from such periods. Furthermore, animals which are mostly bathyal in their distribution are usually poorly represented as fossils from periods later than Cretaceous and Early Tertiary (as fossil marine faunas known since this time are, on the whole, from sublittoral or littoral habitats). A comparison with the surveys given by BALLS (1957) shows that BEURLEN's presentation of the facts is also somewhat simplified, since some of the discussed families actually have a more continuous fossil record than he acknowledges. Thus, the Dynomenidae and Homolidae are known from about the middle of Tertiary, and the Geryonidae from late in Tertiary. Further, the groups discussed are mostly bathyal in their distribution in Recent. The Carcinoplacidae are, besides being represented in bathyal depths, abundant in the littoral region, and the Dynomenidae are actually only sublittoral.

The initial invasion of the deep-sea, i.e. the bathyal region, by the decapod families mentioned, very probably took place while they were most widespread and abundant and thus actively evolving in the shallower depths. Then, after having become successfully adapted for a deep-sea life they may gradually have extended their range to still greater depths (cf. p. 200), while their shallow-water relatives possibly became extinct as a result of changed ecological conditions in their original habitat.

Of the groups considered by BEURLEN only the Eryonidea (represented in Recent by the family the Polychelidae) reach into really abyssal depths, i.e. depths of more than 3000 m (cf. p. 194).

XII. THE FACTORS DECIDING THE VERTICAL ZONATION OF THE DEEP-SEA FAUNA

Apart from food and oxygen being necessary for the existence of a higher marine life, the most important single factor for controlling the distribution of the animals in the marine habitat is unquestionably the temperature. This was more or less clearly realized by the first biogeographers; as was also observed early on (e.g. by WYVILLE THOMSON 1873) that the

extremes of temperature, rather than the means, is the regulating factor.

The known bathymetrical distribution of the Porcellanasteridae constitutes a further support of the, on the whole, well established assumption that in the oceanic deep-sea the upwards limit of the true abyssal fauna (i. e. the boundary between this and the bathyal fauna) is primarily determined by the course of the $4^{\circ}C$ isotherm (or at least coincides with it). Thus, all six abyssal genera (listed p. 180) are known solely from localities with temperatures below about $4^{\circ}C$.

The highest temperature endured by the Porcellanasteridae as a whole, seems to be between 11° and 12° C. One of the three bathyal genera (listed p. 180) is known from localities with temperatures varying from 1.1° to 11.3° C, while the two others, known from only a few finds, lived at temperatures ranging between 6° or 8° and 11.5° C. The absence of the Porcellanasteridae from the abyssal depths in the Mediterranean (where the bottom temperatures are above 13° C) is well in agreement with an upper limit for the tolerances of temperature at about 12° C.

In the warmer regions of the ocean, an important distributional barrier is set (as regards the pelagic fauna) by the so-called thermocline, or discontinuity layer (the water layer where the warmer surface water, sinking downwards due to the evaporation causing increased salinity - and thus increased density – meets and mixes with the underlying colder water of an equal density). The whole water-mass, the hydrosphere, is by this water layer subdivided into a warmer upper water-mass and a colder lower water-mass (called by BRUUN (1955b) thermosphere and psychrosphere, in order "to stress this salient ecological factor"). In the upper warm low-density water-mass (varying in thickness between 20 and 500 m or more) the temperature decreases rapidly from somwhat below the surface and downwards. In the thermocline (varying in thickness from a few to more than a hundred meters) it falls gradually, generally from about 15° to 10°C; while below the thermocline it decreases only very slowly towards the bottom.

The pelagic order of deep-sea fishes the Ceratoidea (i. e. the adults) is pointed out by BRUUN as an example of an animal group with a distribution confined to the psychrosphere: (being represented in the Sulu Sea, where the bottom temperatures are about 10° C, but absent from the Mediterranean deep-sea, where the bottom temperatures exceed 12- 13° C (cf. BERTELSEN 1951)).

The Porcellanasteridae may now be quoted as an example of a benthic group which similarly has its distribution within the psychrosphere.

Since in the oceanic abyssal region the temperature is almost uniform at all depths, most authors, including e. g. MOSELEY (1880 p. 545), have considered it improbable that the fauna there would exhibit any distributional depth zones, or at least, no distinct ones. However, now that more and more abyssal species have been found in wide-spread localities, perhaps even in different oceans, it seems that several of them may actually be confined to rather narrow zones of depth. Thus, within the Porcellanasteridae all fifteen finds of the cosmopolitan *Styracaster horridus* were made between 4040 and 5610 m, and all seven finds of the cosmopolitan *Eremicaster vicinus* between 5200 and about 7200 m.

That the abyssal region s.str. in faunistic respect is to be subdivided into an upper and a lower zone is a conclusion that has been arrived at by various authors working on different groups of invertebrates and fish (and was indirectly suggested in MURRAY's survey (1895) of the number of species occurring in different zones of depth). When surveying the vertical distribution of more than a thousand species of bottom invertebrates from below 2000 m, N. G.VI-NOGRADOVA (1958) found that generally this change in the composition of the species occurs at about 4500 m (varying in different groups from 4000 to 5000 m).

The bathymetrical distribution of the Porcellanasteridae shows the following boundaries: 1) an upper limit for the group as a whole (and for the bathyal genera in particular) at a depth of about 1000 m, and a temperature of about 12° C, and 2) an upper limit for the abyssal genera at a depth of about 2500/3000 m, and a temperature of about 4° C. The latter boundary is at the same time the lower limit for the bathyal genera. Further, there is a change in the composition of the species at about 4000/5000 m (supporting the distinction at this depth between an upper and a lower abyssal zone). The greatest depth at which porcellanasterids have been collected is about 7600 m, which is somewhat down in the hadal zone.

The extreme depths of the oceans (the trenches) are now, as mentioned, distinguished as a separate faunistic region, the hadal zone, since, besides several species, a number of genera and even two families (the benthic actiniarians the Galatheanthemidae and the pelagic amphipods the Vitjazianidae) appear to be endemic there. – MOSELEY (1880 p. 546) also pointed out: "Were there any variations in the conditions of life such as to restrict certain animals to very great depths, as mountain plants are restricted to certain heights on land, then we might expect to find a peculiar fauna in the deep depressions, and especially in the deepest hollows on the bottom of

the sea, where the water is over 4.000 fathoms deep." He concluded, however, that such conditions would not be present. – The upper limit of the hadal region was originally set at about 6000 m, but, according to WoLFF 1960, is better set at 6800/7000 m.

Within the Porcellanasteridae only the cosmopolitan *Eremicaster vicinus* was hitherto recorded from the hadal zone, but having a known bathymetrical range of 5200 to 7200 m it may not be a truly hadal species. (As mentioned p. 181 also *Porcellanaster* has now been found in hadal depths, at about 7600 m).

A possible earlier Palaeozoic element in the hadal fauna has been subjected to the same destructive influence through the progressively lowered temperatures during the Tertiary as has a such element in the abyssal fauna. It is unlikely, therefore, that the hadal fauna should include any elements of more ancient origin than those found in the abyssal fauna. The adiabatic rise in temperature in the depths of the trenches is so small ($\leq 0.2^{\circ}$ C) that one has to dismiss the possibility of a stenothermic species surviving there when the further cooling exterminated it in the abyssal depth.

The trenches are usually considered to have a late geological origin; it being assumed that they were formed in connection with the Alpine foldings, i. e. in Late Pliocene, near the end of the Tertiary period (cf. e. g. UMBGROVE 1947 p. 63). This being so the hadal fauna must be relatively young. However, certain authors, e. g. BIRSTEIN (1959), are of the opinion that the hadal fauna, as known at present, repudiates such a late formation of the trenches (see also p. 212).

The evolution of taxons of higher than specific rank, such as genera and families, must be put back at least into the Tertiary period. Therefore, as discussed in the preceding, such groups which are now endemic in the deep-sea, must have existed there prior to the beginning of the Quaternary period, long before the last glaciations.* It is quite conceivable, however, that those animal groups which seem to be endemic in the hadal depths, have invaded these depths during the Quaternary from the lower abyssal zone. That they have not yet been found there is, of course, no definite proof of their absence.

The hadal fauna, as is the case of the abyssal fauna, also includes a considerable number of forms of a decidedly young origin. WOLFF (1956a p. 152) e. g. came to the conclusion that the hadal isopods had derived from cold areas in the Arctic, and especially in the Antarctic regions. This is an indication that the trenches, at least in part, did not become inhabited with their present fauna until after the cooling at the poles had reached its climax, and stenothermic cold-adapted species had developed in the waters there (cf. p. 196).

Evidently the temperature, although it is an extremely important factor, does not solely determine the vertical distribution of the Porcellanasteridae (or any other group in the deep-sea), considering the very slight differences in the temperatures of the upper abyssal, lower abyssal, and hadal zones. When seeking for another factor to explain these zones of distribution, one might turn to that of pressure. What actual significance this factor may have for the deep-sea animals is rather unknown however; all experiments on the effects of pressure on marine animals having of necessity been made on shallow-water species. (Some of these, incidentally, have shown a surprising resistance to increased pressure, even surviving short exposures to pressures of 1000 atm. (cf. CATTELL 1936 p. 441)).

The boundary between the upper and lower abyssal zones, at about 4500 m, almost coincides with the depth at which the water becomes undersaturated with calcite (cf. REVELLE & FAIRBRIDGE 1957 p. 282). Thus, this and other chemical properties of the water (modified by increased pressure) may be partly the explanation for the faunal change.

That the pressure, however, is a less important factor for the distribution of the deep-sea fauna than the temperature, is borne out also by the findings of ZOBELL & MORITA (1959) that the deep-sea bacteria, which "were unique in their ability to grow preferentially or exclusively at in situ hydrostatic pressures" at the same time "appear to be even more heat-sensitive than pressure-sensitive".

The percentage of species of porcellanasterids in the total fauna of sea-stars varies, as illustrated in the diagram p. 180, from 0 in the depths less than about 1000 m, to 25 % at 4000 m, 50 % at 6000 m and (so far known) 100 % at 7000 m. The apparent absence of the Porcellanasteridae in more moderate

^{*} This seems evident and has also been concluded by most if not all authors since the days of the Challenger Expedition. BIRSTEIN (1959 b p. 228) is incorrect in attributing to BRUUN the view that the abyssal fauna should be "of a recent (Quaternary) origin, derived from batial and sublittoral species". What BRUUN (1956) said in effect was that the glacial cooling of oceanic deep water "must have been catastrophic for the abyssal and hadal fauna" so far as "Only the relatively eurythermic and eurybathic species could survive".

depths, even in the polar regions where some other deep-sea animals may occur in fairly shallow water (cf. p. 196), might lead to the assumption that these sea-stars are dependent on a hydrostatic pressure of a definite size. However, the explanation for the upper limit of their occurrence is more likely to be found in their relations to other animals in the habitat, competitors for food and predators.

Thus, the probable low reproductive rate in the Porcellanasteridae (cf. p. 181) may limit their ability to compete with other deposit-feeding animals in more moderate depths, such as e. g. bivalves. When the Porcellanasteridae are more successful in the greater depths the reason may be that they are better able to thrive on a bottom relatively poor in food than most of their potential competitors. This latter possibility may account too for the apparently fairly uniform distribution of the Porcellanasteridae over the whole abyssal plain (cf. p. 214).

Further, a low reproductive rate will make the populations of Porcellanasteridae very susceptible to attacks from predators. It is possible therefore, that the upper limit of their occurrence is also set as the depth at which the depletion by predators outweighs the reproductive potential. – That in the deep-sea fauna the percentage of carnivores relative to suspension-feeders and deposit-feeders decreases with increasing depth, is a well-known phenomenon (cf. e. g. IMBRIE 1959), and is also illustrated in the diagram referred to above, showing the percentage occurrence of species of the mud-eating porcellanasterids in various zones of depth relative to the total number of species of sea-stars; these animals in general being the most important benthic carnivores.

Other factors which may influence the upwards vertical distribution of deep-sea fauna elements, (in areas where no limit is set by the temperature) are e. g. the water movements (the mud-dwelling deep-sea fauna requires a soft bottom and calm water) and possibly the light. When many deep-sea animals extend their range of occurrence high up in the polar waters, this, as already suggested by MOSELEY (1880 p. 547), may be due not only to the low temperatures but also to the fact that the water here "is dark during most of the year, both from the absence of sun or the obliquity of its rays, and because of the covering of the water by ice and snow".

The boundaries in the vertical distribution of the marine fauna are naturally never sharply defined but are transitional zones. The lower limit for the vertical distribution of a deep-sea species once having become adapted to the abyssal conditions of temperature, is probably always determined by a combination of factors, including perhaps the chemical properties of the water, conditioned e. g. on the pressure, and the correlated condition of the bottom substrates (see p. 213ff). Further, a most important factor must always be the question of food-supply.

XIII. SOME CHARACTERISTICS OF DEEP-SEA ANIMALS

Any fundamental differences between the fauna of the deep-sea and that of the shallow water were not to be expected, since ultimately the former is derived from the latter, and since the environmental conditions in the deep-sea, apart from the pressure, are no different from any that can be found in shallow regions. The characteristic features shown by many deep-sea animals are also primarily correlated with their life in a dark and calm milieu and on a soft bottom.

The affinity of the (known) deep-sea fauna with the soft bottom environment was stressed by MUR-RAY (1895 p. 1434) when he introduced the term "mud-line" for the depths (at about 50-500 m) where the detrital matters with organic particles derived from land and from the death and decay of pelagic organisms, begin to settle on the sea-floor. "Here," he noted, "is situated the great feeding grounds of the ocean". MURRAY further assumed that this region of fine mud was for many species the place of origin, and suggested that: "In all probability the deep-sea was peopled by continuous migrations downwards and seawards from about the mud-line."

The case of the Porcellanasteridae can be taken as an example of a deep-sea group which has originated in the region of the mud-line. The astropectinidlike ancestral porcellanasterids (cf. p. 184) may be assumed to have settled in the upper deep-sea in Late Mesozoic times. Thereafter, in the course of their evolution, they have become adapted to living as burrowers in the loose substratum; completely forsaking the predatory or scavenging way of feeding (which was presumably their original habit) for the mud-eating habit, now one of their distinct characteristics. After having succeeded in this new mode of life, the Porcellanasteridae spread outwards and downwards in the deep-sea simply because the life-conditions, to which they were now adjusted, were also found there.

The Porcellanasteridae in morphological respect, are primarily distinguished by their complicated cribriform organs (cf. p. 181), and simple cribriform organs are found in the sublittoral-bathyal Goniopectinidae. On the whole, the peculiarities of the Porcellanasteridae are merely the adaptation to life on a soft bottom and to feeding on the organic material contained in the bottom substratum itself (the ciliated cribriform organs producing a circulation of fresh water around the animal in its burrow, and at the same time providing a flow of surface substratum down to the animal to feed on).

The "mud-eating" habit is a frequent way of feeding in motile benthic deep-sea animals, and is met with in other echinoderm groups such as e. g. the Elasipoda and the Spatangoida, and e. g. in some polychaetes and crustaceans. Even some species of fish, of the family Macrouridae, feed in a rather similar way.

Light-perceptive organs are absent in the Porcellanasteridae (MEURER 1915) whereas they are found in some other deep-sea dwelling asteroids such as e. g. astropectinids. This fact might be taken as further evidence of the long geological time the Porcellanasteridae may have lived exclusively in the dark deep-sea. However, as is known from other animal groups, the eyes are organs which may easily degenerate if not in use.

A characteristic feature in many sessile deep-sea animals (e. g. some glass-sponges, sea-pens, sea-lilies, and some sea-squirts) is that they are provided with a stalk. This in general is claimed to be a necessary adaptation for a safe anchoring and for lifting the animals above the substratum, the upper layer of which is usually assumed to be in a semi-liquid state.

The photographs of the deep-sea bottom now available, usually seem however, to indicate a fairly firm surface. In the opinion of the writer, the stalk of the sessile abyssal animals may also be an adaptation for raising them above the oxygen-poor water layer close to the bottom rather than for raising them above a semi-liquid layer of ooze. Of course the stalk also keeps the sessile animals somewhat free of the ooze clouds which will be stirred up whenever an animal moves over the bottom. However, in this connection it should be borne in mind that such suspended particles will often be their main source of food.

The peculiar structural feature of a chitinous tube formed around the body in the Galatheanthemidae (the possibly endemic hadal sea-anemone discovered by the Galathea Expedition and described by CARL-GREN (1956)) may be an adaptation analogous to a stalk, since its support allows the oral end with the tentacles to be raised well above the bottom.

In the abyssal tunicate *Culeolus*, the thread-like stalk probably cannot lift the body off the bottom, but serves in keeping it at anchor while, as suggested by MILLAR (1959), it floats by means of periodic unstimulated contractions and the expelling of water, such as has been observed in some shallow-water tunicates. A favourite place of attachment for *Culeolus* is also the stalk of glass-sponges, no doubt because in this way it becomes further raised above the bottom.

The problem of a possible gigantism in the deepsea has been brought forward by various authors. Thus the Challenger scientists, e. g. MOSELEY (1880 p. 593), noted that "Some animal forms appear to be dwarfed by deep-sea conditions of life", while "Others attain under them gigantic proportions".

Pronounced examples of dwarfing are found in the deep-sea species of such sessile suspensionfeeders as the gorgonarian *Primnoella* and the stalked crinoid *Bathycrinus*, and in these cases the dwarfing seems to be well accounted for by the sparse foodsupply available to this kind of animal. But not all sessile suspension-feeders in the deep-sea are small. There are actually giant forms too; the most remarkable example being the gigantic solitary hydroid *Branchiocerianthus (Monocaulus* of authors) of which the Challenger (cf. WYVILLE THOMSON 1875) dredged specimens more than 2 m high, in the mid-Pacific and near Japan at about 5200 and 3500 m respectively. It perhaps may be justified to assume that such large specimens are of great age.

Several abyssal crustaceans show so-called gigantism and e. g. BIRSTEIN (1957) and WOLFF (1960), when referring to this feature, have suggested that it might be due to an especially high metabolic rate, effected by the hydrostatic pressure in the great depths, – experiments having shown that intensified pressure causes an increase in the rate of metabolism. The increased metabolic rate in an animal reacting to such adverse conditions as that of a pressure a hundred times greater than the habitual one is, however, quite another thing than the rate of metabolism in an animal living undisturbed in its natural milieu. As regards that very important ecological factor the temperature, the prevailing rule also seems to be that different populations of the same or related species show roughly the same metabolic rate, regardless of the temperatures at which they live (cf. BULLOCK 1955). No doubt the rate of metabolism in populations of the same or related species will prove to be similarly adapted to the pressure at various depths.

Cases of 'gigantism' may occur in quite different ecological milieus. Marine invertebrate species (and genera) primarily show relatively increased size in the cold regions (the polar seas and the deep-sea), whereas terrestrial species (and genera) primarily show this feature in the warm regions of the tropical rain-forests. However, the giant-clams are examples of 'gigantism' in the tropical shallow-sea, while the giant-earthworms are examples of 'gigantism' in only a moderately warm terrestrial milieu.

Thus, in the writer's opinion, it seems most probable that the phenomenon of gigantism in the deepsea, as understood by e. g. BIRSTEIN and WOLFF (op. cit.), does not really exist. (Dwarfing, or relatively reduced size, induced by the extremely unfavourable conditions in the deep-sea with regard to accessibility of food, is, on the other hand, a well-established phenomenon).

The increased size encountered in some deep-sea forms was suggested by MOSELEY to depend "on lack of enemies rather than on an abundance of food". The progressively fewer predatory species in the benthic fauna with increasing depth and distance from land must also be a factor which allows the abyssal animals a relatively long life in general. -Furthermore, the sparse food-supply may cause a relatively slow growth in the abyssal animals and accordingly, a postponed sexual maturity in comparison with that of their relatives from shallower depths. At the same time the abyssal animals may perhaps attain a great longevity simply on account of the uniform ecological and homothermal conditions in the deep-sea. It is also suggested, by e. g. MACGINITIE 1949, that some deep-sea animals have life spans of perhaps hundreds of years. If this be so, it may well explain some cases of so-called gigantism.

As regards the Porcellanasteridae, none of the

species are especially remarkable in their size. The smallest, *Porcellanaster cæruleus*, reaches a diameter of about 6 cm, and the largest, *Styracaster horridus*, reaches a diameter of 30 cm (but has very slender arms). The total range of size in sea-stars goes from a few centimeters to about three quarters of a meter in diameter, and by far the greater part are from 10 to 30 cm in diameter.

The assumption of entirely uniform ecological conditions in the deep-sea habitat throughout the year will not be true everywhere. The marked seasonal fluctuations in the productivity in the upper layers of the oceans in some areas may be perceptible in the deep-sea too. MOSELEY (1880 p. 592) also noted: "Possibly there is at some places a periodical variation in the supply of food falling from above, which may give rise to a little annual excitement amongst the inhabitants."

This could mean, for the abyssal fauna, a seasonally fixed sexual period (or spawning time). No evidence is available to support the possibility however. It is also commonly assumed that the abyssal species as a rule will not show any definite seasonal period of reproduction but may spawn at any time of the year. What very little can be deduced from the examination of the gonads of a number of porcellanasterids agrees with the assumption that eggs in small numbers may be produced throughout the whole year. A non-pelagic development is considered the general rule for all truly abyssal species, and according to their egg-sizes the Porcellanasteridae also follow this rule.

In the oceanic abyssal region with its rather stable ecological conditions (without considering the gradual change in temperature during an entire geological era), the incentive for new forms to evolve will probably be insignificant. At least, this is the general assumption. The many species and genera, and also higher taxons, which are endemic in the region, are in the main therefore, only the results of those genetic changes which occur in all populations in the course of time (cf. p. 204).

1. The cosmopolitanism

The first naturalists who investigated the distribution of marine animals (e. g. WOODWARD 1851) early observed that the deeper a species (or a genus) lives, the more extensive generally is its horizontal distribution (i. e. towards the higher latitudes, correlated with the downwards decreased temperature). The earlier authors who discussed the deepsea fauna consequently anticipated that it should prove to be cosmopolitan. Thus Lovén in 1863 distinctly expressed the opinion that a deep-sea fauna of the same general character extended from pole to pole, including some very widely distributed species. WYVILLE THOMSON in 1877 similarly concluded that the depths of more than 1000 m all over the world had a uniform fauna, that the abyssal genera were generally cosmopolitan, and the species were the same, or, if differing in remote localities, then markedly representative, i. e. of close genetic origin. The uniform impression given by the abyssal fauna is also amusingly expressed in MOSELEY's remark (1880 p. 547): "We got quite tired on the Challenger of dredging up the same monotonous animals wherever we went."

That the deep-sea fauna should prove to be essentially cosmopolitan, not only as regards the genera, but also to a large extent with regard to the species, was in effect the classical view, based on the assumption that the conditions of environment were identical all over the ocean. (That the zoogeography of the shallow and moderate depths is primarily a question of the distribution of different water masses with which the different species are associated, was more or less clearly realized by the first biogeographers and also alluded to by WYVILLE THOMSON in 1873 p. 42).

The view of a general cosmopolitanism of the abyssal species has been opposed however, by later investigators. MURRAY, when summarizing the Challenger results, thus had to conclude (1895 p. 1439) "with references to species there is no striking evidence of a universal deep-sea fauna spread all over the floor of the ocean". Most recently e. g. N. G. VINOGRADOVA (1959) has expressed the opinion that the deep-sea bottom fauna should be divided into a series of separate zoogeographical regions. This point of view will be discussed in more detail in a following paragraph (cf. p. 209).

It has been amply proved in the course of the ex-

ploration of the deep-sea that the fauna of the more moderate depths, the bathyal fauna, has to be distinguished into a number of different zoogeographical divisions. Their extension and the causes for them does not, however, concern us in the present discussion, which is limited to the truly abyssal fauna.

Within the Porcellanasteridae, nearly all the abyssal genera are known to be cosmopolitan, viz. *Hyphalaster* (2275-5415 m), *Thoracaster* (2600-about 5000 m), *Styracaster* (2550-5610 m), *Eremicaster* (1570-about 7200 m), and *Porcellanaster* (1160-6035 m), while the bathyal genera seem to have a restricted distribution, none of them being known from outside the Indo-Malayan region, viz. *Lysaster* (about 1000 m), *Benthogenia* (905-925 m), and *Sidonaster* (1150-about 2300 m). The remaining abyssal genus, *Abyssaster* (3200-6280 m), is known only from the Indian Ocean and the western Pacific. (A new abyssal genus, *Vitjazaster*, from the Kurile-Kamchatka Trench, will be described by BELYAEV).

A cosmopolitan distribution is undoubtedly the general rule for all truly abyssal genera; the exceptions are few, especially considering how scanty the exploration of the deep-sea still is. A reminder of the possible incompleteness of the faunistic record is e. g. the case of the peculiar tunicate *Octacnemus* which was believed endemic in the South Pacific deep-sea from the days of the Challenger Expedition until 1947 when a specimen was recorded among some unidentified North Atlantic material from the Ingolf Expedition (MADSEN 1947). One may also mention the case of the Pogonophora, which were considered endemic in the Pacific for some time after their discovery (cf. BRUUN 1956), but are now known to be world-ranging.

It may be appropriate, before proceeding with the discussion of the horizontal distribution of the abyssal species, to stress that these are understood to be the species which, always living at temperatures below about 4° C, have their main occurrence in the depths below about 2000 m, and down to 6-7000 m (i. e. to the transition to the hadal zone in which other rules of distribution may be in force, as discussed p. 212).

Every zoogeographical analysis must consider the possibility of erroneous specific determinations. In deep-sea zoogeography however, cases of synonyms among the described species are no doubt more frequent than cases of new species being erroneously identified with earlier described ones. Further, some taxonomists have been so impressed by their knowledge of the zoogeographical regions in different latitudes on land that they have erected new species or subspecies in deep-sea animals for no other reason than that they were collected in localities widely separated from where the related, and, in their morphological characters, indistinguishable forms were known. (Examples of such cases in the history of the Porcellanasteridae are the species *Porcellanaster eremicus* and the subspecies *Styracaster chuni groenlandica*).

Since the abyssal fauna is still only scantily explored, more importance should certainly be given to similarities ascertained in various areas than to apparent differences, which may be due to e. g. accidental information of rare species or of temporary local faunas (see also p. 214).

The writer in 1951a, 1951b, and 1953a, made some surveys of the distribution of the species recorded from depths exceeding 3000 m in some of the classes of echinoderms. (The limit at 3000 m should warrant that the greater part of the not truly abyssal species were excluded). It appeared from these surveys that about 5 % of the species of asteroids in question and about 10 % of the ophiuroids and holothurioids were known to be cosmopolitan, a fair percentage considering the number of species recorded from only a single or a few finds.

A cosmopolitan species, it should perhaps be noted, is here (in agreement with the most usual view) understood to be a species recorded from the main deep-sea basin of each of the three oceans (typically absent from the enclosed basins with bottom temperatures of more than 4° C, and also, in general, from the Arctic deep-sea region where the temperatures are below 0° C).

Within the Porcellanasteridae the following species, according to the quoted definition, may be considered cosmopolitan: *Hyphalaster inermis* (32 finds, 2280-5415 m), *Thoracaster cylindratus* (20 finds, 2600-5000 m), *Styracaster horridus* (15 finds, 4040-5610 m), *Styracaster chuni* (6 finds, 2550-4550 m), *Eremicaster vicinus* (7 finds, 5200-about 7200 m), and *Porcellanaster cæruleus* (86 finds, 1160-6035 m). That is, six species out of the total of fourteen species known from more than two finds, or an ascertained cosmopolitanism of 43 %.

The species thus considered cosmopolitan may have their center of distribution in a defined area however, and at the greatest distance from this area may occur only sparsely and be very scattered. *Por*- cellanaster cæruleus e.g. is known from many finds in the Atlantic and the Indian Ocean, but from only a few finds in the well-explored East Pacific. Styracaster horridus and S. chuni, besides Hyphalaster inermis, also seem to be mainly Atlanto-Indian in their distribution, none of them having hitherto been found in the eastern Pacific.

That the truly abyssal benthic fauna should prove to be essentially cosmopolitan should hardly instigate any serious objections, since the abyssal region forms an ecological unit without pronounced barriers (i. e. disregarding the abyssal depths of such enclosed basins as the Arctic Sea with very low and the Mediterranean with unusually high temperatures).

A similar extensive speciation such as that on land is a priori not to be expected. A new abyssal form when spreading over the deep-sea floor from its center of origin, may in different populations change in different directions however; just as different populations of an "old" cosmopolitan species may develop new distinct characters. This accounts (since the genes responsible for such modifications will not always immediately become spread throughout the whole stock) for WYVILLE THOMSON's observation (1877 p. 353) that deep-sea forms from remote localities often appear markedly representative. (A good example is provided by the two minute deep-sea forms of the gorgonarian Primnoella from opposite regions of the globe: Primnoella jungerseni from the North Atlantic (2137-2448 m) and P.krampi from the South Pacific (5850 m), described by the writer (1944, 1956a). These two forms are clearly distinct, but had they been found in the same area there should have been little objection in considering them individual variants of the same species).

It is usually held (cf. e.g. DAHL 1953) that benthic deep-sea forms with a free-swimming larval phase have generally a wider distribution than those without. However, the absence of a free-swimming larval stage does not prevent an abyssal species in eventually attaining a world-wide distribution. This is evident also from the known cosmopolitan distribution of several of the porcellanasterids, the larvae of which are certainly non-pelagic. (The eggs of course may float along the bottom, as may also the larvae a short time before settling). Any abyssal form, wherever it has first appeared as a separate taxonomic unit, will eventually be able to spread over the whole abyssal region.

The abyssal deep-sea is essentially a very calm milieu, but not absolutely so, and certainly not

to the degree assumed by the early biogeographers, and illustrated e.g. in MOSELEY's remark (1880 p. 543) that: "Any movement taking place in the water at that depth must be of a molecular nature only." There are in most places bottom currents of some velocity, on an average of 2 km per day (cf. DIETRICH 1957). The currents in abyssal depths (2000-4000 m) in the North Atlantic are e.g. recorded showing a range of velocity variation of 0-5 cm/sek (i. e. up to 4.3 km per day), and a change of direction through at least 90°, over periods of a few weeks and over distances of a few tens of kilometres (Swallow & Hamon 1959). Furthermore, earthquakes and volcanic activity may cause stronger currents of a temporary nature which may be of importance as regards the distribution of the animals. - The dispersal of a benthic species from its place of origin and over the whole world ocean, if it e.g. propagates once every year and the offspring settle at a distance of, say, 1 km from the parental populations, might take place in the course of 20-30.000 years (about the time which has elapsed since the last glaciations).

2. Some cosmopolitan species

The taxonomic revision of the Porcellanasteridae undertaken on the basis of the Galathea material, has demonstrated (cf. p. 204) that a considerable number of the species belonging to this group may be termed cosmopolitan (at least they are known to be widely distributed in the oceanic deep-sea). – There are as yet only few taxonomical surveys of deep-sea animals based on sufficiently representative materials for a zoogeographical purpose. But those available (see following summaries) seem strongly to support the assumption that the cosmopolitan pattern of distribution is the general rule as regards the truly abyssal species, i.e. those which are endemic in the region.

One of the more conspicuous animal forms in the deep-sea is the sea-pen *Umbellula*. (During the Galathea Expedition it was collected in 21 of the 74 successful dredgings in depths below 1000 m.) The taxonomy of the genus was revised in 1958 by BROCH, who recognized only 7 distinct species (or 6 species and 1 subspecies) among the total of 39 species which had been named in the literature. (A single name, *Crinillum geniculatum*, refers only to a stalk fragment, and a few nominal species, *U.gilberti*, *U.indica*, and *U.purpurea*, were not definitely referred to any of the valid species. *U.indica* and

U. purpurea are probably identical with *U. pellucida* however.)

The following gives the pattern of distribution shown by the recognized species of *Umbellula*:

Two species, U.lindahli (150-5310 m) and U.thomsoni (about 200-5860 m), are cosmopolitan, (U.thomsoni was collected by the Galathea Expedition in the Panamic region). Two other species, U.huxleyi (about 300-1365 m) and U.durissima (about 570-4450 m), are also recorded from all three oceans, but in the Pacific area only from the regions of the Malay and Japanese archipelagos, and they thus primarily show an Atlanto-Indian distribution.

Two species, *U. pellucida* (220-2000 m) and *U. spicata* (375-1100 m), are known solely from the northern Indian Ocean, and are both confined to the bathyal zone.

The remaining form, *U. encrinus* (180-1500 m), is of an Arctic distribution, and may well be considered an Arctic race of the oceanic deep-sea species *U. lindahli*.

Of the other deep-sea pennatularians, four further species may be termed cosmopolitan (KÜKENTHAL & BROCH 1911), viz. Anthoptilum grandiflorum (230-2920 m), Funiculina quadrangularis (65-2600 m) (unknown from the East Pacific however), Distichoptilum gracile (1190-2830 m), and Scleroptilum grandiflorum (820-4200 m).

The solitary madreporarian coral, *Fungiacyathus* (or *Bathyactis*) symmetrica (150-5300 m), is also cosmopolitan (MOSELEY 1880).

Stephanoscyphus simplex, the only scyphozoan polyp known from depths exceeding 3000 m, was dealt with in detail by KRAMP in 1959 on the basis of the Galathea material. It has a world-wide distribution in the oceanic deep-sea (42 finds) in depths from 430 to 7000 m and at temperatures of 0° C to about 10° C (13° C?), its main occurrence being in depths of more than 2000 m and at temperatures below 4° C.

Only a very few bryozoans are known from more than a single find (SILÉN 1951), but one of these, *Levinsenella magna* (1690-4850 m), is known to be cosmopolitan.

The polychaetes on the whole are to a large extent cosmopolitan. KIRKEGAARD (1956) e.g. recognizes in the hadal fauna, besides a special element of stenobathic and stenothermic species, two other elements: "Eurybathic and eurythermic species, many of them, maybe all, cosmopolitan" and "Eurybathic and stenothermic species with a worldwide distribution". A total of about 45 species of ascidians are recorded from depths of more than 2000 m (MILLAR 1959); and of those known from more finds, half are cosmopolitan, viz. *Culeolus murrayi* (3400-4635 m), *Dicarpa simplex* (2470-4600 m), *Corynascidia suhmi* (2475-4635 m), *Styela sericata* (3510-5860 m), and *Bathystyeloides enderbyanus* (2550-5300 m).

The majority of abyssal pycnogonids are known from single finds only. But one of the 9 species of *Nymphon, N.procerum* (3950-4600 m), and four of the 12 species of *Colossendeis*, viz. *C.cucurbita* (1350-4400 m), *C.angusta* (12-5350 m), *C.colossea* (865-4150 m), and *C.macerrima* (538-3670 m), are known to be cosmopolitan (cf. FAGE 1951).

The cirripeds include 34 species recorded from depths exceeding 3000 m (NILSSON-CANTELL 1955), and the only two known from sufficient finds to be used in a zoogeographical analysis, are both cosmopolitan, viz. *Megalasma hamatum* (365-3660 m), and *Verruca gibbosa* (385-3130 m).

Cosmopolitan species are e.g. among the abyssal isopods: Storthyngura pulchra and Eurycope nodifrons (cf. WOLFF 1956), and among the abyssal amphipods: Orchomenella abyssorum and Halice secunda (cf. DAHL 1959).

The decapod crustacea include a number of cosmopolitan deep-sea species (BALLS 1957) such as *Nematocarcinus ensifer* (535-3650 m), *Polycheles sculptus* (450-2870 m), *Galacantha rostrata* (1600-2900 m), and *Ethusina abyssicola* (1225-4260 m). A number of other species are known to be very widely distributed.

Two of the abyssal species of brachiopods are cosmopolitan (DALL 1920), viz. *Pelagodiscus atlanticus* (1500-5000 m) and *Abyssothyris wyvillei* (1800-5500 m).

Two of the 10 species of gephyreans known from depths of more than 3000 m (E. WESENBERG-LUND 1955) are of a world-wide distribution, viz. *Golfingia flagriferum* and *G.margaritacea*.

Among the echinoderms, e.g. 11 of the species of ophiuroids recorded from depths of more than 3000 m, (about one-fifth of the species known from more than one find) are known to be cosmopolitan (cf. MADSEN 1951 b). As mentioned p. 204, also a fair percentage of the deep-sea asteroids and holo-thurioids are of a similar wide distribution; and a preliminary study of the echinoids collected by the Galathea Expedition has revealed that e.g. also *Echinosigra phiale* is cosmopolitan (MADSEN 1951 *a*, 1953 *a*, *b*).

Taking into account the few abyssal dredgings

which have been performed in relation to the vast distribution of the abyssal region, it is certainly very noteworthy how many abyssal species have been rediscovered in remote localitites. This strongly supports the classical assumption of a uniform abyssal bottom fauna, or, more correctly (cf. p. 207 ff.), of an abyssal bottom fauna in which a large element is the same all over the oceans. It also seems that we now have a fair knowledge of the common forms in this endemic abyssal fauna element, in spite of the somewhat random collecting. Thus the Galathea Expedition obtained porcellanasterids in 27 dredgings spread along its whole circumnavigation route, and not a single one of the species found, was new to science.

The importance which is to be given to the discoveries of the same species in remote localities, will be borne out by the following calculation of how large a part of the abyssal region is hitherto explored. The abyssal deep-sea (with depths exceeding 3000 m) occupies an area of 278 million square kilometers, or slightly more than half the total area of our globe, and the area covered by the dredging operations up to now can at the very most have been 5 km². The information we have of the bottom fauna of the abyssal deep-sea thus covers only onefifty millionths $(2 \cdot 10^{-5} \%)$ of the total area occupied by this fauna.

3. Ekman's considerations on a possible cosmopolitanism of the abyssal fauna

In his important handbook of the zoogeography of the sea, EKMAN (1953 p. 291) states: "The abyssal species have generally a wider distribution than the archibenthal and there are many cosmopolitan species. But the dividing line between the more locally restricted species and the more or less cosmopolitan species with regard to depth should be put at a lower level than the commonly assumed upper limit of the abyssal zone". At the same time he notes: "Not even for the most extreme abyssal species of the benthos can a cosmopolitan distribution, however, be considered the rule.

As will have been evident from the preceding discussion of the horizontal distribution of the truly abyssal species, the writer must disagree with this latter conclusion (which disregards the fact that the majority of the abyssal species are yet known from only a single or a couple of finds). Of course not all animals living in the abyssal region are cosmopolitan. However, if in the analysis of the zoogeography of the abyssal deep-sea, the element of eurybathic species also occurring in the bathyal zone (perhaps even in the sublittoral of the colder regions (cf. p. 208)) is excluded, (besides those species known from too few finds to be of any value for a zoogeographical purpose) then the concept of a cosmopolitan distribution of a large percentage of the species appears well documented.

(EKMAN in his handbook used, for practical purposes, the 1000 m line as the limit between the bathyal and abyssal faunas. – The depth which he (as noted above) refers to as the upper limit of the cosmopolitan species, was suggested by KOFOED (1927), in connection with the distribution of the deep-sea fishes, to be roughly at 2600 m. EKMAN further found in a later analysis of the vertical distribution of the elasipod holothurians (1953 b) that in this typical abyssal group the greatest faunal change occurs at a depth of 2000 m. This depth roughly coincides with the upper limit of the occurrence of eupelagic sediments, and therefore, concludes EKMAN, this limit is also a zoogeographical boundary.)

4. The main subdivision of the lower abysssal fauna

The writer's view compared with that held by Екман.

The writer has suggested (1951, 1953), on the basis of an analysis of the known distribution of the deepsea asteroids and ophiuroids, that if any zoogeographical subdivision of the endemic lower abyssal benthic fauna should be undertaken, there might be distinguished – besides the large cosmopolitan element: 1) An element with a distribution extending over the Atlantic and the Indian Ocean (and, as was also noted, inclusive of the neighbouring region of the Malay Archipelago). 2) An element with a distribution confined to the Pacific. 3) An Antarctic element.

It may be worth noting that these three claimed main faunistic regions in the abyssal deep-sea roughly coincide with the three major areas of different deep-sea deposits, viz. globigerina ooze (in the Atlantic and Indian oceans), abyssal red clay (in the Pacific), and diatom ooze (in the Antarctic).

As was also touched upon in 1953, the impression of an Atlanto-Indian element versus a Pacific element in the abyssal fauna, might be caused by an artefact of collecting, the species in reality being cosmopolitan but not yet proven. Primarily, this tentative suggestion of an Atlanto-Indian and a Pacific abyssal fauna region respectively, was also given as an objection to the view held by EKMAN (1935, 1953 a), of an Atlantic and an Indo-pan-Pacific abyssal subregion respectively.

EKMAN (1953 *a* p. 292) stated that: "one would not go far wrong in maintaining that the abyssal fauna of the medium degrees of latitude may be divided into two main regions, namely into an Atlantic and an Indo-Pacific, the latter reaching east as far as the American coast. The main divide is here not the East Pacific Barrier (cf. p. 212), as in the case of the shelf fauna, as it is apparently navigable for some abyssal species, but it is formed by the two American continents. Thus a difference has developed between the abyssal and shelf fauna in that (as EKMAN underlined) the abyssal fauna cannot be divided into an Atlanto-East-Pacific and an Indo-West-Pacific region, but into an Atlantic and an Indo-pan-Pacific region".

This view was given by EKMAN in very general terms, whereas he otherwise supported the various claimed zoogeographical regions with faunistic surveys. Thus it appears that he primarily wanted to emphasize the marked difference in the abyssal fauna on either side of the American continents (that is, the Atlantic and the East Pacific abyssal faunas respectively) in contrast to the great similarity between the shallow-water fauna on either side of the Isthmus of Panama. – It is only in passing that he referred to an Atlantic and an Indo-Pacific deep-sea region respectively.

At a later stage in the handbook (p. 303) EKMAN noted that "the open-sea abyssal can be divided zoogeographically into only three or four main regions: an Atlantic, Pacific, arctic and perhaps antarctic region". Thus here he took no definite view on the zoogeographical position of the abyssal fauna of the Indian Ocean. In an other paragraph (p. 292) he also pointed out: "How far the abyssal fauna of the Indian Ocean is independent vis-à-vis that of the Pacific may be shown by future investigations". Further he mentioned (p. 292) that: "Several species which are common to the abyssal region of the Indian Ocean and the Atlantic and which were formerly regarded as Atlantic relicts of the Tethys Sea, are now considered as signs of a direct communication between the two abyssal regions south of Africa". - Apparently the conclusion must be that EKMAN's view on the main zoogeographical subdivisions of the oceanic abyssal deep-sea (i.e., the zoogeographical position of the Indian abyssal fauna) does not actually conflict with that held by

the writer. (The probable explanations for a closer affinity of the abyssal fauna of the Indian Ocean with that of the Atlantic rather than with that of the East Pacific, are discussed in paragraph 7, p. 210.)

The writer regrets that the known distribution of the Porcellanasteridae is not of great help in settling the question of the zoogeographical position of the abyssal Indian Ocean. Of a total of 14 species which are known from more than two finds, six (listed p. 204) are cosmopolitan. Styracaster elongatus (7 finds) is known from the Atlantic and the Indian Ocean. Styracaster spinosus (5 finds) is known from the Atlantic, and probably S. clavipes, recorded from a single locality in the Indian Ocean, is the same species. Styracaster armatus (4 finds), Abyssaster tara (8 finds) and Eremicaster crassus (5 finds) are known from the Indian Ocean and the Pacific. Styracaster caroli (6 finds) is known only from the Indian Ocean. Eremicaster pacificus (15 finds) and E. gracilis (23 finds) are known only from the Pacific. Of these eight species of porcellanasterids known from only one or two of the oceans, two range from the Atlantic to the Indian Ocean, while three range from the Indian Ocean to the Pacific.

With reference to the theory of a possible subdivision of the abyssal fauna into an Indo-Atlantic and a Pacific element (besides the cosmopolitan element), attention may be called to the fact that with regard to some deep-sea crustacea, BURKENROAD in 1936 (Penaeidae) and DAHL in 1953 (Eryonidea) similarly found a pattern of distribution indicating a closer relation between the deep-sea faunas of the Indian and the Atlantic oceans than between those of the Indian and the Pacific oceans.

5. The "guests" in the abyssal region

In the writer's opinion it should be sufficiently established from the faunistic surveys given in the preceding that the abyssal zone contains a characterizing fauna of cosmopolitan species. There is no absolute faunistic homogenity however, not even in the lower abyssal zone, since existing side by side with the endemic abyssal species there are considerable numbers of species which may be described as guests in the region (cf. below). The presence of these species naturally makes it possible to distinguish several subregions in the abyssal deep-sea, although these refer rather to the bathyal zoogeography. When stating that the open-sea abyssal can be divided zoogeographically into two or three main regions only (see further p. 207) EKMAN also pointed out (1953 p. 303) that "for the coastal abyssal and especially for the archibenthal we have to postulate a greater number of regions".

The species in the abyssal fauna, here called guests (a name probably used first by WALTHER, 1893-94 p. 168), sometimes also called secondary deep-sea species, have their main distribution in a confined area of the bathyal zone (in the case of the polar fauna maybe even in the sublittoral zone). The individuals or populations which occur in the neighbouring abyssal depths may be only strayers, able to live but at the same time (probably primarily because of scarcity of food) unable to produce a constant series of generations under the abyssal conditions. Such species in order to maintain their abyssal representation will depend on a continuous invasion from the bathyal depths and thus will really confirm to the concept of a guest. - Other species may be better adapted to an abyssal existence but still only able to mature their reproductive products under food-conditions such as found on the terrigeneous deposits (cf. p. 186) and for this reason are of a restricted distribution in the abyssal zone. (When finally a species has evolved the ability to reproduce, also when living on the eupelagic deposits, its distribution over the whole abyssal bottom will be only a question of time.)

The most common 'guest' occurrences in the abyssal zone are shown by species which are abundant in sublittoral-bathyal depths in the higher latitudes, and from there descend into the neighbouring greater depths (cf. p. 195). Examples of such cases are offered by e.g. the following three ophiuroids: the Antarctic *Ophiosteira senoqui* (110-3109 m), the Arctic-North Atlantic *Ophiocten sericeum* (6-4370 m), and the North Pacific *Ophiura lectoctenia* (123-3239 m), (cf. the map published by the writer, 1953 b p. 36, illustrating the principal types of deep-sea distribution within the echinoderms).

Further examples of species occurring in the North Atlantic deep-sea, but apparently having their main distribution in the sublittoral-upper bathyal depths in the Arctic region, are e.g. within the octocorals: *Clavularia arctica* (55-2050 m), *Gersemia rubiformis* (6-3600 m), and *Capnella glomerata* (60-2700 m), (cf. MADSEN 1944), and within the amphipods: *Stegocephalus inflatus* (5-2000 m), *Arrhis phyllonix* (5-2465 m), and *Hippomedon holbølli* (15->2200 m), (cf. STEPHENSEN 1925 p. 129, 1931 p. 232, 1935 p. 71).

It seems probable that a number of the taxodonte

According to VINOGRADOV	A (considering the fauna	According to the writer (considering primarily the endemic abyssal fauna)				
ATLANTIC	ARCTIC SUB-AREA		ARCTIC DEEP-SEA REGION			
WATER		North Atlantic Province	ATLANTO-	NOIE		
AREA	AILANIIC SUB-AREA	West Atlantic Province	INDIAN			
	505111011	East Atlantic Province	(+ WEST	REC		
PACIFIC-	NORTH-INDIAN SUB-AREA	[DEEP-SEA REGION	ITAN		
NORTH INDIAN	PACIFIC SUB-AREA	West Pacific Province		MOPOL		
DEEP WATER		North Pacific Province	PACIFIC			
AREA		East Pacific Province	DEEP-SEA REGION	COSI		
	ATLANTIC SUB-AREA		ANTARTIC			
WATER	INDIAN-	Indian Province	DEEP-SEA			
AREA	PACIFIC SUB-AREA	Pacific Province	KEGION			

Table 2. The zoogeography of the abyssal region

bivalves recorded from the North Atlantic deepsea are also merely "guests" from the Arctic shallow region, e.g. *Nucula tenuis* (5-2250 m) and *Portlandia arctica* (5-2400 m). Other bivalves which show the same kind of distribution are e.g. *Modiolaria discors* (0-1800 m), *Pecten groenlandicus* (6-2000 m), and *Saxicava arctica* (0-2000 m), (cf. MADSEN 1949 pp. 106-112).

Finally, a few examples may be given of species of echinoderms which seem to have their main distribution in the bathyal depths of a confined area in the lower latitudes, while occurring as "guests" in the neighbouring abyssal depths, e.g. the ophiuroid *Ophiotreta matura* (240-4160 m) in the Indo-Malayan area, the asteroid *Rosaster alexandri* (150-3550 m) in the Bay of Mexico (cf. MADSEN 1951 *a*, *b*), and the echinoids *Phormosoma placenta* (170-2340 m) and *Pygmæocidaris prionigera* (660-2860 m) in the Indo-Malayan area, and *Coelopleurus floridianus* (90-2380 m) and *Homolampas fragilis* (550-3550 m) in the western North Atlantic (the West Indian area), (cf. MORTENSEN 1928-51).

6. Commentary on N. G. Vinogradova's view on the abyssal zoogeography

A scheme giving a detailed zoogeographical subdivision of the abyssal deep-sea has recently been published by N.G. VINOGRADOVA. – It is intended to make a few comments on this scheme since it is somewhat at variance with the view of the zoogeography of the abyssal zone held by the writer.

The accompanying table 2 gives a survey of the zoogeographical areas, sub-areas and provinces, claimed in the deep-sea by VINOGRADOVA, comparing them with the regions claimed by the writer. Table 3 gives a survey of the distribution of the cosmopolitan and the more widely distributed porcellanasterids in relation to the sub-areas and provinces of VINOGRADOVA.

It should be noted that while the writer has

Table 3. The distribution of some of the species of Porcellanasteridae; those considered cosmopolitan marked with an asterisk

	North Atlantic	West Atlantic	East Atlantic	North Indian	West Pacific	North Pacific	East Pacific
* Hyphalaster inermis	×	×	×	×	×	×	×
Abyssaster tara				\times		\times	
* Thoracaster cylindratus		\times	×	×		\times	\times
* Styracaster horridus			\times	\times	×		
* Styracaster chuni	×		\times		\times		
Eremicaster gracilis						\times	\times
Eremicaster crassus				\times			\times
* Eremicaster vicinus			\times	\times	\times	\times	\times
* Porcellanaster cæruleus	\times	×	×	×	×	\times	×

confined his considerations on the abyssal zoogeography to the fauna occurring in depths of more than 3000 m, VINOGRADOVA based her analysis on the fauna recorded from more than 2000 m, which means that a number of species of an extended bathyal rather than an abyssal distribution have been included. It will also be immediately evident from table 3 that such a detailed zoogeographical subdivision as that proposed by VINOGRADOVA in her provinces, is unreasonable in relation to such truly abyssal species as the porcellanasterids. VINO-GRADOVA's provinces really relate to the bathyal fauna, and the following discussion will therefore only consider the sub-areas and areas claimed by her.

According to VINOGRADOVA the zoogeographical sub-areas in the abyssal zone are: the Arctic, the Atlantic, the North Indian, the Pacific, the Antarctic Atlantic and the Antarctic Indian-Pacific.

As to the Antarctic deep-sea, the writer agrees with the, on the whole, commonly held opinion (cf. EKMAN 1953 *a* p. 303) that it constitutes a special faunistic region. All three species of porcellanasterids collected in the Antartic Sea, *Hyphalaster scotiae*, *Styracaster robustus*, and *Abyssaster planus*, may also be especially cold-adapted forms which may be endemic in the region. (They are known only from the type-localities.)

It is similarly agreed that the Arctic deep-sea, which is an enclosed basin, is a separate zoogeographical region. (No porcellanasterids are known so far from this area.)

As regards the Atlantic, North Indian and Pacific sub-areas then, the abyssal faunas of the Atlantic and the Pacific obviously show distinct features. The North Indian abyssal fauna, however, is so closely related with the Pacific on the one side and that of the Atlantic on the other side, that from a zoogeographical point of view the Indian abyssal region can not be ranked equal with the two other regions. This is also generally recognized. To which of the two other oceanic abyssal faunas the Indian abyssal fauna has the nearest connection is, however, a point of dissension.

Thus the main point on which the writer disagrees with VINOGRADOVA in her view on the abyssal zoogeography, is with regard to the zoogeographical position of the truly abyssal fauna of the Indian Ocean. While VINOGRADOVA postulates an Atlantic deep-water area as distinct from a Pacific-North Indian deep-water area (a division agreeing with EKMAN'S Atlantic and Indo-pan-Pacific abyssal regions), the writer postulates an Atlanto-Indian region (inclusive of the region of the Malay Archipelago) as distinct from a Pacific region (cf. pp. 207. 208).

VINOGRADOVA found 2.1 % of the more than a thousand analyzed species to be common to the Indian Ocean and the Atlantic, and twice as many common to the Indian Ocean and the Pacific (further, that only 4 % were known to be cosmopolitan). But, as already noted, the surveyed species have included a considerable number which the present writer would not regard as truly abyssal, and a large number have been recorded from only a single or a few localities, and therefore are of little use for any zoogeographical purposes.

7. Possible explanations for an Atlanto-Indian and a Pacific (East Pacific) abyssal fauna element respectively

It is beyond dispute that the bathyal faunas of the northern Indian Ocean and of the neighbouring West Pacific, are very closely related. It is further evident that also the abyssal fauna is largely the same in the Indian Ocean and in the neighbouring region of the Malay Archipelago (also when disregarding the cosmopolitan element and the element of "guests" from the bathyal zone). This fauna is, however, as already mentioned in the preceding, in the writer's opinion more closely related with the abyssal fauna of the Atlantic than with that of the main Pacific, or rather the northern and eastern Pacific. The supposed boundary or, more correctly, the transitional zone between these two claimed main subdivisions of the oceanic abyssal region extends from Southern Japan in a south-eastern direction to east of New Zealand. (The writer thus distinguishes a Pacific abyssal fauna (in the main comprised by VINOGRADOVA'S North Pacific and East Pacific provinces) from the rest of the oceanic abyssal fauna, whereas VINOGRADOVA, and EKMAN, distinguish the Atlantic abyssal fauna from that of the other oceans.)

The marked differences in primarily the bathyal but also in the abyssal faunas of either side of the American continent, have been noted by several authors. For instance in 1953 DAHL says: "In the round-the-world distribution of the abyssal Crustacea the West-Atlantic and the East Pacific probably represent the opposite extremes". – The distribution of the Porcellanasteridae, as known at present, shows exactly the same picture. In the eastern Pacific, Eremicaster is abundant, Abyssaster, Styracaster, and Porcellanaster, are represented but rare, whereas Hyphalaster is unknown. In the Atlantic, Eremicaster is only known to be represented by a single, abysso-hadal species, while Porcellanaster, Hyphalaster, and also Styracaster, are common. In the Indian Ocean these four species all are abundant. Of the two remaining abyssal genera, Abyssaster is primarily Indian in its distribution and unknown from the Atlantic, while Thoracaster seems equally common in all three oceans.

An explanation for the difference between the deep-sea faunas of the eastern Pacific and western Atlantic, may be found in the geological history of the oceans (cf. ARLDT 1919-22; SCHOTT 1912, 1935). In former geological periods, i. e. from Palaeozoic until well up in Caenozoic (Late Tertiary), a great ocean belt, including the recent Mediterranean, stretched across the earth, dividing the land masses into a southern and a northern group. This world-ocean was of a somewhat varying extension in different periods, but already from Early Mesozoic the land masses corresponding to the present North and South American continents were merely separated by a shallow (and narrow) stretch of sea (cf. SCHUCHERT 1935); and at the end of the Mesozoic a land-bridge was erected. (During the middle of the Tertiary this landbridge was broken, but only to permit the interchange of the tropical shallow water faunas of either side of the isthmus; and at the end of the Tertiary it became closed again.) The differences in the recent deep-sea faunas to either side of the American continent is thus well accounted for.

The recent littoral and sublittoral faunas of either side of the Isthmus of Panama, on account of the interoceanic connection during Late Tertiary, are contrariwise closely related and comprise, besides numerous identical genera, many so-called twin species and also several identical species (cf. EKMAN 1953 a p. 30). In the shallow-water fauna of the tropical belt the greatest contrast is to be found between the fauna of the western American coast and that of the Indo-West-Pacific region, which, far back in the geological history were continuously separated by a broad and very deep ocean (EKMAN's East Pacific Barrier).

The claimed close connection between the abyssal fauna of the Atlantic and that of the Indian Ocean (inclusive of the region of the Malay Archipelago), also illustrated in the distribution of the Porcellanasteridae, is similarly accounted for both by the present wide connection between the two regions south of Africa and by the past history of this part of the world-ocean (cf. ARLDT 1919-22).

From Late Mesozoic and into Early Tertiary the regions corresponding to the recent Atlantic and Indian Oceans were in wide connection both north and south of the later African continent (whereas during this period the regions corresponding to the recent Indian and Pacific oceans were to a large extent separated by land or by shallow water). It was not until Late Tertiary that the part of the world-ocean stretching across from the Indian to the Atlantic region, (the so-called Tethys Sea) was replaced by the recent conditions, with a separation of the Indian Ocean, the Mediterranean, and the Atlantic.

The Atlantic region suffered a marked deterioration of climate in connection with the glaciations in its northern part, whereas the ecological conditions remained rather stable in the Indian region during the Tertiary as well as the Quaternary period. The bathyal, and in part, relatively primitive porcellanasterids found in the Indian Ocean, may therefore (as noted in the preceding) be regarded as the last survivors or direct descendants of the ancient species of porcellanasterids which inhabited the bathyal depths of the Tethys Sea, and have now perished in the other regions.

(As pointed out by EKMAN (1953 *a*), the rather stable ecological conditions prevailing for such a long time in the Indo-Malayan region offer a better explanation of the general faunal richness found here in comparison with the Atlantic and Pacific, than the assumption that the Indian Ocean has been a center of creation.)

It is assumed that in the oceanic abyssal region there are no zoogeographical barriers of such importance that they can definitely prevent any species, (when first adapted to the ecological conditions in the great depths) from eventually spreading over the whole world-wide abyssal region. Since, however, a dispersal over that vast area by species whose young must typically settle near their parents, may take thousands of years, a species originating in the Atlantic would be common to this and the Indian Ocean for a long time before spreading to the Pacific, and vice versa for a species originating in the Pacific.

The very long geological period during which the abyssal regions of the western Atlantic and the eastern Pacific have been separated is a natural explanation of existing differences in their faunas. Are there also, however, any reasonable explanations for zoogeographical boundaries elsewhere in the abyssal oceanic deep-sea? Certainly the land mass formed by the European-Asian and African continents constitutes a kind of zoogeographical barrier which will take time to circumvent. Some kind of barrier may also be formed between the Indian Ocean and the Pacific by the Australian continent, supplemented to the south by the extremely cold Antarctic water and to the north by the islands of the Malay Archipelago.

Finally, to all appearances, the so-called East Pacific Barrier, referred to above as the most important zoogeographical boundary in the circumtropical shallow-water region, is also a boundary for the abyssal fauna. The abyssal region stretching from the western North Pacific southwards to the east of Polynesia is a poor feeding ground for benthic animals. It is sparsely populated therefore, and apparently even comprises extensive desert-like areas (cf. p. 214). It must be relatively difficult for an abyssal species to spread from either the western or the eastern Pacific through this sterile region where no large populations can be maintained. Evidently the spreading of the abyssal species in the eastern Pacific also takes place primarily in southwards and northwards directions through the food-rich areas near the continents, and the spreading from west to east in the Pacific, or vice versa, may mainly take place in its northernmost region.

Porcellanaster cæruleus and Eremicaster gracilis (inclusive of *E. crassus*) may be species which are in the course of spreading over the abyssal deep-sea from the bathyal western North Atlantic and from the bathyal eastern Pacific respectively. They also seem to dominate widely in the abyssal depths of the mentioned regions, and being young and apparently vigorous types of porcellanasterids, they may have been serious competitors to older types of this group which possibly lived there earlier.

(It would seem that the Porcellanasteridae in general may not be very exacting in their demands on the substratum, at least some of the species being able to thrive equally well on a wide variety of bottom (cf. p. 213). This may be one reason accounting for the fact that these animals apparently are less apt to speciation than some other deep-sea animals, e.g. isopods and amphipods. Thus, the distribution of the various species of porcellanasterids must correspond exceptionally well with the main zoogeographical divisions of the abyssal region.)

8. The alleged endemism in the trench faunas

At this point a few remarks may be made on the zoogeographical position of the hadal fauna. Tectonically the trenches and deeps are rather well circumscribed; this feature probably accounting for a certain isolation of their faunas, and a hereby caused speciation. The possibility must also be considered that the hydrostatic pressure in the hadal zone may require special physiological adaptations of its inhabitants, which subsequently might become unable to thrive under other conditions and so be prevented in spreading from the trenches or deeps. However, this is a possibility which the writer does not think feasible.

It is true that a considerable number of the species recorded from more than 6000 m, are unknown from smaller depths, but this could be partly accounted for by incomplete knowledge of their distribution. From WOLFF's survey (1960) it also appears that of the hitherto identified 23 hadal species of echinoderms, more than half, viz. 14, are known to have a more or less wide distribution in the abyssal zone too.

The trenches are usually considered to be of a comparatively young geological age; it being assumed that their formation was connected with the Alpine foldings (cf. p. 199). In the writer's opinion the facts known about their faunas do not dismiss such an assumption. - The degree of endemism recorded for the various trench faunas is partly on the subspecies level, and from this it can not be concluded that the trenches are of any great age. Incidentally, it should always be possible to point out minute differences between different populations, especially as long as only small numbers of individuals, or materials which may only comprise siblings, are available. With regard to the trench faunas it may often be difficult to judge therefore the degree of endemism. Very probably many of the hadal subspecies which have been erected, can not hold when more material becomes available and the range of variation better elucidated. (See also pp. 213, 215).

9. The distribution of the abyssal fauna in relation to the condition of the bottom

Evidently the abyssal fauna is to a large extent composed of comparatively few species which occur in a relative abundance of individuals. This is a feature which is shown also by the cold shallowwater faunas and further by the infauna as a whole. In the former case the feature may be traced back to the fact that only relatively few species survived the Tertiary fall in the temperatures. In the latter case the reason is the relatively few ecological niches available (in comparison with the number available for the epifauna). Known samples of the abyssal fauna also primarily represent the infauna, since almost all successful deep-sea collecting has been done on the soft level bottom. (THORSON, 1957 p. 466, estimates that the total number of epifauna species in the sea is at least four times as large as that of infauna species.)

Although the abyssal deep-sea bottom is mainly flat, areas with an uneven, hard and rocky bottom, are apparently of a more common occurrence than was suspected before the introduction of the echosounder. The fauna in such places is yet only very fragmentarily known, and though probably rather poor, may include many unknown forms. Also the general assumption that the character of the bottom substratum is entirely uniform over vast areas may not be true in all places. Areas covered with a very loose substratum of fine ooze may thus include seamounts with a coarser grade of bottom, since here the currents may remove the finest deposits.

Incidentally, the old deep-sea expeditions which had to risk their collecting gear at random, were more likely to obtain samples of the abyssal epifauna than modern expeditions, which, guided by their echo-sounders, have as far as possible used their costly gear for dredging only on the level bottom. Why the hadal fauna seems to be rather different from the known abyssal fauna, is perhaps in part due to the fact that the fauna living on the fairly steep slopes which bound the rather narrow trenches, send strayers out on the enclosed flat bottom areas where the collecting has been largely performed.

The Porcellanasteridae are infauna animals which live from the basal food in the milieu (i.e. eating the bottom material proper and deriving their nourishment from the organic matter (detritus and bacteria) contained in it). Thus their populations, though probably patchy and scattered, may be expected to be comparatively abundant in individuals. Some catches of porcellanasterids have also yielded a rather large number of individuals (though small in comparison with the number of elasipod holothurians obtained in some deep-sea hauls). Examples are: 32 individuals of *Hyphalaster inermis*, 18 of *Thoracaster cylindratus*, and 86 of *Eremicaster graci*- *lis*. But of course these individuals could have been relatively scattered, since the dredge may have worked over a considerable area.

The three species abundant in individuals, *Hyphal-aster inermis, Thoracaster cylindratus,* and *Eremi-caster gracilis,* are at the same time (with 32, 20, and 23 finds respectively) some of the most frequently recorded porcellanasterids, and are thus among the dominant abyssal benthic species. The two first-mentioned species are also known to be cosmopolitan. (Incidentally, a world-wide distribution may be expected to apply also to some at least of the abyssal species of porcellanasterids known hitherto from but a single or a few individuals; the species in question being rare and, therefore, more accidentally caught.)

The kind of substratum covering the deep-sea floor (its composition and structure) might be expected to exert some controlling influence on the distribution of the Porcellanasteridae (cf. pp. 207, 212). – Some other marine animals are apparently very sensitive to minute differences in the concentration of various organic and inorganic elements in the bottom substratum as well as in the water (cf. WILSON 1951, URSIN 1960 p. 100). – From the information hitherto available very little can be deduced about this question however.

The Porcellanasteridae are always found on a soft level bottom. In about half of the 110 cases where information is available, the bottom was registered as greyish, greenish, or bluish mud; in about onethird of the cases as ooze (usually globigerina ooze, but in a few cases radiolarian ooze, and in one case diatom ooze), and in one-fifth of the cases as bluish, yellowish, brownish, reddish, greenish, or blackish clay. Finally, in a few cases the bottom was recorded as being of green or black sand. It may be noted, however, that the nature of the bottom recorded may not always have applied to the whole dredged area.

A species such as *Eremicaster gracilis*, in spite of its name a fairly robust form, has been found seven times on a bottom of ooze (globigerina, grey, and diatom ooze), nine times on mud (green, grey, or blue mud), once on clay, and once on sand, -a rather wide range of bottom types. A delicate species such as *Styracaster armatus*, is found exclusively on globigerina ooze (4 finds), whereas the more robust *Styracaster chuni* is recorded exclusively from clay or sandy clay (6 finds, but the kind of bottom was not recorded in two of the cases).

The Porcellanasteridae are mainly known from

areas where the deposits are more or less terrigeneous, thus with a fairly high content of organic material. These areas are however, those which have been most extensively dredged, and nothing definite can yet be said about the occurrence of porcellanasterids in other areas. Perhaps the substratum in places may be too soft for these burrowing sea-stars to thrive on, and this in part, could be the explanation for their general absence in the hadal depths.

It should be noted that as early as 1877, WYVILLE THOMSON stated that: "The distribution of life evidently depends in a marked degree either upon the nature of the bottom or upon the conditions which modify the nature of the bottom". To illustrate this he mentioned that "over the vast areas where the calcareous matter of the foraminifera has been removed, and the bottom consists of red or grey clay, animal life is scarce; and is represented chiefly by shell-less orders, such as the Holothurioidea and the Annelids".

A difference in the composition of the bottom faunas in the eastern and mid-Pacific deep-sea on the one hand, and the Atlantic and Indian deep-sea on the other hand, thus (as also touched upon p. 207) may be partly accounted for by the, on the average, somewhat different substrates in these two regions: primarily abyssal red clay in the former region, but calcareous ooze in the latter.

The general impoverishment of the deep-sea bottom fauna with increased distance from land (and from oceanic areas with a high productivity in the photic layer) and also with increased depth, is a phenomenon which was noted early on in the exploration of the deep-sea and has been amply confirmed e.g. by the recent Russian explorations of the Pacific and Indian oceans (cf. FILATOVA 1959 and BELYAEV 1959). However, in the upper abyssal region the Porcellanasteridae apparently gradually replace the bathyal fauna elements extending out there, becoming eventually one of the dominant animals in the lower abyssal zone. Thus the Porcellanasteridae may be fairly uniformly spread over most of the oceanic deep-sea, having their main occurrence at depths of about 4000 m, and disappearing only when the abyssal depths pass into the hadal ones.

10. The possible fluctuations in the abyssal populations

In the deep-sea with its stable ecological conditions and no marked seasonal variations (cf. p. 202), the animal populations probably maintain themselves for very long periods in those areas where they have once become successfully established. As long as a population comprises a sufficient number of individuals it will be almost impossible for a competing form to gain a foothold in the same area. The deep-sea animals allegedly have a considerable longevity and, if this be so, fluctuations in the populations and the composition of the local faunas probably take place only over relatively long periods.

The Porcellanasteridae (especially their young) may be preyed upon by other kinds of sea-stars, crustaceans, or bottom fishes. (In the deepest regions however, they can have only few enemies, if any at all). Further, they may be attacked by parasites, the most damaging being ascothoracid barnacles. Due to these conditions a population of porcellanasterids may be exterminated or the number of individuals so diminished that it becomes possible for a competing form to settle. A population of porcellanasterids may perhaps also simply exhaust the available food-supply and so die off. - Incidentally, extensive areas in the deep-sea may perhaps for long periods be totally or almost barren of life, except for bacteria and protozoa. This assumption seems borne out by the many photographs of the deep-sea floor showing no life nor any trace of life (cf. e.g. LAUGHTON 1959). Desert-like areas in the main Pacific have also been recorded by various deep-sea expeditions (cf. e.g. A. AGASsiz 1906 p. 9). It may further be noted that the phenomenon of a bottom area "Lying fallow in periods" is also known from the sublittoral zone (cf. THORSON 1957 p. 484).

When a population of porcellanasterids (or other deep-sea forms which feed in a similar way) disappear from a given area, the type of species conquering the vacant space may be completely accidental. The succeeding species will be those, which at the right moment, happen to produce viable progeny. For such reasons, well-defined animal communities comparable to those known from the shallow marginal seas, probably do not exist in the abyssal region. In the Kurile-Kamchatka and Bougainville trenches, over 90 % of the bottom fauna (by weight) consists of the holothurian *Elpidia* glacialis, in the Kermadec Trench 70-95 % consists of bivalves, and in the Tonga Trench 50 % consists of amphipods and isopods (BIRSTEIN 1959). It is quite possible that these differences are not a permanent feature. The faunas mentioned may be temporary only and possibly subject to considerable fluctuations over periods of sometimes only a few scores of years. (But of course, the different amount of terrigeneous material and organic material from the upper water layers which settle in the various trenches, will account for some permanent differences in their faunas.)

XV. SUMMARY

The porcellanasterid sea-stars are exclusively deepsea animals, known only from depths exceeding about 1000 m. Prior to the Galathea Expedition they were recorded from 165-170 dredgings, in a total of 600-650 individuals. Fifteen genera and 57 species were named. The Galathea Expedition brought back 469 specimens obtained in 27 dredgings, and this material formed the main basis for a study and revision (see the preceding paper in this report) which resulted in a division of the group into only 9 genera and less than 25 valid species. One new genus, *Abyssaster*, was erected to embrace some of the species formerly included in *Hyphalaster*, but no new species were found.

In the introduction to the preceding paper a survey on the morphology of the Porcellanasteridae is given, and the characters which may be used taxonomically are discussed. Some notes are also appended on their possible mode of life. Included in the systematic section is, besides the rather detailed description of the Galathea material, references to and discussions of all previously recorded porcellanasterids.

The knowledge gained of the taxonomy and distribution of the Porcellanasteridae has thereafter formed the basis for the present review and discussion on some of the general problems of the abyssal fauna – its geological origin, and especially, the zoogeography of the abyssal region.

The now known distribution of the species of Porcellanasteridae, supports the concept of an essentially cosmopolitan lower abyssal level-bottomfauna. Six of the 14 species of porcellanasterids known from more than two dredgings, have been found in all three oceans. The greatest difference in the abyssal fauna of porcellanasterids is between the faunas of either side of the American continents (the Atlantic and the East Pacific abyssal faunas respectively). The zoogeographical boundary in the abyssal region, next in importance to that formed by the American continents, is apparently constituted by the ecologically unfavourable mid-Pacific deep-sea, corresponding with the so-called East Pacific Barrier, so important in the zoogeography of the shallow and moderate depths.

The Porcellanasteridae seem to have originated (probably in Late Mesozoic) in the bathyal depths of the Tethys Sea from astropectinid-like ancestors. All three exclusively bathyal genera (two of which may be the most primitive porcellanasterid genera) are confined to the region of the Indian Ocean, which on the whole comprises the greatest number of different forms. Some of the world-ranging species of Porcellanasteridae seem to have a rather confined bathymetrical distribution. The porcellanasterid genera hitherto recorded from the greatest depths are probably the youngest phylogenetically. This and other considerations, support the assumption that in the main the recent abyssal fauna is younger than the bathyal and littoral faunas, and that probably on the whole the ancestors of the oldest types of abyssal animals today, did not invade the abyssal habitat until Early Tertiary.

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