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ZOOGEOGRAPHY OF THE SEA

By

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PREFACE

In 1935 the Akademische Verlagsgesellschaft in Leipzig published my book *Tiergeographie des Meeres*. When, some time ago, it was proposed to bring out an English edition, it was evident to me that a simple translation would not suffice because the progress made in marine zoology since 1934 made it necessary to revise the text, making additions and corrections where required. When I set to work I found that the revision had to be more comprehensive than I thought. It is true that the recent war made scientific expeditions into the world's oceans almost impossible, but work on the collections of earlier expeditions was continued and a considerable number of other advances in marine zoology had been published. The revision, therefore, had to be thorough-going.

To elucidate the various zoogeographical regions and their faunas I have, in a number of cases, drawn up tables for the occurrence of various groups of species and genera within the fauna in question, the data being expressed in figures for the absolute number and the percentage. It goes without saying that these tables cannot be absolutely correct, but merely reflect in an approximate way our present knowledge, incomplete as it is. They constitute an attempt to present the faunistic facts as objectively as possible, arranged in such a way that the important features are brought out by and for comparison with other faunas.

It is not only the individual animals which live; the faunas also appear to us as living units. Since a fauna has developed from an earlier fauna, in the course of time it changes, perhaps grows old and will in future be replaced by a new one. The attempt, by growing refinement of method, to find out more and more of the life history of these faunas provides a particular stimulus for the zoogeographer. In so doing he must combine various disciplines. In the sphere of zoology he combines faunistics with taxonomy, ecology with its fundamental science, physiology. In its methodology zoogeography closely resembles plant geography, the results of which it uses, in addition to those of oceanography, present and past climatology, geomorphology and palæontology. Animal geography thus represents a gratifying example that even today, when an ever-increasing specialization is often a condition of progress, there are still sciences left which find in the opening up of frontiers and in the

collaboration with other sciences the condition for their own progress. It is my hope that in the following account even the dry lists of names and the tabulated figures will make their contribution to the understanding of the ever-changing life of the faunas.

It is a pleasant duty to express my thanks to those who assisted in the inception and preparation of this book: to Professor H. Munro Fox, London, on whose initiative this English Edition was undertaken; to a great number of scientists who by offprints or letters have contributed much by way of advice and suggestions; among these I should like to make especial mention of Professor T. A. Stephenson, Aberystwyth, with whom I had the pleasure of discussing the position of the South and South-west African fauna, and Dr. Joel W. Hedgpeth, of Berkeley, California, who among other things placed at my disposal as yet unpublished informations about the fauna of the Gulf of Mexico. I also express my thanks to the Zoological Institute of the University of Uppsala (Director Professor S. Hörstadius) for the excellent facilities it provided for my work, to Dr. Elisabeth Palmer, London, who has carried out the translation into English, and, not least, to the publishers, Sidgwick & Jackson Ltd. and its Managing Director J. S. Knapp-Fisher, with whom it has been a pleasure to collaborate.

SVEN EKMAN

Uppsala,
April, 1952.

CHAPTER I

THE WARM-WATER FAUNA OF THE SHELF: INTRODUCTORY SURVEY

THE first chapters will deal with the sea-floor fauna in shallow waters of up to 200 m. depth. This fauna has long been called littoral (as in my *Tiergeographie des Meeres*). But at an early date, and with greater frequency in recent times, the term littoral has been reserved, both in zoology and botany, for the upper layer of water, and nowadays there seems to be a general tendency to restrict the term to the inter-tidal fauna and the comparable faunistic zones. We encounter here one of the characteristics of a young science: marine zoogeography as yet lacks a fixed and generally accepted terminology. But to avoid adding to the confusion of terminology I shall not use the term "littoral" in its widest sense. In that case, however, it needs to be replaced by another term. Both English and American authors make frequent use of the term "shore fauna" and "coastal fauna". These have the advantage that they are easily understandable, but they are not fully adequate with regard to the lower limits of the fauna in question. I therefore suggest the term "shelf fauna". The English "shelf" means just the region which is concerned, namely the sea-floor on the continental shelf as far as its edge, where it falls away steeply. This edge lies usually at a depth of about 200 m., more rarely at a greater depth (300–400 m.). In oceanographic or purely geographical literature the word "shelf" is in general use. Its use in zoogeography would fill a real need. The objection that "shelf fauna" is not applicable to the numerous oceanic islands which do not possess a shelf is hardly valid, since the so-called shore fauna of these islands is in origin a real shelf fauna which developed on a continental shelf and then spread to the islands, although possibly not in the form of present-day species but in that of their ancestors.

The term "neritic fauna", which of course refers mainly to the water above the shelf, is a planktological term and cannot be extended to include the sea-floor fauna.

According to this suggestion the term shelf fauna will include the fauna of the sea-floor from the inter-tidal zone as far as the outer edge of the shelf.

It must be emphasized, however, that we still lack the detailed

investigations which would enable us to determine with reasonable accuracy where the shelf fauna ends and the deep-sea fauna begins. In any case the zone in question is a transitional zone with no clearly marked delimitation. Many observations make it reasonable to suppose that it lies round about the edge of the shelf, but the crucial question here, as in other borderline cases, is: where does the most pronounced change of fauna take place? There are strong reasons for believing that in general this coincides with the "mud-line", or the upper limit for loose mud sediment. The zoogeographical significance of this was clearly perceived by John Murray and stressed by him in his reports on the collections made by the "Challenger" expedition. The mud-line seems in general to coincide with the edge of the shelf. Even at this stage we may say that the boundary zone lies at different depths in different regions and that it does not depend wholly, or even mainly, on the depth, but on the interplay between various hydrographical factors and the nature of the animals concerned. It is also an open question to what extent the fauna in the lower zone of the shelf may be arranged in regional groups, the surface-projected boundaries of which correspond to those of the upper layers of coastal waters. Both experience and theoretical speculations suggest that conformity with the upper layers decreases with increasing depth. In this state of affairs currents play a decisive part. In some cases it may seem justifiable to include in one and the same regional group the fauna of 150–200 m. depth and that of 0–50 m. depth, whereas in other cases this would do violence to nature.

The relationship between the tropical, the northern and southern subtropical, and the northern and southern temperate faunas may be expressed in the following way. The tropical fauna is the richest, containing the largest proportion of the warm-water animal world. This includes numerous elements which, chiefly because of their special need of warm water, do not penetrate into the subtropical regions bordering on it. It is therefore particularly characterized by endemic elements. The subtropical faunas are more or less thinned-out warm-water faunas which have most of their constituents in common with the tropical fauna and a much smaller number in common with the neighbouring temperate fauna. But it too contains a number of endemic elements which are, however, considerably inferior in numbers and taxonomic importance to the tropical endemic elements. The subtropical faunas, therefore, cannot be ranked with that of tropical waters. But they offer a greater contrast with the temperate than with the tropical fauna. They form a unit with the tropical fauna which will be discussed under the heading "warm-water fauna".

Since it seems indubitable that temperature is the most important factor in the division of faunas, the borders of the tropical and subtropical zones have been identified with particular isotherms. The tropical fauna would thus occupy a region between the isotherms for 20° C. water temperature at the coldest time of the year, while the subtropical faunas in the north and south respectively are limited by a yearly minimum temperature of about 16°–18°. This is probably correct in the main. We shall return to the problems of delimitation when we describe the various warm-water zones.

The relative homogeneity of the warm-water fauna

It is common knowledge that the tropics are much richer in life than the colder regions and this is also true of the tropical seas. A large number of genera, families and systematic groups of a higher order are wholly or almost entirely confined to the warm-

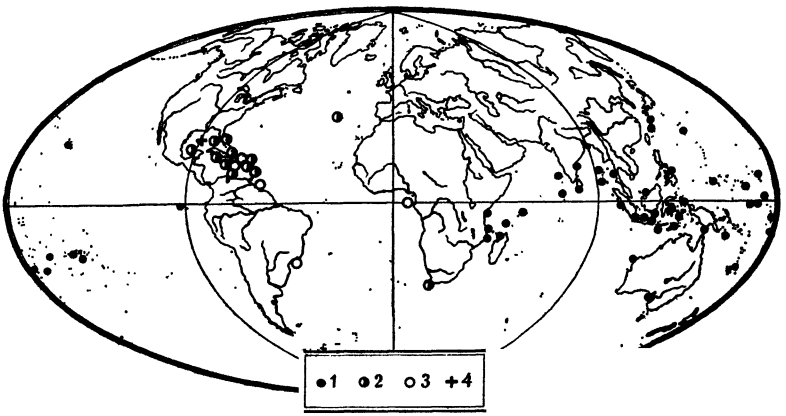


FIG. 1.—Distribution of *Holothuria atra* and its varieties. 1. var. *atra*; 2. var. *floridana*; 3. var. *grisea*; 4. var. *nitida* from a single locality in the Gulf of Mexico. (After Panning, redrawn.)

water zone. Many of them occur in all main divisions of this zone, that is, the Atlantic, the Indo–West-Pacific and the East Pacific, and are thus *circumtropical*; this term is applicable only to those animals which occur in every one of these three divisions and, as regards the Atlantic, preferably both on the African and American side. Such a circumtropical distribution is not only to be found among many genera and higher taxonomic groups but also among several species. Such are, to mention only a few examples, *Holothuria atra* (fig. 1), the brittle-star *Amphipholis squamata*, which also occurs in the temperate zone, the crabs *Grapsus grapsus*, *Planes minutus* and

Plagusia depressa, which often attach themselves to floating seaweed, driftwood and even swimming turtles and medusæ and thus may be conveyed passively over wide pelagic areas—an example of the importance of animal habits for zoogeography. Of circumtropical fishes we may cite *Zygæna malleus*, the hammer-head shark, and the porcupine-fish *Diodon hystrix*, disregarding the more particularly pelagic species. Nearly all the marine turtles (*Chelonia mydas* and *C. imbricata*, *Caretta caretta*, *Dermochelys coriacea*) provide further examples. But of the enormous numbers of tropical species the circumtropical represent only a tiny fraction.

With these brief remarks we may leave the question of circumtropical distribution for the moment; we shall return to it again when we discuss the history of the warm-water fauna. We now turn to two associations of animals which occupy a dominant position in certain parts of the tropics, namely the coral reefs and the mangrove swamps.

Coral reefs

Coral reefs are found only in the tropics and flourish best in areas where the mean annual water temperature rises to at least 23·5° C. Where the temperature in the colder season falls below 20° C. no reef formation of any size occurs. But temperature is not the only determining factor. On the west coasts of Africa and America the temperature is not too low, but the reefs are nevertheless poorly developed; this has been considered to be due to upwelling water or the lack of suitable bedrock. In other regions, for instance in India, large stretches of the coast are free from reefs without any plausible explanation having been suggested. But on the whole coral reefs are so characteristic of the tropics that the northern and southern extremes of their occurrence may be regarded as constituting the boundaries of the tropical zone (fig. 2).

The big reefs are, however, not always mainly formed by corals. In many places, coralline algæ of the genera *Lithothamnion*, *Halimeda* and others are quantitatively as important or even more important, while the Foraminifera, too, often predominate quantitatively. In the well-known deep boring executed on Funafuti (see p. 9) Foraminifera were found to be the quantitatively dominant reef builders, followed by coralline algæ, the corals being only third in importance. Limestone reefs, where no corals at all are found, also exist. In such cases, the name "coral reef" is misleading.

Apart from the temperature there are other factors which influence reef formation. The corals are typical inhabitants of shallow water, reaching their optimum development in water of less than

30 m. depth. The new formation of reefs stops at a depth of about 50 m. This partiality for the upper layers may be due to the fact that corals live in symbiosis with small algæ. At low tide large areas of the reef are above water. Clear water and high salinity are other vital factors for corals, and they are therefore unable to live where large rivers flow into the sea.

It must be emphasized that the same species of corals which form the great reefs occur also outside the coral zone proper but without combining to produce large formations, for instance in West Africa, South Africa and Japan.

The importance of the coral reefs for animal geography lies not only in the fact that they constitute gigantic biocœnoses of their own which characterize a distinct zoogeographical region, but also

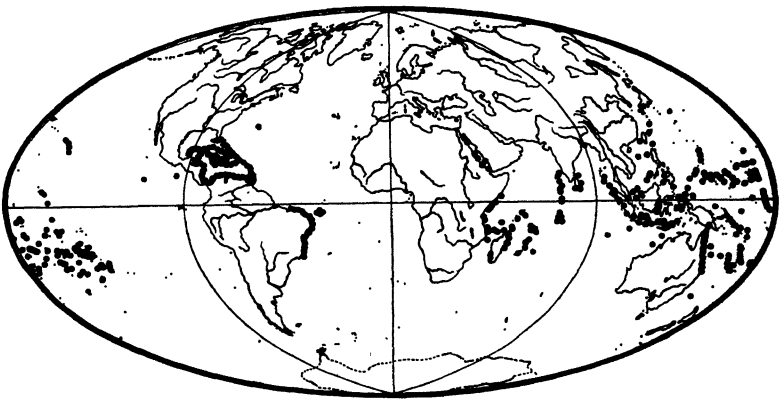


FIG. 2.—Distribution of reef-corals, omitting occurrence of reef-corals without reef formation. (Mainly after G. Schott, 1926, 1935.)

because they are the habitat of a special fauna of great variety. No other animal association can compare in this respect with the coral reefs in zoogeographical importance.

In describing this biocœnosis we may begin with the small unicellular algæ which we have just briefly mentioned, the zooxantellæ, most of them belonging to the flagellate group Cryptomonadinæ, some probably to the Dinoflagellata. Similar small algæ have been found to occur also in company with cœlenterates other than corals, e.g. hydrozoans, medusæ and anemones, and also in other animal groups (radiolarians, molluscs, ascidians), but from a general biological point of view their regular and abundant occurrence in the corals is the most important. In this case they live intracellularly in the ectoderm and it may be regarded as proven that they are of vital

importance to the corals in providing oxygen (not, however, assimilates, as was once believed). On the other hand, they receive from the corals carbon dioxide, nitrogen, phosphorus, etc. (Yonge & Nicholls;[593] Yonge.[592]) The preference of corals for the upper layers of water and for clear water is probably connected with the fact that the zooxantellæ need light for photosynthesis.

A hydrozoan which appears as a reef builder, thanks to its considerable calcium precipitation, is the athecate hydroid genus *Millepora*, which superficially resembles an ordinary colony of corals. Among the Alcyonaria, too, there are two reef-building genera, each forming a family of their own, *Heliopora* and *Tubipora* (organ-pipe corals).

The other animals found on the reef make use of the advantages offered by the reef-building species: a firm basis for attachment, cavities for protection, the rich hunting ground it provides, the calciferous sediment for digging themselves in, the loose limestone of the corals easily penetrated by boring or corroding. Only a few examples of the various animal groups inhabiting the coral reefs can be mentioned here.

The sea-anemones are represented by the large species of the genera *Discosoma* and *Actinodendron*, the Octocorallia by the fleshy alcyonarians *Sarcophyton*, *Lobophytum* and *Sinularia* which thickly carpet large stretches of the reefs, the polychæts by the well-known palolo worm (*Eunice viridis*) from Samoa, Fiji and the Gilbert Islands, large multi-coloured turbellarians and nudibranch molluscs in a rich variety of species. Small lamellibranchs (*Lithophaga*, *Lithodomus*) eat their way into the coral chalk and the giant *Tridacna* sits there encased in limestone peeping out of an opening. The snail *Magilus antiquus*, which lives inside the *Mæandrina* coral colonies, lengthens the last convolution of its shell in a straight line during growth and thus keeps pace with the increase in thickness of the corals.

Among the large number of crustaceans of the coral reef there are those which are more or less confined to the reef, such as many species of the families Xanthidæ (*Trapezia*, *Leptodius exaratus*, stated to be "the most common of coral-crabs in the Indo-Pacific" and others) and Pinnotheridæ, as well as the family Porcellanidæ of the Anomura. The most peculiar example of a biocœnosis with corals is provided by the circumtropical family Hapalocarcinidæ, where the three genera *Hapalocarcinus*, *Troglocarcinus* and *Cryptochirus* live in the galls which they cause to develop on the branches of the corals. They have been so transformed by their mode of life that it is very difficult to determine their systematic position. Even a prawn, *Paratypton*, has adapted itself to a similar mode of life.

Sea-urchins belonging to the genera *Diadema*, *Eucidaris*, etc., live in the hollows of the coral limestone, and holothurians (*Holothuria*, *Stichopus*) live in large numbers in the calcareous mud of the reefs.

Not the least interesting section of the coral fauna is represented by the fishes. Coral fishes are to be found among most tropical fish families. Most of them are highly coloured. Here we find the majority of the roughly 200 species of the family Chætodontidæ, which, because of their vivid colouring, are generally known as butterfly-fishes. They possess sharp, bristle-like teeth and often an elongated snout with which they can pull out smaller animals from the holes in the coral rock. The genera *Chætodon*, *Holocanthus*,

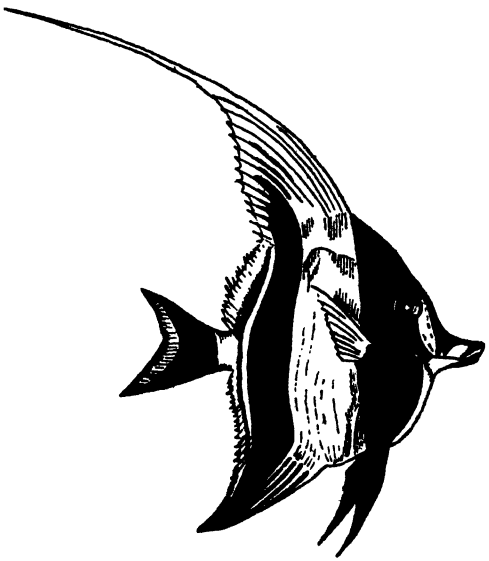


FIG. 3.—A "butterfly-fish" *Zanclus cornutus*. Distribution: Japan, Hawaii, Polynesia and the Pacific coast of Mexico. A second species of the genus was discovered in the Italian Eocene. (After D. S. Jordan.)

Pomacanthus and *Angelichthys* may serve as examples of butterfly-fishes. Other coral fishes are the Moorish idols (*Zanclus*) (fig. 3), the surgeon-fishes (*Acanthurus*) and the trunk-fishes (*Ostracion*), the file- or trigger-fishes (*Balistes*, *Monacanthus*) and the gorgeous genera *Scarus*, *Sparisoma*, etc., as well as the family Labridæ, most of whose species live in the tropics, and the closely related genera *Julis*, *Thalassoma*, *Gomphosus*, *Halichæres*. Other families containing large numbers of coral fishes are the Pomacentridæ, Blenniidæ and Serranidæ.

Many of these coral fishes have large, sharp front teeth whose gnawing capacity is greatly increased by their being more or less fused to form a single tooth plate. They are thus able to gnaw through the coral limestone in their search for food. A large number of invertebrates, too, play an important part in the history of the reef's development because of their effect on the limestone, which suffers decomposition on a considerable scale. Soundings undertaken in the vicinity of coral reefs have shown that each reef has an outer belt of loose chalk sediment. Around the atolls, coral sand and coral chalk mud descend to a depth of as much as 2000 m. The material of this sediment was first produced in the live upper parts of the reefs.

The origin of coral reefs and their history have been much discussed. We shall confine ourselves here only to those aspects which concern zoogeography.

As is well known, the first comprehensive theory was put forward by Darwin,[109] after he had acquired first-hand knowledge of the coral reefs on his voyage round the world in the "Beagle". He started from the supposition that reef-building corals are exclusively shallow-water animals. The fact that a reef often grows from considerable depths, where corals are unable to live, he explained by assuming that such reefs began as coastal reefs, which, because of the subsidence of the sea floor, were forced to constant upward growth. This would explain the peculiar shape of atolls. Darwin brought the three main forms of the reefs, the fringe, barrier and atoll reefs, into causal relationship with one another by explaining the barrier reefs as former fringing reefs which through the subsidence of the land had increased their distance from the coast. The atolls he regarded as one-time fringing reefs around an island which later sank below the surface of the sea. If the floor subsides so quickly that the building activity of the corals cannot keep pace with it, its development will be interrupted. In actual fact there do exist examples of such "drowned" reefs. One of these is the well-known Chagos archipelago in the Indian Ocean. It consists of scattered small coral islands which rise from a 10–15 km. wide ridge enveloping a considerable area of from 150 to 200 km. diameter and with an average depth of from 70 to 80 m.

The well-known American geologist and zoologist Dana supported Darwin's theory in 1849. But since then different views have been put forward by Semper, Alexander Agassiz and others. In a review of all theories and hypotheses which had been put forward up to that time, Langenbeck[296] sided with Darwin, since his theory provided the most generally valid explanation, while his opponents were more concerned with exceptions, and the same view was put

forward by others.[112, 113, 293] A striking confirmation of Darwin's theory was furnished by the results of the deep boring undertaken by The Royal Society of London in 1897–98 on the atoll of Funafuti (north of the Fiji Islands) which rises from a depth of 5400 m. The borings were continued down to a depth of 334 m. and showed that the constitution was the same in the lowest part of the reef as on the surface; *inter alia*, the part played by the Madreporaria was no less evident in the structure of the deeper parts than on the surface. The borings thus proved that the sea floor had subsided at least 300 m. and probably considerably more. The coral reefs of the West Indies have, however, a different history in certain ways from those of the Pacific.

In the Quaternary glacial period an interruption in the earlier development of the coral reef took place, probably due to climatic conditions but also to another cause. The retention of precipitation around the poles in the shape of firm ice caused a lowering of the ocean's surface which was greater in the tropics than elsewhere because the polar ice masses attracted water from the equatorial regions. The consequences of this lowering of the surface of the water and the following post-glacial rise were made clear by Daly[104] in his "glacial control theory". In another direction, too, Darwin's theory has been supplemented. It is now considered probable that the reef-building organisms themselves may cause a subsidence on the sea floor by precipitating the soluble lime contained in the sea-water in the form of coral limestone. The loss of limestone debris from the reefs, which is washed out and forms a sediment in the vicinity, amounts in the course of time to considerable quantities. It has been calculated that in a group of islands of the size of the Maldives limestone production at the present rate would in 368,000 (minimum)–1,960,000 (maximum) years reach an amount sufficient to overcome the solidity of the earth's crust and cause isostatic subsidence. In geological terms the time mentioned is not particularly long, because 1,960,000 years ago the earth was at the end of the Pliocene period and 400,000 ago it was in the middle of the Pleistocene (Quaternary) period (see table 9 p. 66).

The mangrove fauna

Along nearly the entire tropical coastline we find mangrove formation, but only on sites which provide ground favourable to the mangrove trees, which are species of the genera *Rhizophora*, *Avicennia* and others. These grow on swampy sea coasts where there is a rich sediment of loose mud. From this mud the aerial and stilt roots shoot up into the air and among them many animals find hiding-places or burrow into the loose ground which is

alternately covered and uncovered by the ebb and flow of the tides. In the mud of the floor, made foul by dead organisms, there thrive land, fresh-water and marine animals, great in numbers but few in species.

The marine animals are in several respects specially adapted for life in this peculiar environment. They are able to tolerate considerable variations in salinity, i.e. they are euryhaline. They are amphibious, living both in air and in water; many of them are mud-eaters and live in holes which they dig; others again live during low tide on the surface, such as for instance several species of oysters, among them *Ostrea glomerata*, often found attached to coral limestone, as in the Great Barrier Reef of Australia. But this species also forms large colonies among the roots of the mangrove and thus gives rise to the sailors' stories of the oysters which grow on trees. A fish, too, the well-known mud-skipper, *Periophthalmus kœlreuteri*, belongs here. It is as much a land as a sea animal and can actually climb short distances along the stilt roots. The crabs of the mangrove fauna are made up principally of species of the genera *Uca*, *Sesarma*, and *Sarmatium*; there are also members of other groups of crustaceans, such as the anomuran genus *Thalassina*, and among the hermit crabs *Cœnobita*. The well-known king-crab, *Tachypleus gigas* (=*Limulus moluccanus*), inhabits the mangrove swamps and other soft coastal floors of the Indo-Malayan archipelago.

After this short survey of the general conditions in the warm-water zone we now pass on to the various main regions.

CHAPTER II

MAIN REGIONS OF THE WARM-WATER FAUNA OF THE SHELF

In view of the more or less close relationship existing between the shelf faunas of the various warm-water zones of the oceans we are able to divide these faunas into two main regions—the Indo-West-Pacific and Atlanto-East-Pacific.

1. INDO-WEST-PACIFIC

The greatest wealth of animal life is to be found in a region which contains the tropical and subtropical portions of the whole Indian Ocean and the western and central part of the Pacific. This region may conveniently be called Indo-West-Pacific.[145, 146] The name is intended to indicate that the warm-water fauna of the Pacific within the region of the shelf does not constitute a single unit, but that the American part belongs to another main region, the Atlanto-East-Pacific.

For reasons which will be discussed later, the Indo-West-Pacific may be defined in the following way; in the west the east coast of Africa provides a natural boundary stretching from the Red Sea down to South Africa a little south of Durban. In the north-east, on the eastern coast of the Asiatic mainland the northern limit lies roughly in the Korea Strait, while on the north-western coast of Japan the boundary may be placed even further north, and on the oceanic coast of Japan it lies east of Tokyo. In the east, the furthest outposts are Hawaii, the Marquesas Islands and the Tuamotu (Paumotu) archipelago; in the south the limit may be placed on the east coast of Australia roughly around Sydney and on the west coast south of Sharks Bay. New Zealand lies outside the warm-water zone. It need not be emphasized that the said "boundaries" are far from being sharply defined. They are, as in all similar cases, transitional and mixed zones rather than boundaries in the strict sense.

General characteristics

The general abundance of animal life in this region, its independence and geographical delimitation have been attested by accounts of numerous zoological expeditions. Here we can mention only a

few of the findings derived from the general surveys. In so doing we shall be particularly concerned with phenomena which serve to mark the eastern boundary of the fauna.

For the sponges of the group Cornacuspongida this region is regarded as harbouring most species,[222] and the same is true of the Madreporaria. Among the specifically Indo-West-Pacific genera special mention must be made of *Fungia* (fig. 4), which, together with four other genera, forms a special family whose 46 species, except for one, *F. elegans* from western America, are confined to

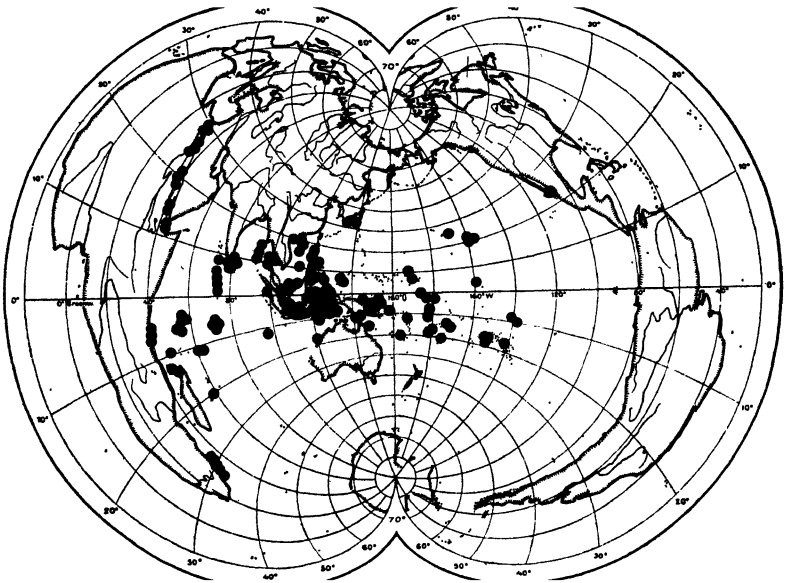


FIG. 4.—The distribution of the coral family *Fungiidae* (5 genera with about 46 species). Only one species, *Fungia elegans*, is to be found in America at three localities on the west coast of Mexico.

the Indo-West-Pacific zone. The same distribution also holds good for the coral genera *Seriatopora* and *Goniopora*. Crossland, who had personal knowledge both of the Central Pacific and the West American coral reefs, stresses the clearly marked difference between the two:[93] "The corals afford a striking example of the contrast between the two main regions"; and he therefore designates the two regions mentioned as "two contrasted oceanographical regions". The same view was expressed by Bigelow[47] as regards the medusæ (which at one stage of their development are coastal animals). As regards the distribution of the Octocorallia, all nine families of the

Alcyonaria are to be found in the Indo-West-Pacific, three of them exclusively there, among them the Helioporidæ, which in their appearance resemble Stony Corals. Purely Indo-West-Pacific are also the alcyonarian genera *Sarcophyton*, *Lobophytum* and *Sinularia*, which are to be found growing over large stretches of the surface of coral reefs. They do not reach further east than Polynesia (fig. 5). The same is roughly true of the Gorgonaria, too. All 12 families of this order are represented in the Indo-West-Pacific region, two of them and several genera being found exclusively there, among them the well-known *Isis*.[294] The same distribution is found among a number of Pennatularia.[235] The polychætes, which are to a large extent cosmopolitan and therefore generally do not throw much light on regional zoogeography, also show the boundaries between

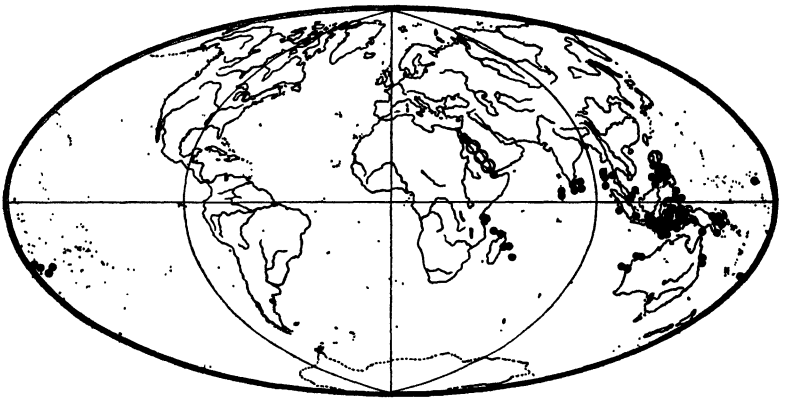


FIG. 5.—Distribution of the Alcyonarian genus *Sarcophyton*. The open circles mark finds not precisely indicated.

the West and East Pacific, which is a good indication of the effectiveness of this boundary. Hempelmann[219] states that although the polychæt faunas on both sides of Central America greatly resemble one another and contain much the same species, yet the deep zone in the eastern Pacific forms a barrier which has prevented Polynesian polychætes from spreading to the American coast.

The region's molluscan fauna has been estimated at 6000 species. Simroth[481] enumerates a large number of species which live entirely or almost entirely in the large Indo-West-Pacific region and a large number of genera, too, are exclusively domiciled there. Among them are many familiar as decorative objects, such as, for instance, *Hippopus*, *Tridacna*, *Malleus*, as well as *Nautilus*, the only surviving representative of the tetrabanchiate Cephalopods. Twenty-six

molluscs (among them only one lamellibranch) are found in identical development also on the tropical-subtropical coast of America or the neighbouring islands, or else they are represented by subspecies or "analogous" or geminate species[231] (cf. p. 30). But in relation to the very large total of West-Pacific molluscs the 26 mentioned represent an insignificant percentage. Of crustaceans, the decapods provide excellent testimony for the region's zoogeographical independence and wealth of species. There are about 100 endemic genera, among them many with large numbers of species. A number of groups of a higher taxonomic order are also endemic, for instance the sub-family Polydectinæ, which are well known for their habit of carrying actiniæ on their chelæ. Among the endemic species, too, many are distributed over the whole of this immense area: for instance, the swimming crab *Neptunus pelagicus*, which is found from Africa to Tahiti and is known for its size and edibility, and the robber- or coconut-crab *Birgus latro*. It is the pelagic zoëa larva which has made the widespread distribution of this land crab possible. Its furthest limits are formed by the islands on Africa's east coast, Madagascar, the Riu-Kiu Islands, New Caledonia and Tuamotu Islands, and the crab inhabits even such remote islands and groups of islands as the Chagos, Mauritius (now extinct), Marshall, Ellis, Cook, Tahiti, Gambier, Tuamotu, Marquesas and Fanning Islands.[438] A third widely known crab species from the coasts and the island groups of the Indian and Pacific Oceans is the spiny lobster *Panulirus japonicus* (East Africa–Japan–Tahiti). Of the crabs of the Red Sea no fewer than 30% are also to be found in Hawaii.

Among the rest of the arthropods we may mention the stomatopod crustacea, which because of their prolonged larval stage have been able to spread over the whole enormous area from Africa to Hawaii and Tahiti (*Squilla nepa* and others); and of the class Xiphosura the sub-family Tachypleinæ with the two genera *Tachypleus* and *Carcinoscorpius*, which are endemic in the region but do not inhabit the extreme boundary zones.

We now come to the echinoderms. All families and sub-families of crinoids are represented in the Indo-West-Pacific with the exception of the monotypic West-Indian Holopidæ. The group Comatulida, which in contrast to the stalked crinoids inhabits for the most part coastal waters, comprises 14 families and about 70 genera, of which 6 and about 45 respectively are exclusively Indo-West-Pacific. The starfishes, brittle-stars and sea-urchins may be treated together here. The Indo-West-Pacific houses about 550 purely tropical or subtropical species. Apart from the circumtropical brittle-star *Ophiactis savignyi* only five species, that is not quite 1%,

are found on the West American coast. Of the endemic species 38 inhabit the Indo-West-Pacific region in its entirety, from East Africa or the Red Sea to Hawaii and Outer Polynesia; for instance, the well-known sea-urchin *Diadema setosum* (East Africa-Tahiti). Of about 120 exclusively warm-water genera in this region, 72% are endemic and only 5% are also represented in West America. The geographical position of the sea-urchin family Temnopleuridæ with its 80 species has been described by Mortensen in the following words: "The Temnopleurids are almost exclusively confined to the tropical and subtropical regions of the sea, excepting only the West American region, where not a single Temnopleurid is found."

Hartmeyer[211] says of the ascidian fauna of Polynesia that it is in the main connected with the fauna of the Indo-Malayan archipelago and he adds that there are no known instances of a connection with the tropical west coast of America.

The fish contribute largely to the homogeneity of the region. This is doubtless due to the fact that even pronounced coastal forms among them are able to be transported by the ocean currents over wide stretches of pelagic regions. Not only in the larval but also in the adult stage a fish has about the same specific gravity as water and there is no risk of a coastal fish sinking to a depth which would be fatal if it is carried away from the coast by an ocean current. There are thus great possibilities of its passive disposal to remote coasts. Chance, therefore, plays a larger part in the possibilities of distribution for the fishes than for most other shelf animals. The investigations carried out by ichthyologists provide many examples of this. Thus Schmidt[467] found that 166 (=36%) of the fish species near the Riu-Kiu Islands are found distributed over an area from the east coast of Africa to Polynesia. Günther, as long ago as 1886, expressed an opinion which still seems valid: "Die Zahl der Arten, die von dem Rothen Meere und der Ostküste Afrikas bis nach Polynesien, selbst bis zu dessen östlichsten Inseln reichen, ist in der Tat sehr gross. Dennoch erreicht diese Indo-pazifische Fauna die pazifische Küste Südamerikas nicht." The last sentence is particularly noteworthy. Examples of its general validity have also been provided by later authors. Weber[578] maintains, in connection with work on the material from the "Siboga" expedition, that the Indo-Pacific fish fauna does not extend further east than Hawaii and the Tuamotu Islands. Further east the East Pacific forms a barrier which is only surmounted by very few species. Jordan & Evermann (1898) have demonstrated that the superfamily Labriformes is represented in West America by different species and even genera than in the islands of the Pacific. For a résumé of older and more recent information with regard to the fish fauna of the shelf we may quote the views

expressed by G. S. Myers in 1940. He maintains that the Indo-West-Pacific contains practically all the families and a considerable number of genera of the tropical fish fauna of the world within the region of the shelf (only four families, and they contain few species, are missing) and that this region houses many families and genera not found elsewhere. The fish fauna of the Indo-West-Pacific is very much richer than that of the rest of the main tropical regions—the West Indies, the Panama region and West Africa. The position of tropical Pacific America Myers characterizes by saying that the fauna of Panama is "trenchantly distinct from the Indo-Pacific. The fact that a few Indo-Pacific shore forms have reached the Galapagos, Cocos and the Revilla Gigedo Islands and still fewer have gotten to the American mainland, is of little consequence."

Among the reptiles, too, we find a family which is very characteristic of the Indo-West-Pacific, namely the sea snakes, Hydrophidæ.[333, 486] They are so well adapted to marine life that from a zoogeographical point of view they come under the same heading as water-breathing sea animals. The family, which contains 15 genera and more than 60 species, ranges from Africa over the whole Indian Ocean and Pacific, but only one single species, *Pelamydrus platurus*, has been reported from West America. Finally we may mention in this connection a small group of sea mammals, the genus *Dugong* (=*Halicore*) among the Sirenia, whose three species inhabit the region stretching from the Red Sea and Madagascar to Australia, New Guinea and possibly southern Japan.

Subregions

In so extensive a region as the Indo-West-Pacific, homogeneity can only be relative. It is possible to distinguish several subregions, but the present incomplete knowledge of faunistic facts does not allow as yet any precise delimitation of the various subdivisions. In fact it is only in a few cases that the evidence is at all decisive for a division into subregions. The following division must therefore be regarded as merely provisional, in general merely marking out certain faunistic centres of distribution or certain regions which show marked divergences.

The Indo-Malayan region

The faunistic centre of this region is the Malay archipelago. Assuming that the coastal fauna of the Philippines and south China is in the main conformable to that of central Malay, as seems reasonable, we can situate the north-eastern boundary in the northern part of the Riu-Kiu Islands, i.e. between the northern Linshoten Islands and the rest of the islands. Balss[28] states that a sharp dividing-line

exists here as regards the distribution of crabs, since 70 tropical species stop short at this line. The most northerly coral reefs are also to be found here, which means that it is also the northern limit for many coralophile animals. Jordan[266] describes the fish fauna of the Riu-Kiu Islands as in the main East-Indian because the species are the same as off Java or Celebes, and the results of Schmidt's[467] investigations point in the same direction. For the mainland the boundary is said to lie off the province of Chekiang.

In the south the boundary runs between the Kei and Aru islands, of which the first-mentioned belong to the Malay and the latter to the Australian zone. As is the case in some other regions, too, the 1000-m. depth-contour provides here the dividing-line.[82, 151, 432] However, different groups of animals show divergences in this matter and we may leave the question open whether it is a dividing-line between two main regions or between two subdivisions of a large Indo-Australian main region (see p. 26).

The Indo-Malay archipelago is the world's greatest archipelago and contains large areas with a depth of less than 200 m. It is therefore not unexpected that an abundance of animal forms should have developed here, no region in the world being so rich in species. A list of the most important animal groups will, therefore, be a repetition of what we have already said, and we can confine ourselves to certain items, while for the fauna as a whole we may refer to the results of expeditions which have made collections in this region, as for example the expedition of the "Siboga" led by M. Weber and the expeditions of the "Investigator" based on Calcutta; their collections, however, were mainly of deep-sea material.

Döderlein,[129] as a result of his investigations on the ophiuroid group Euryalæ, delimited a region characterized by its extraordinary richness in species to which he gave the name Ambonesian after one of the Molucca Islands, Amboina, which has become renowned as the locality of pioneer investigations on the Malayan animal world. The Ambonesian region includes, according to this author, the Philippines, the Moluccas, the small Sunda Islands and Celebes, and is therefore equivalent to the Wallacea archipelago in terrestrial zoogeography. This view was upheld by Mortensen[352] on the basis of the distribution of certain sea-urchins. A. H. Clark[79] in his monograph on the crinoids of the Indian Ocean states that the greatest abundance of genera and species in this group is to be found within the triangle Luzon–Borneo–New Guinea and that this group of animals may serve as a zoogeographical indicator, although they are individually restricted in their distribution since they have a very short larval stage and are sessile during the later stages. A large number of the species of this group live, however, in

deep water. A list of the fish fauna of this region was compiled by Fowler.[167, 168]

A comparison between the Indo-Malayan and the other subdivisions of the Indo-West-Pacific region brings out clearly the fact that the first-mentioned is the centre and focus from which the others recruited the main contingent of its fauna. The further one moves away from this centre in any direction, the more the fauna appears as a progressively impoverished Indo-Malayan (Indo-Australian) fauna, where the addition of endemic elements only to a minor extent makes good the loss of Indo-Malayan forms. The other faunas occupy marginal regions which can therefore not be ranked with the Indo-Malayan central region in zoogeographical importance.

The islands of the Central Pacific excluding Hawaii

The impoverishment which we have just mentioned also distinguishes the region east of the Indo-Australian centre. The coastal fauna of the Pacific Ocean islands in question is, however, only imperfectly known. We do not know, therefore, where the boundary marking it off from the Indo-Malayan central fauna should be drawn, nor do we know whether there is in fact any definite border or transitional zone or whether the transition is gradual and uniform. It may seem *a priori* probable that the boundary of the fauna coincides with the eastern limit of the ancient continent which geologists suppose to have had its most eastern outposts in the Tonga and Fiji Islands, the Solomons and Bismarck archipelago (Schott[472] p. 50), and which included Melanesia. But as yet there are no faunistic facts to support this theory. For instance, as far as the echinoderms are concerned, a detailed examination has shown that the divergences between the Indo-Malayan archipelago and Melanesia are on the whole greater than between Melanesia and Micronesia (Marshall, Gilbert, Ellice and Samoa islands), which lie on both sides of the boundary of the ancient continent, the so-called Andesitic line. This is true for the distribution of both genera and species.

The zoogeographical position of the region may be made clearer by the following extracts from faunistic literature.

Little is known, says Crossland,[94] of the distribution of corals in this region except that the fauna becomes poorer in the east. The number of species in Samoa may be estimated at about two-thirds of that of Northern Australia. Even the very modest coral fauna in the Marquesas Islands, which are lacking in reefs of any great size, is only an offshoot of the western fauna and shows no affinity with that of the Panama region. In Tahiti 16 genera are missing which are

to be found in Samoa or Fiji, among them the well-known *Seriatopora, Euphyllia, Symphyllia*, etc. One of the reasons for this may be that the ocean currents run in the main from east to west.

But this poverty is less marked for several animal groups; in particular the fish fauna might even be called rich. An imposing amount of material has been examined by Günther and Jordan. In 1905 Jordan & Seale listed 475 species of fish from Samoa of which 92 (or 19%) were new to science although they belonged to Indo-Australian genera. All these species were collected on coral reefs. The great number of endemic species among the Samoan fish fauna which we have just mentioned suggests that the present faunistic connections between Polynesia-Micronesia and the Indo-Australian centre of distribution are rather weak. The isolation has lasted so long that new species have been able to develop. But a number of species which at first were regarded as endemic in certain groups of the South Sea islands have later been shown to exist also in other regions.

Hawaii

In spite of their fairly considerable faunistic resemblance with the South Sea islands just discussed the islands of Hawaii must be distinguished from them because of the relatively large numbers of endemic forms.

The reef corals have been investigated by Vaughan.[566] They are closely related to the west of the Indo-West-Pacific coral fauna and contain practically no endemic genera. Many reef-builders which are common further to the south-west are missing in Hawaii, for instance the whole families Oculinidæ, Eusmiliidæ, Astrangiidæ, Mussidæ, Faviidæ, while the genus so characteristic of the Indo-Malayan coral reefs as *Acropora* (=*Madrepora*) is sparsely represented.

Of the molluscs, whose distribution has been summarized by Edmondson,[135] the majority shows affinities with the rest of the Indo-West-Pacific as regards genera, while the species, especially the mussels, are largely endemic. A number of species common to both Hawaii and western America are also to be found, but they only represent a small percentage of the large total (see p. 14).

The same picture of distribution—a distinct kinship with the rest of the Indo-West-Pacific fauna but with a fairly high percentage of endemic species and a very slight affinity with the West American fauna—is also exhibited by the rest of the animal groups whose occurrence in the Hawaiian fauna has been closely examined, e.g. among the crustaceans the Brachyura and Macrura as well as echinoderms and fishes. Many species of crustaceans are found from the

Red Sea to Hawaii. Edmondson[135] has shown, on the basis of his and Miss Rathbun's investigations on the crustacean fauna, how the closeness of the relationship with the south-western part of the Pacific decreases, and the similarity to Hawaii increases as regards the isolated oceanic islands the further to the east they are situated. Thus Wake Island shows a strong affinity in both directions, while Johnston Island, which lies nearer to Hawaii, has only 10% south-west Pacific, and 90% Hawaiian elements in its crustacean fauna. The same is true of the echinoderms according to H. L. Clark,[85] who together with W. K. Fisher[162, 163] has considerably added to our knowledge of these animals in the Pacific. Of the exclusively warm-water species of starfishes, brittle-stars and sea-urchins found in Hawaii, some 74 in number, 36% are endemic, and of the 43 Hawaiian warm-water genera of the same echinoderm groups distribution all are found in the Indo-Malayan region, except for three endemic forms.

The fish fauna of Hawaii has been investigated by several authors [167, 230, 266, 368, *et al.*] It agrees in its general zoogeographical aspect with the aforementioned animal groups, but it seems to be less well provided with endemic species than these, while the West-Pacific traits are possibly more pronounced. Thus of the fish found in the Riu-Kiu Islands 68 species (=15%) are also found in Hawaii.[467] This is due to the ability of most fishes to make use of the ocean currents for transport, as has already been pointed out. A proof of this is that the isolated Marcus Island, situated 1300 km. from the Mariana and Bonin Islands, has a typical south-east Asiatic fish fauna and that a small number of fish species of pronounced West-Pacific origin have been able to spread to the Galapagos Islands, some other islands off tropical America and even to the mainland waters. Such species are to be found, for instance, among the porcupine-fishes (*Diodontidæ*), which are able to inflate themselves and to drift about passively on the surface of the sea; among the pipe-fishes (*Syngnathidæ*) and the puffers or globe-fishes (*Tetrodontidæ*). On the other hand among the sharks, which lack pelagic stages of development, none of the purely coastal species has reached the Hawaiian group.[151]

In a comparison between the fauna of Hawaii and that of the Pacific region special attention must be paid to Hawaii's position with regard to America. The distance from America is certainly very considerable, but no greater than from the nearest larger island groups in the South Sea and much less than the distance from Japan. It might therefore be supposed that the affinity of Hawaii's fauna with the American shelf fauna, to which the fauna of the Galapagos Islands belongs, would be as close as its relationship to the Japanese

or Polynesian fauna. In fact the fauna of the Galapagos has been grouped with that of Hawaii and outer Polynesia as "Eastern Polynesian" fauna. But nature herself contradicts such an arrangement. Both the above-mentioned groups and also many other groups of animals exhibit in their distribution a much nearer relationship between Hawaii and the western Pacific than between Hawaii and America (see p. 15). Thus of the 43 exclusively warm-water genera of echinoderms which we have mentioned, 40 appear in the Indo-Australian region but only 17 in western America, and of the 70 tropical starfish species none lives in America. On the other hand four sea-urchin and brittle-star species occur in both regions; one of these, however, is circumtropical. They represent barely 5% of the total number of tropical species in Hawaii. The broad belt of the eastern Pacific which, being bare of islands and with an uninterrupted abyssal region, divides Hawaii and Polynesia from America (with the Galapagos) clearly forms an effective barrier to dispersal. This *East Pacific Barrier* will be discussed later.

The migrations to the islands of Hawaii and other isolated islands of the Pacific can be imagined as having taken place in different ways. Under present geographical conditions active migration is possible only for species which are able to endure conditions in the wide abyssal zone which surrounds these islands, but this is quite out of the question for the tropical shelf animals which are here under consideration. Passive migration is, however, possible for some of these species. Several possess planktonic larval stages, but on the whole the planktonic stage is too short to account for a dispersal over thousands of kilometres. For a small number such a possibility remains open, but our knowledge of the duration of the larval stages in most animals is very meagre (see p. 12–16). The mode of distribution practised by a larger or smaller number of species is without doubt drifting attached to seaweed or other floating material. A number of animals, for instance many snails, mussels with byssus, brittle-stars, starfishes, sea-urchins, polychæts, ascidians, bryozoa, hydroids, normally live attached to seaweed. Any other mode of traversing wide stretches of ocean is hardly conceivable for such animals as the brittle-star *Amphipholis squamata*, which is viviparous and thus lacks a planktonic stage, yet despite this it is distributed from the Red Sea and South Africa all the way to Hawaii and the Society Islands (and West America, where it might have arrived by circumnavigating South America; it is found also at the southern tip of South America and in the Atlantic).

In whatever way the distribution may have taken place, it is clear that even small and widely dispersed oceanic islands between the Asiatic mainland and Hawaii have played a part in populating

the Hawaii Islands. The Kuroshio Current may also have helped. A further factor is probably to be found in the fact that the coastline of the mainland lay further to the east during the Tertiary period and thus influenced the ocean currents at that time.

Subtropical Japan

The Japanese marine fauna has long been regarded as one of the most interesting, and at an early date it became the subject of zoogeographical discussions, among other things because of certain similarities with the fauna of the Mediterranean. At present it is one of the best known among the Asiatic coastal faunas.

It must, however, be strongly emphasized that Japan does not constitute a unity with respect to its fauna. It consists of a northern and a southern part which belong to two different zoogeographical regions. For all animal groups which have so far been investigated with regard to their distribution around Japan it holds good that there is a northern group of species on the oceanic side of the islands extending in the main to about 36° N., while a southern group of species has its northern boundary on about the same degree of latitude, that is east of Tokyo and Yokohama. Sagami Bay thus belongs to the southern Japanese, the northern Hondo (for example Sendai Bay), the Tsugaru Strait and Yezo to the northern Japanese region, which is temperate. On the inner side of the islands, in the Sea of Japan, which is for the most part dominated by the cold Oyashio Current, the boundary between the two zones is quite indistinct and lies somewhat to the south, about the northern part of the Korea Strait.

The position of these boundaries, or rather transitional regions, is due to hydrographical circumstances. Japan receives warm water from the south by means of the ocean current Kuroshio, whose main mass passes the south-eastern coast, while a smaller branch forces its way through the Korea Strait into the Sea of Japan and is there called Tsushima Current. At the large bend of the coast east of Yokohama the Kuroshio leaves the coast and flows out into the open sea under the influence of the cold Oyashio or Kuril Current, which comes from the north and here wedges itself between the land and the Kuroshio. The latter has an August temperature of 25–28°C. and a February temperature of 11–17°C. off the south-eastern shore. The difference between the summer and winter temperature is greater (10–14°C.) than in most of the other warm-water zones, and in the boundary zones between the two antagonistic streams, according to which of the two preponderates, the temperature may vary a great deal within a short time. In one and the same locality one may meet warm-water plankton in 0–50 m. depth, but a pronounced

cold-water plankton at a depth of 200–400 m. In the Sea of Japan the difference between summer and winter temperature is even greater than in the ocean.

The southern Japanese region is not tropical as regards sea temperatures but at the most subtropical, and this also applies to the shelf fauna. Moreover a small number of northern and a number of southern forms also occur. True coral reefs are not found north of the Riu-Kiu Islands, so that a number of corallophile species are excluded from subtropical Japan. Other tropical species are, however, to be found in fairly large numbers north of the islands mentioned. The subtropical fauna is sometimes called Honshu-fauna after Japan's largest islands, Hondo or Honshu.

Among the echinoderms the Asteroidea, Ophiuroidea and Echinoidea are best known and they may be regarded as fairly representative of the fauna in general. A detailed investigation of the zoogeographical position of this group of echinoderms has led to the result given below. This investigation only took into account the species which are exclusively or almost exclusively found in the shelf region, and deep-sea forms are therefore not included. The main results can be summarized as follows:

Total number of species	160
In common with subtropical Japan and the north and middle part of the Indo–Malayan region (Riu-Kiu, Philippines, Moluccas, Malacca, South China)	52%
More or less pronounced endemic species of southern origin.	28%
Total of all species of southern origin	80%
Species of northern origin or belonging to deep-sea genera .	20%

Compared with the purely tropical fauna the subtropical fauna of Japan is characterized, apart from the endemic element, by a considerable reduction of its tropical elements. Of the roughly 400 species belonging to the above-mentioned echinoderm group and living in the northern and middle Indo-Malayan region only about 20% reached Japan north of the Riu-Kiu group. Various authors have furnished surveys of several other groups of animals (but have usually omitted to separate subtropical from temperate Japan, or they survey the whole Japanese empire including the Riu-Kiu group, or include both shelf and deep-sea fauna).

According to a survey carried out by Balss[28] and Yokoya[591] the decapod crustacean group Reptantia includes about 360 south Japanese species in the shelf region, of which 32% are endemic. One of the latter is *Ibaccus ciliatus*, depicted in fig. 6. M. Sasaki[456] in his exhaustive work on the Japanese cephalopods cites no less than 125 species for the whole country. The fish fauna, too, is rich in species. It has been investigated by Günther, Franz, P. J. Schmidt

and especially by Jordan and his collaborators Evermann, Tanaka, Snyder and Metz. In a valuable zoogeographical analysis Tanaka[538] emphasizes the division of the Japanese fish fauna into a southern and a northern element with a dividing line roughly near Chosi east of Tokyo on the Ocean side and at Hamada on the inner side of the islands. He counts 734 southern species, 658 of which live in the shelf region, and 134 northern species. A further 88 are common to both regions. In a list which excludes the Riu-Kiu Islands but includes the Kuril and deep-sea region Jordan, Tanaka and Snyder[271] record 1236 fish species. For the southern Japanese region including the Riu-Kiu Islands and Formosa Engelhart[151] reports 78 species of Selachii belonging to 44 genera, representing half of the number of species known for the whole world.

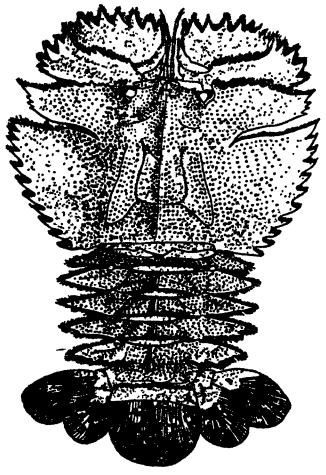


FIG. 6.—*Ibaccus ciliatus*, a little reduced. (After de Haan, *Handbuch d. Zoologie.*)

The position of southern Japan as regards its fauna may, however, be more complicated than the above survey suggests. Let us first consider the water temperature. The following figures apply to the oceanic side of Japan:

TABLE 1

WATER TEMPERATURES OFF THE OCEANIC COAST OF JAPAN

	Surface		200 m.
	February	August	Mean Temp.
North of Riu-Kiu Islands . .	19°C.	28°C.	15°C.
Oceanic coast east of Tokyo . .	13°	25°	10–15°
Tsugaru Strait (Hakodate) . .	6°	20°	—
Outside (east of) Tsugaru Strait . .	—	—	1–2°

We see, particularly in northern Japan from Tokyo to the Tsugaru Straits between Honshu and Yezo, that the temperature of the water decreases rapidly although the distance between the two regions amounts to only six degrees of latitude. The coastal fauna in the strait of Tsugaru and north of it is without doubt a cold-temperate one, and if the whole of the southern Japanese fauna up to the coast east of Tokyo is called subtropical, there seems to be

no room left for any warm-temperate fauna. It is quite possible that such a fauna did not develop in this region of the sea since the changes in temperature in a horizontal as well as a vertical direction are so great. But it is also possible that what above has been called southern Japanese and subtropical is not uniform, but that southern Japan contains a subtropical fauna near the islands Shikoku and Kiushu and in the faunistically rich "Japanese Mediterranean" between Hondo and Shikoku, but contains a warm-temperate fauna off the middle of Hondo. But the surveys at our disposal provide little evidence in the shape of endemic species which would suggest that the last-mentioned area is of an independent character.

Tropical (and Subtropical) Australia

In Australia, as in East Asia, a tropical and probably partly subtropical faunistic region is contrasted with a temperate one. In Australia investigations of several animal groups have shown that the southern limit of the warm-water fauna on the west coast may be situated at about 29° S. Here the Houtman or Abrolhos Islands with their coral reefs represent the most southerly outposts of the tropical fauna. The corresponding boundary or transitional region on the east coast seems to be at 32°–34° S., that is to say in the area north of Sydney and Port Jackson. As far down as 30° S. coral reefs are still met with, while in Lord Howe Island out in the open sea they reach 31° of latitude, the most southerly spot in the world's oceans where true coral reefs exist. In the boundary zone on the west coast the annual temperatures in the open sea range from 19 to 23° and in the boundary zone on the east coast from 17 to 24°. In both tracts the boundary region is marked by the meeting of cold and warm currents, i.e. the westwind drift and its ramifications on the one hand and the south equatorial current on the other.

On the southern side of both these boundary regions we find a different fauna which is clearly distinguished from the northern. We shall discuss this when we describe the temperate region. No distinct subtropical fauna, characterized by any notable number of endemic elements, seems to emerge from the investigations at present available. The number of species is not as large in the tropical shelf region of Australia as in the Indo-Malayan region, but many species are nevertheless common to both. Many others are endemic in Australia, but they belong on the whole to genera which are also represented in the Indo-Malayan fauna.

Of all the animal groups to be found on the Australian shelf it is the echinoderms which have been most completely analysed from a zoogeographical point of view. This is due to the investigations carried out by H. L. Clark, who published his final results in 1946.

There seems reason to believe that his results are in the main also applicable to the rest of the warm-water fauna of Australia. Clark distinguishes three provinces in tropical (and subtropical) Australia, of which one would seem to possess insufficient claims to independence (see below). The names he uses for these provinces were those given previously by Australian naturalists.

The *Solanderian province* comprises the north-east and north coasts of Australia from the Torres Strait in the north to a southern boundary which, according to a regional division previously given for the mollusc fauna on rather meagre evidence,[217] should be placed at Wide Bay. Clark mentions, however, that certain Solanderian species extend their range to the vicinity of Port Jackson and to Lord Howe Island (31° S.) where, as we recently learnt, true coral reefs mark the tropical nature of the fauna; he regards Lord Howe Island also as Solanderian. It seems probable that one may have to include in this province or in the subtropical mixed zone which lies between it and the south-Australian faunal region, also the region of Port Jackson, although this part, according to Hedley[217] and Clark[88] is to be included in an independent *Peronian province*, which extends southwards ending in the southern part of Tasmania which is markedly temperate. The species which are particularly characteristic for the Peronian province are, as may be gathered from Clark's list, either mainly south-east Australian and so could well be regarded as members of the temperate fauna, or they are only known from the vicinity of Port Jackson and may possibly be southern outposts of the Solanderian province. This province is essentially the Great Barrier Reef area. It contains about 208 echinoderm species, of which most are Indo-Malayan and 87, that is 42%, purely Australian. Those which are not found in any other Australian province occur also in the Indo-Malayan region. The province thus lacks endemic echinoderms. Its position as a member of a great tropical-Australian unit is greatly strengthened by the possession of 42% purely Australian species, but it is more closely connected with the Indo-Malayan faunal region than any other Australian province. Its independence *vis-à-vis* north-west Australia Clark explains by the fact that the Torres Strait, which is extraordinary shallow, being only 10–20 m. deep, until the late Quaternary period was above the surface of the sea and therefore constituted a barrier between these two regions. The Great Barrier Reef represented the coastline at that time and stood in closest faunistic contact with the eastern coast of New Guinea.

The north-west Australian faunal region, the *Dampierian province*, because of these geographical circumstances shows less resemblance to the Solanderian province than might have been expected from

recent oceanic connections. The province is so called after the peninsula of Dampier Land in its centre and it comprises the coast from the Torres Strait to the boundary of the temperate region; Clark places this boundary at the Abrolhos Islands and Geraldton (about 29° S.) on the south-west coast. It is clear that in this as in other similar cases the two neighbouring faunas overlap. The Dampierian fauna, in spite of the fact that considerable parts of this region have as yet not been investigated, is richer in species than the Solanderian. Of its 290 echinoderms 50% are purely Australian. If one examines the distribution of the 42 species which are not found in any other part of Australia it will be seen that 25 of them, that is 8–9% of the whole number of species of the province, are to be found neither in the Indo-Malayan nor any other region and are therefore genuinely endemic as far as our present knowledge goes. The Dampierian province is therefore more independent than the Solanderian province. Of its endemic species, we may note among the sea-lilies the uncommonly large and beautiful *Comanthina belli*, among starfishes the fine *Stellaster princeps* and *Goniodiscaster australiæ*, and the brittle-stars *Macrophiothrix scotia* and *Ophiothrichoides smaragdina*. The province also contains a few endemic genera, namely *Monilimetra* among the sea-lilies with four species and *Pseudoreaster* among the starfishes with only one species.

The Indian Ocean

The northern and western parts of the Indian Ocean are on the whole not so systematically investigated that their zoogeographical position can be determined. But Alcock's (1895–1900) study of the crustacean fauna of the Indian peninsula and surrounding coasts gives us an important basis for comparison. The John Murray expedition of 1933–34, which was sent out by the British Museum, collected zoological material from large parts of the ocean, while antarctic and deep-sea expeditions have collected material there on their passage. Two Danish expeditions in 1937 and 1938 explored the Persian Gulf, which yielded rich catches of fish[49] and crustaceans.[505] The Persian Gulf lacks endemic species of fish, but 11–12% of its 215 species seem to be confined to the north-western part of the Indian Ocean, 42% are distributed over a great part of the Indian Ocean and about as many are found only in the north-eastern part of the Indo-Malayan archipelago. Much the same distribution is to be found among the crabs, of which roughly 73% live in the Indo-Malayan region. It is therefore possible to say of both fishes and crabs that the rich Indo-Malayan fauna is distributed over a large part of the Indian Ocean but that the number of species constantly decreases as we proceed in a westerly direction. This is also

strongly supported by A. H. Clark[84] in a survey of the crinoids of the Indian Ocean. The western and south-western parts of this sea have considerably fewer species than the eastern, but contain some 50 species in the shelf region, nearly all of these being of Indo-Malayan type. The number of species continues to decrease towards the south-west, and in Natal and to the south of it they are reduced to a mere eight. As regards other groups of animals we may mention that between the Gulf of Oman and Malacca 10 species of sea snakes are to be found, which, as far as our knowledge of their distribution goes, are endemic in this region. Only one sea snake, the most pelagic of all, *Pelamydrus platurus*, is attested with certainty from the Indian Ocean west of the Gulf of Oman. This species is also found as far down as South Africa. The sea snakes, which are viviparous, are independent of dry land and may be classed zoogeographically with other sea animals.

That the most south easterly region of Africa and its coast contains a subtropical fauna of independent character cannot be regarded as definitely established since the boundary marking off the fauna, which in the following account will be called warm-temperate, is little known. The surface water in the region of Durban has a completely tropical temperature (20° mean temperature in the coldest month of the year, August) and at 200 m. depth the mean annual temperature is actually higher than in any part of the Indian Ocean north of the equator with the exception of the Red Sea. It is true that there are no real coral reefs so far south on the African coast but the same species of corals which form the reefs in the Mozambique channel and in Madagascar are also to be found off Durban, although they do not combine into reefs. The same conditions are to be found in most of the other outer limits of the tropical region and also in the whole of tropical West Africa. The faunal boundary, which a number of authors agree in placing in Algoa Bay, is possibly the southern limit for a subtropical fauna which in this case would extend from there to the area of Durban.

The *Red Sea* occupies an exceptional position in several respects. The temperature of the water even at 200 m. depth is as high as 21–25° and the salinity is exceptionally high because of the great evaporation between the Arabian and the African deserts. It is actually somewhat higher than in the Persian Gulf and the salinity on the surface varies between 36·5 and 41·5‰. How far this affects the constitution of the fauna is not precisely known. The number of endemic species is considerable. For the crinoids the unusually high figure of 70% is given, which may be partly due to the fact that the deep-sea species have been included and also that we have only imperfect knowledge of the shelf fauna in the rest of the Indian

Ocean. Of some 170 species of the Decapod Macrura of the Red Sea 31% are endemic, and 33% of the 260 species of the Brachy-ura.[297, 539]

These figures are of some interest for the course of the evolution of new species in the animal groups in question. We know with considerable accuracy the amount of time which has been available for the formation of new species in the Red Sea. This sea came into existence at the end of the Pliocene or the beginning of the Quaternary period (Pleistocene), when the large inland sea which formerly covered the "erythræic" depression, first joined up with the Mediterranean and later on with the Indian Ocean. The transition from Pliocene to the Quaternary period occurred roughly one million years ago (p. 66), and this time was accordingly sufficient for a fairly large number of animal species to undergo changes of a magnitude which differentiated them as new species.

The Red Sea has been given its name because of the "water-bloom" caused by dinoflagellates, which in this sea, as on many other coasts, dye the water red at certain seasons of the year. Water, rich in nourishment, welling up from the sea floor in combination with a considerable increase in temperature seems to be the main reason for this (cf. p. 193).

CHAPTER III

MAIN REGIONS OF THE WARM-WATER FAUNA OF THE SHELF (*continued*)

2. ATLANTO-EAST-PACIFIC

WE now proceed to the second great warm-water region—the Atlanto-East-Pacific. This comprises an American and a West African subregion. The West African subregion, however, neither qualitatively nor quantitatively exhibits the same independence as the American and consequently it cannot be ranked with it in importance from the point of view of regional zoogeography.

A. TROPICAL AND SUBTROPICAL AMERICA

In spite of the fact that the isthmus of Panama nowadays represents an unsurmountable barrier for sea animals, the tropical eastern Pacific and the tropical West Atlantic constitute nevertheless a faunistic unit. This emerges not from a one-sided consideration of the distribution of the species but becomes all the clearer if we consider the genera. This state of affairs, as we shall see later on, may be attributed to historical causes.

COMMON TRAITS OF TROPICAL-SUBTROPICAL AMERICA'S ATLANTIC AND PACIFIC COAST

As early as 1867 and 1868 it was pointed out by the well-known zoologists Verrill and Günther that there is a closer resemblance between the fish faunas of the eastern and western coasts of Central America than would be expected from their present isolation from each other. Other investigators have since endorsed this view and supported it by examples from other groups of animals. Some species, though only few in number, are found in identical development on both sides of Central America. In other cases Atlantic and Pacific species are to be found more closely related to each other than to other species. This suggests that they must have evolved from a common ancestor. Because of their simultaneous "birth" from a common parent species, the American ichthyologist D. S. Jordan[267] introduced the term "geminate species" or "twin species" for them; synonyms in the earlier and later literature are

"representative", "analogous" or "vicarious" species. Finally, the affinity between the two marine regions is also proved by the great number of genera which are common to both zones but do not occur outside America's warm-water zone.

In determining the relationship of the various faunas to one another and the history of their distribution it is important that conclusions should be drawn not from a more or less subjective general impression of faunistic studies but as far as possible from numerical statements about the composition of the fauna which will permit statistical comparisons. In an analysis of warm-water faunas it is just as important to keep the stenothermal warm-water forms separate from cold-water or eurythermal forms. In conformity with this principle I have assembled all the information available to me with regard to the distribution of all American species and genera of two groups of invertebrates which seemed particularly suitable for this purpose because of the taxonomic and faunistic investigations carried out on them: the crabs, which are investigated by Mary J. Rathbun[423–426] in an extensive modern systematic monograph, and the echinoderm groups Asteroidea, Ophiuroidea and Echinoidea, whose systematic position and distribution are better known than that of most other large groups of invertebrates, thanks to the work of W. K. Fisher, Mortensen, H. L. Clark and others.

We may begin with a glance at the adjoining table:

TABLE 2

CRABS (BRACHYURA) AND ECHINODERMS (ASTEROIDEA, OPHIUROIDEA AND ECHINOIDEA) IN THE TWO AMERICAN WARM-WATER REGIONS

	Crabs		Echinoderms	
	Species	Genera	Species	Genera
Total number	750	196	385	135
	As percentage of the total number			
Endemic in the warm water of America:				
In Pacific but not Atlantic America .	38%	7%	41%	15%
In Atlantic but not Pacific America .	36%	13%	33%	4%
Both in Pacific and Atlantic America.	2%	18%	0·3%	10%
Sum	76%	38%	74%	29%
Other stenothermal warm-water forms (circumtropical, etc.) . . .	6%	31%	7%	31%
Eurythermal forms, also in temperate or deep-water regions	18%	31%	19%	40%

It can be seen that both groups of animals (crabs and echinoderms) are in close conformity. There are only very few species which are

common to both the Pacific and the Atlantic warm-water region, that is to say amphi-American and at the same time endemic to this common region, while the Pacific has a very large and the Atlantic a slightly smaller number of endemic species. This is due to the fact that the two faunal regions began to wend their own way and develop their own particular species at the time when the isthmus of Panama constituted a barrier between them. The species which are common to both, whether they are endemic in America or are more or less circumtropical, seem to be all extremely ancient species which have not changed in their external morphology since the time



FIG. 7.—Distribution of the crab genus *Mithrax*. The genus is endemic in America, it possesses 21 species (about 540 localities) on the Atlantic side, and 11 species (about 70 localities) on the Pacific side. 12 species form twin-pairs.

when the barrier was formed. The genera, however, present a completely different picture. Among them, those which are both endemic and amphi-American are much more numerous, 18 and 10 compared with 2 and 0·3% for the species. So far as the crabs are concerned the number is higher for their common region than for any of the subregions. This is a good illustration of the close affinity of the two faunas as parts of a common American (amphi-American) thermophile fauna. As examples of endemic amphi-American genera we may mention *Mithrax* (fig. 7) and *Pyromaia* among the crabs,

among echinoderms the well-known keyhole urchins *Encope* (fig. 8) and *Mellita.*

The graphic representation in figs. 9 and 10 brings out the same distribution for the crabs as was shown by the table and also gives a more detailed picture of the distribution of eurythermal species and genera. We may observe here the comparatively slight resemblance between the warm-water fauna and the northern and southern temperate faunas. It is true that the South American temperate fauna is not well known, but even the better known temperate north Atlantic region shows few elements in common with the warm-water region as compared with the number of species and genera endemic in the latter (39 as against 270 and 3 as against 26 respectively). This is a good illustration of the point already emphasized earlier, namely that the contrast between the faunas of warm and temperate water is very pronounced and considerably more marked than the very small differences which divide tropical and subtropical faunas.

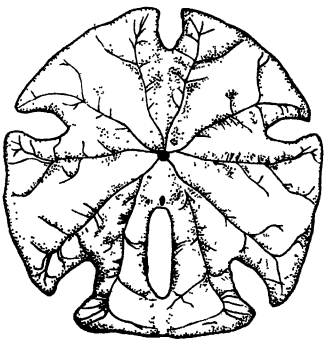


FIG. 8.—*Encope* sp. (After Agassiz, redrawn and simplified.)

The crabs and echinoderms may be regarded as fairly representative of the fauna in general as far as distribution on the American warm-water shelf is concerned. We shall only cite a few other groups of animals as examples. There is a comparatively small proportion of amphi-American species among molluscs; one of them is the well-known oyster *Ostrea virginica.* Among the fish the corresponding figure seems to be round about 10% according to Meek & Hildebrand, who have surveyed the richly diversified fauna of tropical West America. One of the amphi-American species is the peculiar *Manta birostris* generally known as sea devil, which reaches a length of six m.

Endemic amphi-American genera are of course more numerous than species. As has been mentioned already, they amount to 18% of the total number of crabs and 10% of all echinoderms. It will suffice to give examples from some well-known fish genera (according to Jordan, Evermann & Clark). The number of fish genera in question is fairly considerable.

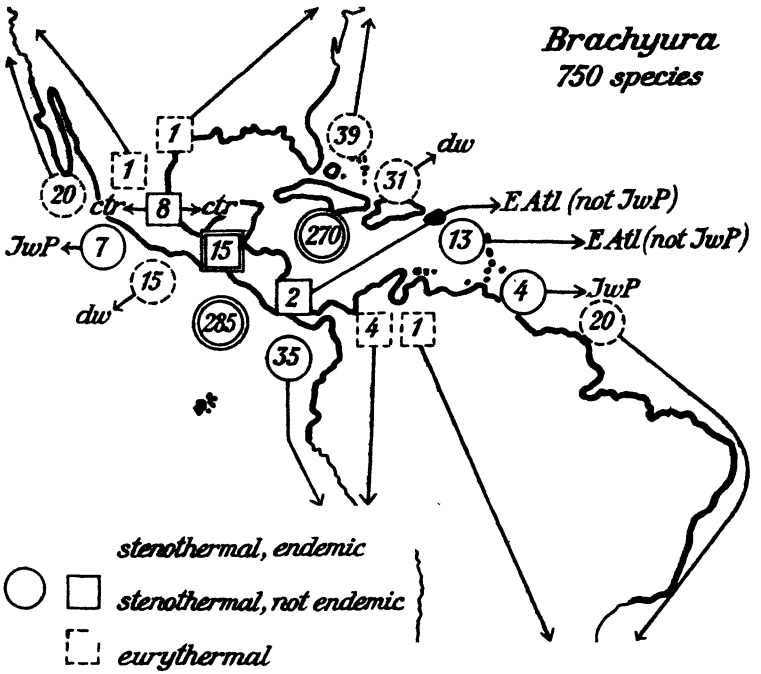


FIG. 9.—The circles off the Atlantic and Pacific coast respectively denote the number of species which are to be found in one region but not in the other; the squares in Central America contain the number of species common to both regions. The arrows denote distribution outside tropical America: *IwP*=Indo-West-Pacific, *EAtl* = East Atlantic, *dw*=deep water, *ctr*=circumtropical. In several cases the same species is marked on two spots.

	Atlantic species	Pacific species
Hæmulon (grunts) .	10	2
Calamus (porgies) .	8	3
Cynoscion (weak fishes, etc.)	10	10
Menticirrhus (kingfishes)	4	5
Bairdiella (mademoiselles)	3	2
Iridio (doncellas) .	15	4
Citharichthys . .	7	7
Achirus (American soles)	4	7
Gobiesox (clingfishes) .	13	3
Manta (devil fishes) .	1	1

Twin species, which together with the common genera are the clearest indication of the close relationship between the faunas on both sides of Central America, are numerous among several animal groups and represent a comparatively high percentage of the fauna. Among genuine warm-water crabs, Rathbun[422–425] distinguishes roughly

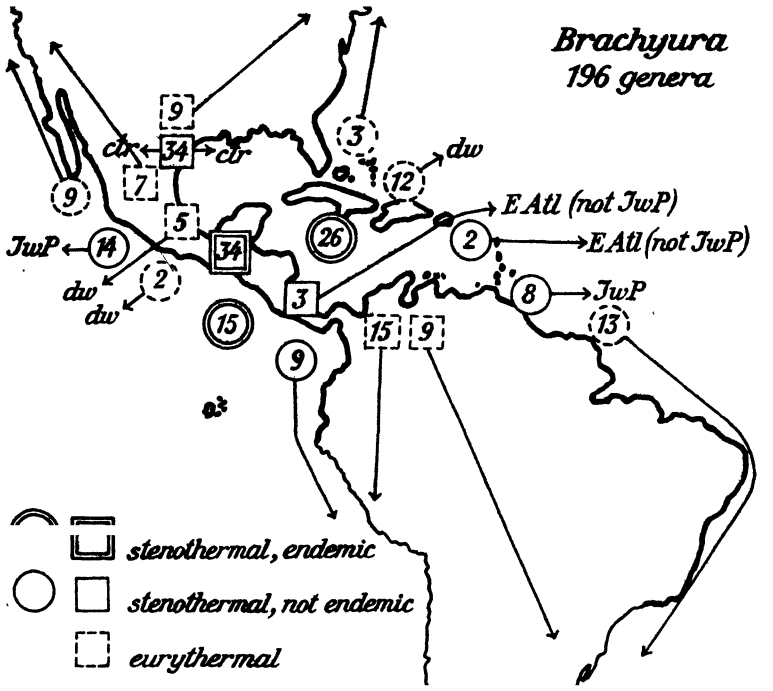


FIG. 10.—Distribution of the 196 genera of tropical America. Cf. caption of fig. 9.

80 pairs, and with additions [160a] the number rises to more than a hundred. Among the starfish, brittle-stars and sea-urchins about 40 pairs are known and they occur also among the pycnogonids[216] and other invertebrates, such as, to quote a familiar example, the spiny lobsters *Panulirus interruptus* and *P. argus*. Finally, as regard the fishes Jordan, as we have already mentioned, was particularly interested in twin-pairs. He mentions at least 100 of them, among them the following:

Atlantic	Pacific
Centropomus undecimalis	*C. viridis*
Epinephelus adscensionis	*E. analogus*
Lutianus apodus (cf. fig. 11)	*L. argentiventris*
Hæmulon parra	*H. scudderi*
Kyphosus incisor	*K. analogus*

The connection between America's two warm-water zones is illustrated to a lesser extent by such elements as also occur both in

the warm-water and temperate zones. As examples of these we may mention the pennatularian genus *Renilla* whose distribution is given in fig. 12.

This close Atlanto-Pacific resemblance led certain authors quite early on to propose that the faunas of the two coastal regions should be combined into a larger unit. Günther's view with regard to the fishes has already been mentioned, McMurrich in 1889 made a similar proposal founded on the distribution of the Actiniaria. In the present century others have expressed similar views, for instance with regard to the pennatularians,[25] and Euryalæ.[129]

We shall now attempt a causal explanation of the facts mentioned above. To explain the close faunistic resemblance between the two coastal regions which are now separated by the isthmus of Panama we must postulate a direct connection between the two in the past.

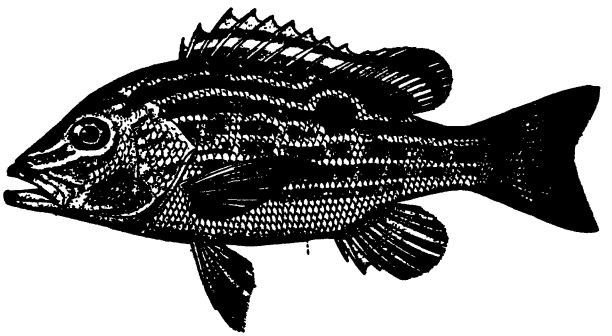


FIG. 11.—*Lutianus synagris*. (After D. S. Jordan.)

For the fauna in question consists of stenothermal warm-water animals which could not round the cold-temperate southern tip of South America. This conclusion of a former direct connection was reached by Günther before the geologists demonstrated an ancient channel across what is now Central America and his views were subsequently fully confirmed by geology, an example of the legitimacy of drawing in certain cases geophysical conclusions from purely zoogeographical premisses. The relatively small number of amphi-American species shows that the channel must have ceased to exist before the bulk of the species had reached their present morphological development. The age of the barrier is thus greater than the average age of the species. On the other hand, the great similarity between the two members of the many pairs of twin-species shows that the marine connection must have existed still at a, geologically speaking, comparatively recent date.

These somewhat speculative conclusions agree very well with palæontological and geological evidence. It has been shown that for long periods of the Palæozoic and Mesozoic eras the Pacific had a direct connection with the Atlantic across the present Central America. In the Tertiary period this seems to have changed. In the Eocene, Oligocene and Miocene the two oceans had a direct connection for considerable periods, and according to Schuchert,[474] who has most recently devoted a voluminous monograph to this question, it existed even in the lower Pliocene. Since then the land barrier has existed without interruption. The last connecting channel seems to have been fairly narrow and was situated south-west of

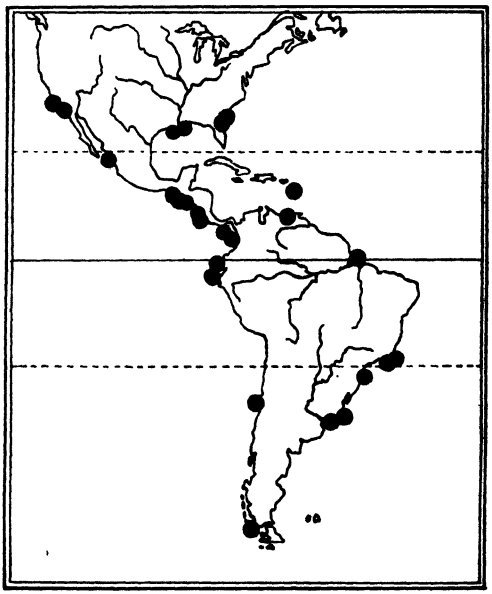


FIG. 12.—Distribution of the exclusively American genus *Renilla*. Localities not precisely indicated have been omitted. An occurrence should be noted also on the Texas coast.

Yucatan. A palæontological witness to unimpeded faunistic communication during the Eocene is for instance the mussel *Venericardia planicosta*, which was common both in the Gulf of Mexico and in California and Oregon. The Atlanto-Pacific communication affected the deep-sea fauna to a far lesser extent than the shelf-fauna and it would thus appear to have been generally shallow. The continuation of these conditions for very long geological periods must have resulted in the formation of a fairly uniform fauna in the

sea which was subsequently divided into two by Central America, which emerged as a barrier during the Pliocene.

On the whole the Atlantic fauna is richer than that of Western America and although this does not seem to be the rule with regard to crabs and echinoderms, to judge by the findings so far, it nevertheless holds good even for certain groups among them, as for instance the genus *Mithrax* (fig. 7). Jordan[266] remarks of the fish fauna that the West American fishes are in the main of Atlantic origin and a similar view is expressed by Ihle[249] regarding certain groups among decapod crustaceans. Vaughan[567] holds the same view concerning the Lower Pliocene corals and v. Ihering[248] expresses himself even more definitely with regard to the fossil fauna of western South America.

AMERICA'S PACIFIC WARM-WATER REGION

Boundaries and hydrography

There is fairly general agreement among experts as to the rough delimitation of the warm-water zone in its north and south extremities. The tropical zone comprises in the north the whole of the Bay of California, but only the southern tip of Lower California, where many tropical elements stop. Further to the north we find a subtropical transitional fauna which in the region of San Diego changes into a temperate fauna. The northern limit of the warm-water fauna may therefore be regarded as being roughly coincident with the border between the United States and Mexico, but it is by no means clear-cut. The southern limit lies at a remarkably low degree of latitude: in northern Peru off Point Aguja, Payta, or even further north, Guayaquil Bay at 3°–4° S. on the border between Peru and Equador. Point Aguja is situated at 6° S. Further south the fauna must be regarded as temperate, while between 3°–6° S. there exists possibly a transitional zone containing a subtropical fauna. The Galapagos Islands must be regarded as belonging to the region of the tropical fauna. This is true of the surface layers of water. For the stratum 100–200 m. depth the position is different, as will now be shown.

The distribution of the fauna is influenced to a high degree by the hydrographical conditions which are both peculiar and very variable. From the south comes the great cold Peruvian Current or Humboldt Current, whose main part turns west at the well-marked bend in the coastline at Point Aguja in the direction of the Galapagos Islands. The upwelling of cold water from the sea floor increases the cooling influence of the current and is a contributary cause for the shifting of the southern limit of the warm-water zone to a position further

north than on any other coast. Such upwellings exist also on the ocean coast of Lower California and occasionally also in the Gulf of Panama. Because of these circumstances the temperatures are extremely variable in the whole warm-water zone. In fact, the surface temperature in the Gulf of Panama may for a short time sink to 16° C. while at 200 m. depth the prevailing temperature is at the most 12° C. in the whole region between the northern and southern limits mentioned, and only 8–10° C. on the oceanic coast of Lower California. If one takes the same temperatures as in other parts of the oceans as marking the depth limit of the warm-water fauna, the lower limit in western America cannot be placed deeper than about 100 m.

The general characteristics of the fauna

A glance at the maps on p. 34 and 35 and table 3, p. 40 shows the following state of affairs: of about 390 species of crabs in the West American warm-water zone, nearly three-quarters are endemic to this region. West America shows thus a considerable degree of independence even compared to the West Indian fauna so far as species are concerned, but its connection with the last-mentioned fauna is made fairly clear by the high percentage of common genera, which is considerably more than twice as high as the percentage figure for community of genera with the warm-water zone in the other direction, that is the West Pacific. It is also worth noting how weak the affinity is with both the southern and northern temperate zones. We should add the proviso that this affinity may turn out to be slightly stronger when our knowledge of the temperate fauna in the Pacific and Southern Atlantic is more complete, but no radical alteration of the picture is likely. Here, as in other cases, in making statements, for example about the number of endemic species, we must always do so with the reservation that the figures are only provisional and that greater or smaller corrections may have to be made in future.

It emerges partly from the survey made in table 3 that the echinoderms present much the same picture as the crabs. The endemic genera, however, both for crabs and echinoderms are very poor in species and in most cases contain only one species, i.e. they are monotypic.

We may give prominence to the following examples of species and genera endemic to this region. One of the well-known crabs is the large, edible *Ucides occidentalis*, which the natives dig out of its holes on the mangrove coasts. The genus is purely American. Among the Alcyonaria the genus *Eugorgia* with at least nine species is endemic, and five other genera, among them *Gorgonia*, have their main habitat here. The pennatularian genus *Leioptilum* is also

endemic, likewise about two hundreds of fish genera, for instance the economically important genus *Paralabrax* of the serranid family. These examples could be multiplied.

TABLE 3

CRABS (BRACHYURA) AND ECHINODERMS (ASTEROIDS, OPHIUROIDS AND ECHINOIDS) OF THE PACIFIC AMERICAN WARM-WATER REGION

	Crabs		Echinoderms	
	Species	Genera	Species	Genera
Total number	390	155	210	95
Stenothermal warm-water forms:	As percentage of the total number			
Endemic to Pacific America	73%	10%	75%	20%
Both in Pacific America and the Atlantic Ocean, but not elsewhere	4%	24%	1·5%	18%
Both in Pacific America and the Indo-West-Pacific, but not elsewhere	2%	9%	2%	7%
Circumtropical forms	2%	16%	0·5%	24%
Circumtropical forms, exclusive of East Atlantic	—	6%	—	—
Eurythermal forms:				
Both in the warm-water region and also in the temperate North Pacific	5%	10%	8%	12%
In the temperate South Pacific	10%	15%	2%	5%
In the deep-water below the warm-water zone	4%	10%	11%	14%

Of particular interest is the relationship of the West American fauna to the West and Central Pacific. We have found earlier on that the bulk of the species of the last-mentioned fauna and even a substantial part of its genera did not spread further east than Polynesia and so did not reach the American coast. As regards those animals which did reach this coast, of the 26 molluscs which showed such a distribution half the number are in the American Pacific only found near the islands which lie far from the mainland, such as the Clipperton or Galapagos Islands, etc., but not near the coast of the mainland.[231] The same is true also of some other species (see below on p. 42 *Ostraciidæ* and *Sparisomidæ*).

Several West Pacific genera which are absent from the west coast of America are to be found in the West Indian region, and this is true of so many that the warm-water fauna of Pacific America actually shows a somewhat weaker connection with the Indo-Pacific than does that of Atlantic America. In view of present geographical conditions such a distribution is unexpected. The following examples may be given.

Of the warm-water Gorgonaria in the Pacific there are only two genera, *Psammogorgia* and *Heterogorgia*, which are represented both off its eastern coast and in its western parts. But in the Atlantic six genera are to be found which possess species in the West Indian warm-water region and occur elsewhere only in the Indo-West-Pacific. Such a distribution characterizes the whole of the family *Gorgonellidæ* (fig. 13). The *difficilis* group of the genus *Holothuria* is circumtropical, except for a gap on the west coast of America (fig. 14). The same applies to the crinoid sub-families *Perometrinæ* and *Thysanometrinæ*; the crinoid group is, as A. H. Clark particularly stresses, a good example for this type of distribution. Decapod

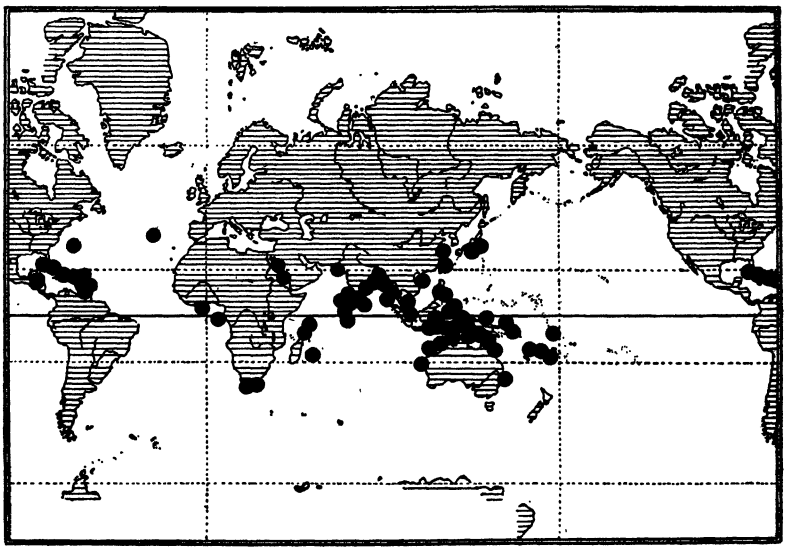


FIG. 13.—Distribution of the Gorgonarian family *Gorgonellidæ*. A mark generally indicates many localities.

crustaceans with the same distribution are the genus *Scyllarus* and at least 10 crab genera. Other examples are the whole order Xiphosura, which is, however, not rich in species, and further several molluscs, for instance the decorative snail *Dolium* and 12 species of *Triton*, which Simroth[481] considered as six pairs of twins of which one twin lives among the Antilles and the other in the Indian Ocean. Hartmeyer[211] and Huus[246] mention several ascidians which occur both in the West Indies and south-eastern Asia, but not on the west coast of America, as for example *Microcosmus exasperatus* and the genera *Rhopalæa* and *Rhodosoma*.

Other examples may be taken from the fish; but unfortunately

no complete analysis has been carried out. Several genera with species both in the West Indies and the Indo-West-Pacific are absent from the west coast of America. In general they are, however, poor in species even in the West Indies. Others again possess no, or only very few, species on the west coast of America but are preponderant in Atlantic America and are also well represented in the West Pacific, for instance the butterfly-fishes *Chætodon* with many species, two species being found in Pacific, seven in Atlantic America, and *Epinephelus* (groupers: 3+10 species). The same distribution is shown by the family *Scaridæ*, (corresponding number of species 4 and 19), *Lutianidæ* (Snappers: 8 and 22) and *Sparidæ* (porgies:

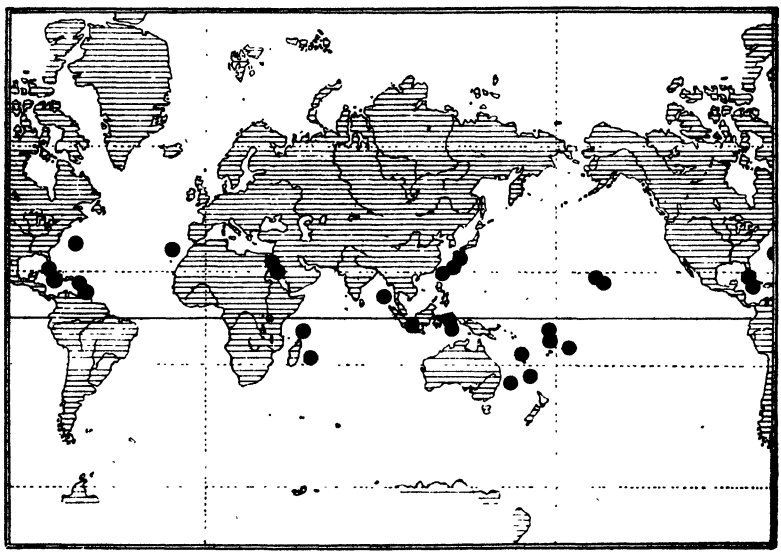


FIG. 14.—Distribution of the *Holothuria difficilis* group. (After Panning, 1929, simplified.)

1 and 21). There are also whole families which are by and large circumtropical except for the mainland coast of West America, where they are missing. Such are, for instance, *Ostraciidæ* (trunk-fishes) with four and *Sparisomidæ* (parrot-fishes, fig. 15) with 24–25 species in the West Indies. Of these families, however, one has two and the other one species on the islands far distant from the coast of West America (Galapagos, Clipperton, Socorro islands and Revilla-gigedo archipelago).

Other examples of this nature are, further, the eels *Anguilla* and *Conger*, with the proviso that the larval stage, the well-known *Leptocephalus*, is pelagic and partly lives in deep water and that the

post-larval stage of, for instance, the Atlantic *Anguilla anguilla* and *A. rostrata* are eurythermal and therefore have partly a northern distribution. The distribution of the genus *Anguilla* may be seen from fig. 16. *Conger* agrees in the main, but is not found in the Central Pacific. As J. Schmidt has shown in his well-known investigations on the life history of the eels,[464] it is probable that this distribution is to a large extent regulated by the availability of suitable breeding grounds. But if the eastern Pacific lacks suitable spawning grounds, this cannot, as has been maintained, be held to disprove the opinion that the East Pacific is an obstacle to distribution of those fishes, too. On the contrary this would explain why it constitutes such an obstacle.

Finally, the mammals provide examples of this type of distribution. The whole of the suborder *Sirenia* belongs here, for one of the three families, the *Manatidæ*, inhabits the east and west coasts of

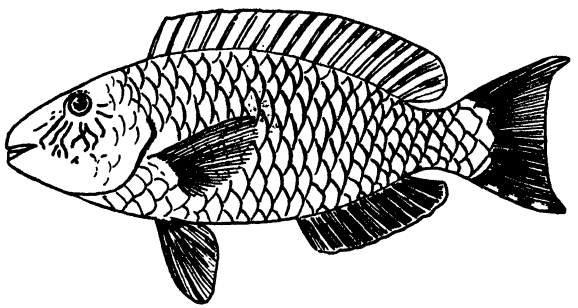


FIG. 15.—*Sparisoma abildgaardi*. (After D. S. Jordan, simplified.)

the tropical Atlantic and another, the *Halicoridæ*, the Indo-West-Pacific region from the Red Sea to Australia, New Guinea and the Riu-Kiu Islands, and the third, the *Rhytinidæ*, which is indeed not tropical, has inhabited during historical times the Asiatic coast of the Pacific. This suborder is not represented on the American Pacific coast. Among the seals, the genus *Monachus* has a distribution which includes the tropical and subtropical seas with the exception of Pacific America. *M. albiventer* inhabits the Mediterranean, *M. tropicalis* the Caribbean and the Gulf of Mexico and *M. schauinslandi* the central Pacific, where it is known at least from Laysan west of Hawaii. Even the whales provide a few interesting examples of a distribution which seem to imply a connection with the former Tethys Sea. We are here concerned with the fresh-water whales. The family *Platanistidæ* contains four genera. Of these *Lipotes* lives in an inland sea in China, *Platanista* in the large rivers

of India, *Inia* and *Stenodelphis* in the Atlantic rivers of South America. The species of the genus *Sotalia* which belongs to the dolphin family, have a very similar distribution in rivers and river mouths in China, Australia, India and South American Atlantic rivers. We must assume that a former continuity preceded the present discontinuous distribution of the fresh-water whales and that this must be looked for in a region of the sea.

The examples given show that a fairly large number of otherwise circumtropical genera (and sometimes families) which are to be found both in the West Indies and the Western Pacific are absent from the American Pacific. We do, indeed, find also genera of

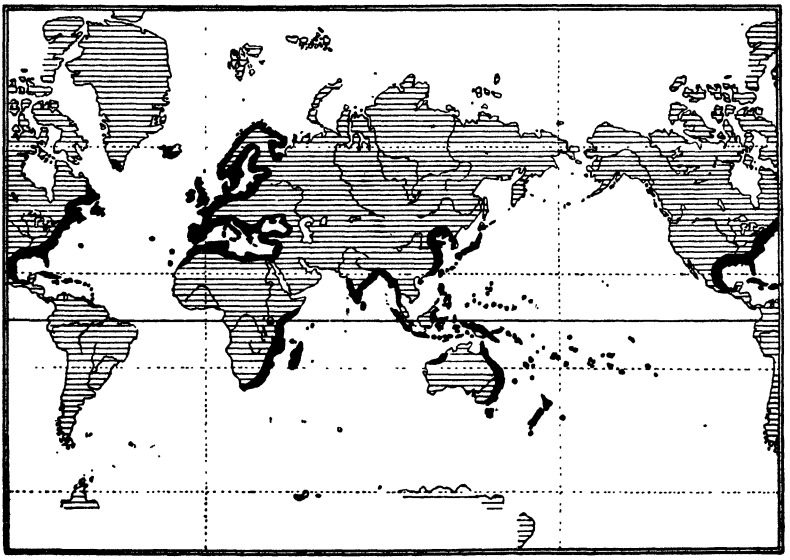


FIG. 16.—Distribution of the genus *Anguilla*. (After Johannes Schmidt.)

several animal groups which in contrast occur both in the West and East Pacific but are absent from the West Indies. Among the crabs (but not the echinoderms) there are at least as many of these genera as of those of the first-mentioned mode of distribution, and the fishes provide further examples, though these are comparatively few. The main impression is, however, that the Pacific coast of Central America, despite its geographical position, shows a lesser degree of affinity than the Atlantic coast to the Indo-West-Pacific. This is doubtless due to the fact that both the West Indian and the Indo-West-Pacific fauna were formerly parts of the same original fauna, namely that of the Tethys Sea (see p. 63).

Subregions

The shelf-fauna of the Pacific coast of Central America is by no means homogenous but shows clear differences in different geographical regions. As far as can be seen at present it seems reasonable to distinguish three subregions.

The Gulf of Panama represents the centre of such a subregion. The question of how far it reaches to the north and south and whether there is a subtropical fauna in the south with endemic elements as a positive character, or whether the tropical fauna is merely reduced and mixed with other elements before it is replaced by the temperate, awaits closer investigation. A fairly large number of animals are known from the Gulf of Panama which are not to be found in the neighbouring regions, but to what extent this is due to our incomplete knowledge of the latter is not known. Of the 28 Gorgonaria known from the Gulf of Panama, the majority are to be found exclusively there and a number of crabs, echinoderms and species of other groups may, with the above reservation, be provisionally regarded as endemic.

The term "Panamic Province" is often used in the literature for the whole of the Pacific warm-water zone of America. Since, however, the fauna of the Gulf of Panama is clearly distinguished both from that of the Gulf of California and that of the Galapagos islands, the fauna of the Gulf of Panama has better claim to the title "Panamic fauna".

The Californian Gulf exhibits, to judge by the investigations carried out so far, an unexpected measure of independence from the Panamic fauna (in the limited sense). Glassell[184] analysed the distribution of the cancroid, grapsoid and spider crabs, 195 species in all, and found 40% of them endemic in the Gulf of California, while 48% were "Panamian" and 12 were common to the fauna found north of Magdalena Bay on the west side of Lower California. The Gulf of California houses also a not inconsiderable number of species of Octocorallia and Cirripedia, which are not to be found in other regions.

Finally, the Galapagos Islands show a strong faunistic affinity with the Central American mainland and also with the West Indian region. But they also exhibit some degree of independence with a fairly weak connection with the western Pacific, although this is less weak than in the coastal fauna of the mainland.[231] J. S. Garth[176] has carried out a zoogeographical analysis of the crab fauna which includes 120 species. As can be seen from this analysis, there is an almost equally strong affinity to the distant Californian Gulf as to the considerably nearer Gulf of Panama. In the Galapagos Islands, too, the connection with the West Indian crab fauna

attested by 38 twin species, is considerably closer than with the Indo-West-Pacific. Compared with the Californian Gulf, which has almost double the amount of crab species (about 220), the Galapagos fauna is fairly meagre, and this holds good also for other animal groups. It is probably due to the relatively low water temperatures which in spite of the equatorial position of the islands is somewhat lower than in other tropical regions and may also account for the absence of true coral reefs. Among the crabs there are 18 endemic species to be found, as far as our present knowledge goes, which is a particularly low percentage (15%). Other animal groups also contain endemic species. The Peruvian Current has carried a small number of temperate elements to the islands. One of these is the penguin genus *Spheniscus*, which occurs with one endemic species *mendiculus*. The penguins, because of their loss of the ability to fly, may be classed for distributional purposes as genuine aquatic animals.

AMERICA'S ATLANTIC WARM-WATER REGION

General natural conditions

While the Indo-Malayan archipelago is the world's largest archipelago and possesses the richest fauna, the West Indian archipelago is the next largest and contains a shelf fauna of impressive richness, particularly as compared with the rest of the Atlantic fauna.

The warm-water zone comprises to the north the islands of Bermuda, the northern coastal limit being situated at Cape Hatteras or a little to the south. It has been shown for some animal groups that the faunistic change is most pronounced roughly at this point,[96, 220] but the superficial and the deeper water shows a difference in this respect. In 100–200 m. depth where the warm water of the Gulf Stream flows, certain warm-water elements spread further north than Cape Hatteras, while the species of a temperate fauna reach further to the south in the surface water near the coast. T. A. & Anne Stephenson[512] found that there is a marked zoogeographical boundary in northern Florida as far as the inter-tidal fauna is concerned, and that this fauna has a different composition between Florida and Cape Hatteras from that of southern Florida, possibly depending on the fact that the sea floor consists of a material of looser constituency.

The southern boundary of the region is more difficult to assess, largely because of our insufficient knowledge of the coastal fauna of Brazil. West Indian species represent more than 50% of the molluscs in the area of Rio de Janeiro, which also houses a number of endemic species,[252] and 40% West Indian species of the same group

are found as far south as the mouth of the La Plata river[248] at 35° S. Presumably it would be correct to place the southern boundary of the region in the neighbourhood of Rio or a little to the south. The coral reefs and mangrove swamps with their characteristic fauna also stop roughly at Rio. In the north we find coral reefs in the islands of Bermuda and particularly on the west coast of Florida, where they stretch without interruption for nearly 240 km. and even reach a width of 10–15 km.

Hydrographically the tropical West Atlantic is dominated by warm ocean currents. The strong South Equatorial Current, which comes from the Gulf of Guinea in West Africa and reaches South America at the sharp bend between Pernambuco and Cape San Roque, divides in this region into a southern branch, the Brazil Current, and a northern one. The latter follows the coast W.N.W., alongside of the Northern Equatorial Current, or Antilles Current, which in the main continues on the outside of the Antilles, while the branch of the South Equatorial Current just mentioned flows into the Caribbean and the Gulf of Mexico. It then leaves this sea through the straits between Florida and Cuba and, assuming a northerly direction, joins the Antilles Current under the name of the Florida Current and so gives rise to the Gulf Stream. All coastal water between 30° N. (North Florida) and 20° S. (north of Rio) has, therefore, passed through equatorial regions where it has been heated. It has a mean annual temperature of at least 25° C. and even in the coldest time of the year it is warmer than 20° C. Between Cape Hatteras and northern Florida the surface water temperature in February is, however, only 15–20° C. and so is equivalent to the subtropical temperature in other parts. Even at a depth of a few hundred metres the temperature is high in the tropical region, being in general higher than at the same depth in the Indo-Malayan archipelago. On the other hand, a cold current flows along the north American coast from the north which continues even south of Cape Hatteras near the coast.

America's tropical Atlantic coast is well provided with coral reefs in a number of places but on the whole they are not of such luxurious growth as in the Indian Ocean or the Pacific, nor are the species and genera of coral nearly as numerous as in the other two oceans. Vaughan[567] enumerates more than a score of Pacific coral genera which are absent from the Atlantic. The Atlantic coral reefs are most prolific in the Bahamas, their most northerly limits being on the southern tip of Florida, in the northern Gulf of Mexico and in the Bermudas, and their southern limit at Cape Frio east of Rio de Janeiro. Long stretches of the coast are free of reefs, partly because of an unsuitable sea floor or the influence of the fresh

water brought by the large rivers. A corallophile fauna rich in species inhabits the reefs, such as, for example, the large gasteropod *Strombus gigas* and among the fishes *Scarus cæruleus* (blue parrot-fish), *Teuthis cæruleus* (blue surgeon) *Pomacanthus arcuatus* (black angel), *Angelichthys ciliaris* (blue angel) *Ocyurus chrysurus* (yellow-tail), to mention only a few of the most common.

The endemic fauna

In comparison with other Atlantic regions the West Atlantic warm-water region is marked by an extremely large number of endemic species and even genera. We can only mention a few here.

For the crabs and echinoderms the table on p. 49 may be consulted. From this we see that of the crabs the number of endemic species amounts to nearly 70%, while the endemic genera amount to 17% of the total number found in this region. The percentage calculated with reference only to genuinely tropical-subtropical elements (stenothermal warm-water elements) would be even higher. The



FIG. 17.—*Carpoporus papulosus* ♂. (After Mary J. Rathbun, redrawn.)

echinoderms agree as regards species fairly closely with the crabs, while the genera show a slight divergence, with a lower percentage of endemic genera and a higher one for genera which are common to both the West Indian and the Indo-West-Pacific region .The last-mentioned percentage would prove even higher, about 53%, if eurythermal circumtropical genera, possessing species also in the temperate Atlantic, were included. Examples for endemic genera of crabs are *Lupella* and *Carpoporus* (fig. 17), each with only one species. Among endemic species well-known examples are the wharf-crab, *Pachygrapsus gracilis*, and the beach crab, *Sesarma ricordi*, the former one of the mangrove crabs and the latter an amphibian crab. For the echinoderms we may single out for mention the peculiar crinoid genus *Holopus*. This forms a family of its own which contains only 1–2 small species which are found near Cuba and in the Lesser Antilles. All the crinoid species of this region are said to be endemic.[83] All endemic genera of the echinoderm groups in the table are monotypic (i.e. contain only one species).

TABLE 4

CRABS (BRACHYURA) AND ECHINODERMS (ASTEROIDEA, OPHIUROIDEA, ECHINOIDEA) OF THE ATLANTIC AMERICAN WARM-WATER REGION

	Crabs		Echinoderms	
	Species	Genera	Species	Genera
Total number	385	150	200	95
	Percentage of total number			
Stenothermal warm-water forms:				
Endemic to Atlantic America	70%	17%	67%	6%
Both in Pacific America and the Atlantic Ocean but not elsewhere	4%	25%	2%	15%
Both in America and East Atlantic but not elsewhere	4%	4%	8%	6%
Both in Atlantic America and Indo-West-Pacific (including circumtropical forms)	3%	28%	2%	42%
Eurythermal forms both in the warm-water and also				
In the temperate North Atlantic	11%	8%	3%	20%
In the temperate South Atlantic	5·5%	15%	2%	15%
In the deep water below the warm-water zone	6%	11%	16%	12%

Other animals, too, contribute to the remarkably high percentage of endemic elements. All the Atlantic genera of reef-corals (Madreporaria) are represented in the West Indian fauna[177]; it is impossible at present to give more detailed data showing the distribution of species because the systematics of this group is inadequately established owing to the large individual variability. Of the endemic genera of Gorgonaria, *Rhipidogorgia* is well known. Among arthropods other than crabs we may mention *Limulus polyphemus*. The species is to be found as far north as Maine, but it is fairly characteristic of the warm-water region. There are many endemic fish genera but in general they are poor in species. An exception is the genus *Sparisoma* (parrotfishes), which possesses 17 species within the American warm-water zone and only one outside it, namely in the East Atlantic.

Relationship to the East Atlantic

We may begin with a comparison with the East Atlantic tropical-subtropical region, which also includes the Mediterranean. In attempting to arrive at conclusions about possible connections, both present-day and those of an earlier date, between the eastern and western Atlantic warm-water regions, we must confine our analysis to the genuinely warm-water fauna, that is to say the stenothermal

tropical-subtropical elements, because the eurythermal elements may conceivably have spread from one region to the other by way of the temperate parts of the North Atlantic or through the cold water of the deep sea.

The following table illustrates the amphi-Atlantic relationship (between East and West Atlantic) for the crabs and echinoderms and also provides a comparison with the amphi-American affinity (across present Central America). First, as far as the species are concerned, it will be seen that the amphi-Atlantic connection is very slight; only a few of the present-day species have managed to migrate from one side to the other. There may be many reasons for this. The ocean currents flow from Africa to America and the water only returns to Africa after a long detour. The sparse West African fauna has not a great deal to send while the journey is too long for the rich American fauna. But the slight extent of the interchange also shows indubitably the existence of a *mid-Atlantic barrier* which has been fairly effective during the period of present-day species, the cardinal factor being that the distance between the African and American coasts is so great that the time taken to cross it by drifting with the currents is longer than the pelagic juvenile stage of the animals concerned. A comparison with the corresponding facts relating to the amphi-American communication shows that it is even slighter. This is quite natural since amphi-American communication has been absolutely impossible for stenothermal warm-water animals since the time when the isthmus of Panama joined together (probably middle Pliocene), so that only exceptionally old species, which existed prior to this, now live on both sides of Central America.

TABLE 5

AMPHI-ATLANTIC AND AMPHI-AMERICAN COMMUNICATIONS IN THE FAUNAS OF STENOTHERMAL WARM-WATER CRABS (BRACHYURA) AND ECHINODERMS (ASTEROIDEA, OPHIUROIDEA AND ECHINOIDEA)

	Crabs		Echinoderms	
	Species	Genera	Species	Genera
Total number	300	115	160	62
	Percentage of total number			
Amphi-Atlantic forms . . .	8%	22%	15%	42%
Amphi-American forms . . .	6·5%	62%	2·5%	48%

For the genera the amphi-American affinity is distinctly greater than the amphi-Atlantic as regards the echinoderms and with a much more marked difference in the case of the crabs (62% as against 22%).

Our knowledge of the West African fauna is of course at present imperfect, but the difference may to a certain degree persist even with improvement of our present knowledge. This is quite natural, for the history of the dispersal of the genera goes back to the early Tertiary Period and we have already seen that an open sea communication existed for the greater part of the Tertiary Period across present-day Central America. This communication was of a littoral character and thus it was much easier for the coastal fauna to pass across than the central Atlantic. But even the latter seems to have been passable for animals with a long pelagic larval stage or where there were opportunities for passive transport by floating seaweed and so forth.

Other animal groups show much the same picture of distribution which is connected with the general paucity of the East Atlantic tropical fauna. All 26 Atlantic genera of reef-corals are thus found in the West Indies but only five in West Africa, while the 12 Atlantic genera of the so-called mæandric Astræidæ are exclusively American.[177] The holothurian fauna of West Africa differs greatly from the West Indian; and so on.

There is, however, a small number of genera which show that the tropical-subtropical Atlantic has some slight degree of unity in that they possess species in both the eastern and western parts, but not outside the Atlantic. Among the crabs we may instance *Cryptochirus* with its single species *corallicola*, which lives in the limestone-walls of the corals and causes the formation of galls; further the fish genus *Sparisoma* (fig. 15) just mentioned; among the mammals *Manatus*, which is the sole member of the family Manatidæ among the sirens, with four species, of which three live in tropical America and the fourth in West African rivers and Lake Chad. Among the species which are evidence of an amphi-Atlantic communication we may mention the crabs *Panulirus guttatus* (spiny lobster), *Stenorhynchus seticornis* and *Lysiosquilla scabricauda*.

Among the amphi-Atlantic genera, too, twin-pairs have been found, for instance among the ascidians. Thus the East Atlantic *Diazona violacea* is regarded as a twin to either of the two West Atlantic species *Diazona gigantea* and *D. geayi*.[246]

Relationship to the Indo-West-Pacific

In the preceding chapter we have already discussed the relationship of the West Indian fauna to the Indo-West-Pacific when we compared it with the American Pacific fauna. We will now compare its relationship to the Indo-West-Pacific fauna with its relationship to the East Atlantic and in doing so we shall find that the West Indian coastal fauna shows a closer affinity with the fauna of the Indian

ocean and the Malayan archipelago than with the East Atlantic, and this despite the fact that the last-mentioned fauna lives in the same ocean whereas the Indo-West-Pacific is much further distant and also isolated from the West Indies by land masses (West Asia and Central America) or by cold-water regions (south of Africa and South America).

We have already seen that of the stenothermal warm-water genera of West Indian crabs 22% are also represented in the eastern Atlantic. The percentage of genera which are also represented in the Indian Ocean or West Pacific is 36·5. To these belong for instance the queen

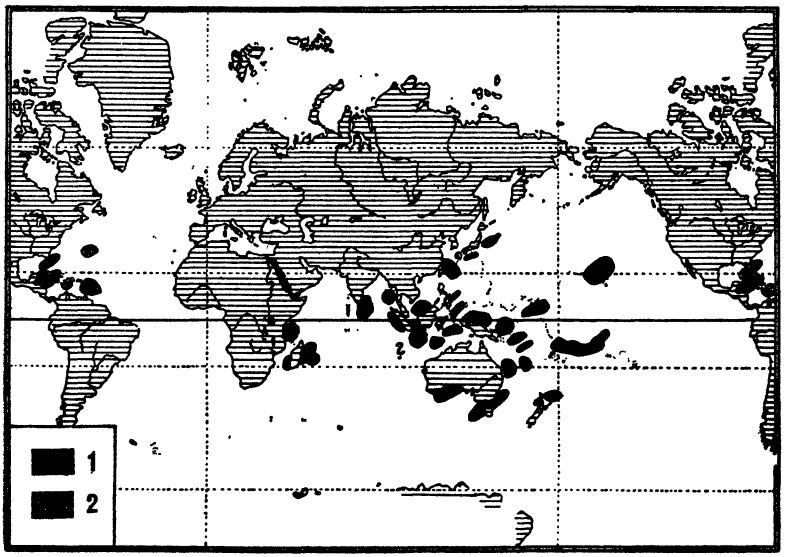


FIG. 18.—Distribution of the squid genus *Sepioteuthis*. Species which are certain members of the genus may be divided into two groups taxonomically: the purely Indo-West-Pacific *lessoniana*-group (1) and the, at least predominantly West-Indian *ehrhardti*-group (2). (After Wülker, 1912.)

crabs, *Carpilius*. For the echinoderms the figure for East Atlantic common elements is 42% and for the Indo-West-Pacific 64–65%. Among other animal groups, too, roughly the same proportions have been found. An example of such a group are, according to Chusman,[96] the Foraminifera. Of the 26 genera of reef-corals of the West Indies 21 are to be found in the Indo-West-Pacific (Gerth[177]) and only five in West Africa. The genus *Sepioteuthis* (fig. 18) among the squids has the same distribution. Tortugas and Bermuda possess Indo-West-Pacific species of the alcyonarian family *Plexauridæ*.[521] The historian of the Atlantic Ocean, H. v. Ihering (1907), in his

account of the Tertiary and Recent mollusc fauna, has furnished several examples of the same distribution, which he considers due to the extent of the Tethys Sea in the Tertiary Period. The snail genus *Fusus*, known for its decorative shell, is one of these examples.[186] As far as the ascidians are concerned, Huus[246] and Michaelsen[337, 338] have stressed the West Indian–Indo-West-Pacific affinity. Van Name[369] notes that the relationship of the same group of animals with West Africa is weaker than might be expected and continues: "It is to the fauna of the Indian Ocean, Red Sea and Malay region that the most significant relationship exists." Other examples might be adduced.

What has been said so far applies to the genera. But as regards the species the West Indies have a somewhat greater resemblance to West Africa than to the Indo-West-Pacific, as emerges from the table (p. 49) on the distribution of crabs and echinoderms. These proportions may be regarded as fairly representative for most animal groups. This greater degree of relationship for species in the amphi-Atlantic distribution and for genera in the West Atlantic–Indo-West-Pacific distribution can only mean that in modern times and as long as the species existed in their present development, communication with Africa across the Atlantic has been easier—the passage to the Indo-West-Pacific being at present completely blocked for stenothermal warm-water animals—but that in earlier times there was an open communication with the Indian Ocean prior to the evolution of the present-day species but within the lifetime of present-day genera. This question will occupy us again later (Chapter IV).

Subregions

The great region which is occupied by the Atlantic warm-water fauna of America (we shall occasionally, for the sake of brevity, refer to it by the perhaps not quite accurate term "West Indian") is too little known in detail to enable us to divide it with any degree of certainty into zoogeographical subdivisions. Some authors regard the long-stretched archipelago from Florida to Venezuela as forming a separate Antillean subregion. Whether it differs faunistically from the mainland coast of the Caribbean and the Gulf of Mexico in anything but abundance of species must at present remain undecided. Henderson[220] regards the Antillean subregion as comprising the whole region between Cape Hatteras and Brazil and he bases his view on the distribution of the scaphopods. H. L. Clark[86] places the southern limit for the Antillean echinoderms at the southern tip of the curve formed by the Antilles. It is possible that Brazil represents a subregion of its own as is the case, in fact, regarding the alcyonarians of the shallow water (E. Deichmann[119]),

but for several other groups the investigations at present at our disposal seem to show that its main characteristic is a pauperization of the rich profusion of the West Indian species.

The fauna of the Bermudas has been investigated from a zoogeographical point of view by Verrill.[570, 571] He maintains that these islands have received their fauna to an overwhelming degree from the Antilles, particularly from the Bahamas, under the influence of the Gulf Stream and to a large extent through the agency of floating seaweed. The fauna of the Bermudas is, therefore, a branch of the fauna of the Antilles, although impoverished. This view was confirmed for echinoderms.[86] All of the 50 crabs and 40 starfishes, brittle-stars and sea-urchins of the Bermudas are found also in the West Indies. Other animal groups show in addition to the main mass of West Indian species a slight admixture of northern elements. The coral reefs of the Bermudas are of particular interest. According to Vaughan[567] they rest on a Quaternary bedrock, which is not an old reef formation. They are, therefore, the result of a relatively recent colonization. In addition to the madreporarians of the genera *Porites*, *Mœandra*, *Mussa*, *Oculina*, *Astræa*, *Symphyllia* and others, the hydrocoralline *Millepora* forms the main constituent of the reef. Reef builders of a peculiar kind are certain polychæts of the family *Serpulidæ* and the snails of the genus *Vermetus* and related genera, whose chalk tubes together with the madreporarians form the main constituent of the miniature atolls which are known as "serpulid atolls" or "boilers" and have a diameter of only a few or at the most about 30 m.

The *northern part of the Gulf of Mexico* also occupies a special position in that both the fauna and hydrographical conditions differ from the neighbouring regions in possessing features which are more akin to warm-temperate regions, for instance off Beaufort south west of Cape Hatteras. I have to thank Dr. J. W. Hedgpeth for the following, as yet unpublished results. The temperature conditions may be seen in table 6.

TABLE 6

MEAN SURFACE TEMPERATURES DURING THE COLDEST AND WARMEST MONTHS AT THE GULF COAST OF MEXICO (GALVESTON 29° 20′ N., 94° 46′ W.; Port ARANSAS 27° 52′ N., 97° W.), CAPE LOOKOUT OFF BEAUFORT 115 KM. S.W. OF CAPE HATTERAS, DAYTONA IN N.E. FLORIDA, AND S.E. (WARMEST) FLORIDA.

	Coldest month	Warmest month
Galveston . .	12.0° C.	28·5° C.
Port Aransas . .	11·1	29·3
Cape Lookout .	12·5	26·7
Daytona . .	15·5	27·2
S.E. Florida . .	22·2	28·8

In the surface coastal water off Texas the summer temperature is thus completely tropical but the winter temperature, because of cold northern winds, is not even subtropical but warm-temperate, even a little lower than off Beaufort. This influences the fauna of the shallow water in such a way that certain mainly temperate species which are missing from southern Florida, are found along the northern coast of the Gulf. Such a species is *Littorina irrorata*, which reaches its south-western limit at the Mexican boundary. For the same reason certain species, which spawn during the summer off the temperate eastern North America, have shifted their spawning to the winter and early spring season off Texas. One of them is the economically important oyster *Ostrea* (*Crassostrea*) *virginica*, which, it is true, is also found further south but occurs as a community dominant only off the north coast of the Gulf of Mexico and off the east coast of America north of Florida. Possibly some hydroids also, for instance *Tubularia crocea* (which is, however, also tropical in the Pacific) are examples of the same peculiarity, viz. that (southern) Florida forms a distinct break in the distribution of several not tropical species which occur both to the north and west of the peninsula.

The temperature in the coastal water off Texas may sometimes fall below 5° C. or even lower, resulting in mass mortality of fish in enclosed waters. The low winter temperatures seem, however, to be confined to the surface water, since off Texas and Louisiana there stretches a belt of about 40 patches of small live coral reefs at about 50–70 m. depth.

B. TROPICAL-SUBTROPICAL WEST AFRICA

In an account of the warm-water fauna of West Africa it will suit our purpose to combine the fauna which is normally regarded as tropical and is called the Guinea fauna with the fauna adjoining it to the north, the so-called Mauretanian fauna. The marine fauna of West Africa is, it is true, one of the less well-known warm-water faunas, but what has emerged so far suggests that the Mauretanian fauna has so many elements in common with the Guinea fauna, that it should to a considerable extent be regarded as subtropical. It contains, however, many components which may justify our regarding it as a mixed fauna forming a transition to the northern warm-temperate fauna. But to make our account comparable with that of warm-water faunas discussed above, we shall include in the treatment both the Guinea fauna and the Mauretanian fauna, extending as far north as the Straits of Gibraltar.

To begin with we shall, however, confine ourselves to the Guinea

fauna. Examination of a number of animal groups on the west coast of Africa, for instance by the expedition led by W. Michaelsen, has made it probable that the boundaries of the tropical faunal region, indefinite though they are, should be placed in the north roughly at Cape Verde (15° N.) and in the south in the southern part of Angola, roughly at Mossamedes (15° S.) or possibly a little further south, near Great Fish Bay (16°–17° S.). Whether this southern limit is really the boundary of the tropical fauna or that of a subtropical or mixed fauna, has not been fully established.

The tropical region is considerably smaller on the African than on the American side of the Atlantic (fig. 19). The reason for this is to be found in the ocean currents and these in their turn are affected by the rotation of the earth. The result is that West Africa resembles western South America in that on both coasts branches of the southern West Wind Drift are forced up towards the north and cool down the water climate closer to the equator than in other oceanic regions. Along the south-west coast of Africa the cold Benguela Current flows, whose cooling influence is increased by upwelling water from the sea floor. It is only on the north coast of the Gulf of Guinea that a warm current flows close to the land. The contrast with the Atlantic coast of America, where warm currents flow past the land for considerable stretches, is obvious. Besides this, the warm water forms a considerably thinner layer along the African coast. The temperature at 100 m. depth brings out this contrast. It is (the annual mean) about 26° off Bahia, Brazil, and 24° off the Antilles, whereas off Africa it reaches 18° or 19° only in a small region just around the equator, in the Gulf of Guinea it is only 15–16°, while to the south and north of it within a region which comprises almost half of the tropical coast it is no more than 13–15°. In the deeper parts of the shelf the water is colder at Cape Verde than off Morocco and no warmer than in the latitude of Portugal (fig. 20). Here again we see a likeness with the west coast of America. On the west coast of Africa the tropical fauna is restricted to a considerably thinner surface layer of water than in any other tropical region. This may be the cause of the communication between the northern and southern temperate fauna which has been suspected, and in some cases demonstrated, along this coast (see p. 195).

The West African tropical fauna is poorer than any other tropical coastal fauna. Michaelsen, who studied the fauna on the spot, found the determining causes of this in the temperature of the water, the constitution of the sea floor, which here consists of sand, and in the open situation of the coast, which provides no shelter from the surf. The sandy material of the sea floor does not provide a suitable basis for coral reefs. Some reef-corals are found, of course, but

they do not form real reefs,[543] so that many corallophile species are also missing, which constitute such a considerable and interesting part of the fauna in other tropical seas. Upwelling water can inhibit

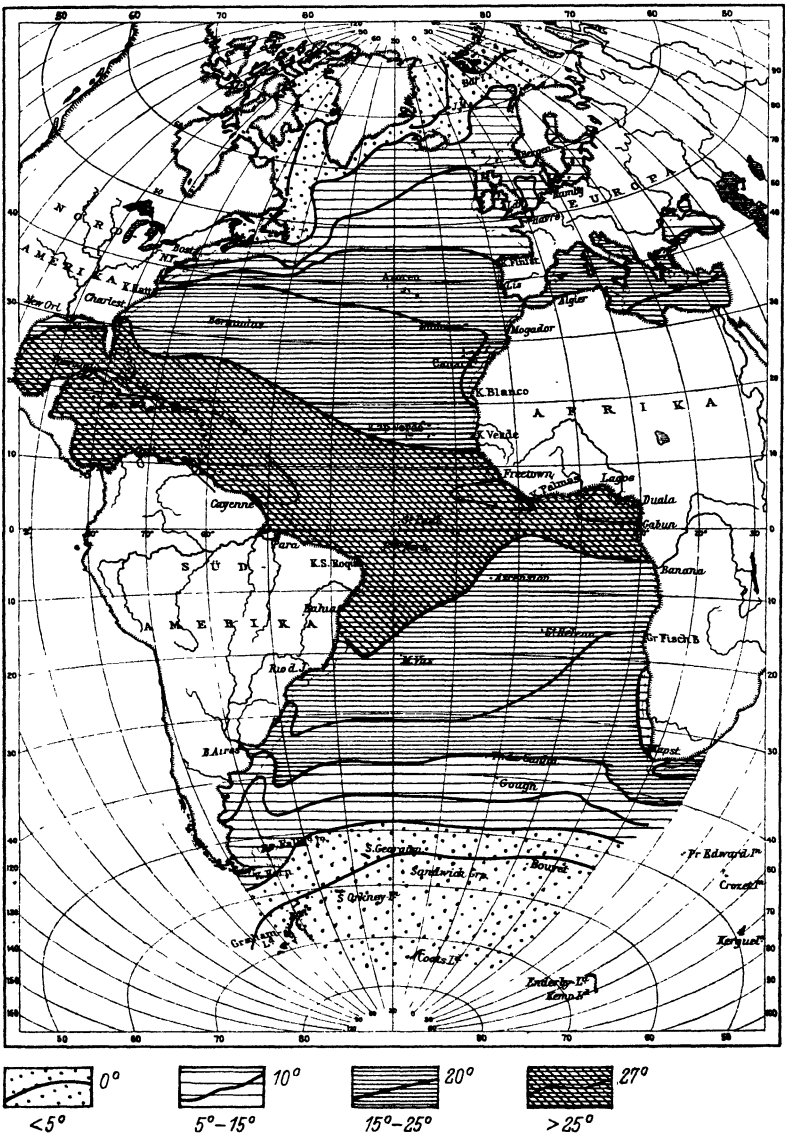


FIG. 19.—Mean annual temperature of the surface water of the Atlantic. (After Schott, 1926; slightly simplified.)

the proliferation of the fauna by its low temperature but not, as has been supposed at times, by lack of food, since on the contrary it contains plenty of plant food and favours a rich algal flora.

The region contains only an insignificant number of endemic

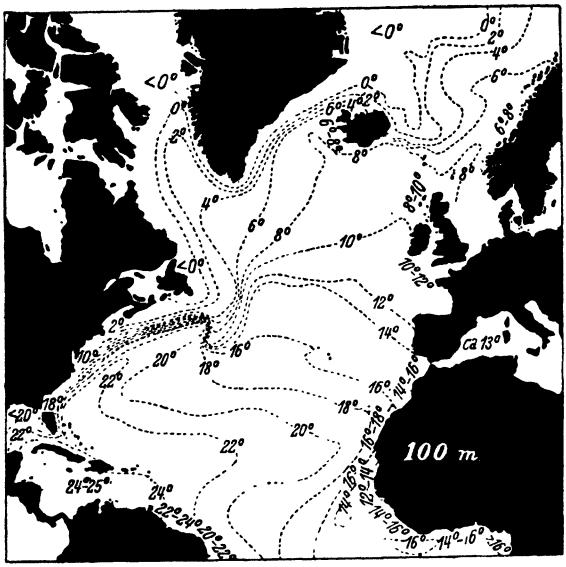


FIG. 20.—Temperature 100 m. below the surface in the northern and middle Atlantic. (After Murray & Hjort.)

genera. Among the crabs we find only one of these, the monotypic *Atlantotlos*, which was given its name because of the close relation with the Pacific genus *Tlos*. Among the gastropods we may mention *Pusionella* with at least 10 species,[529] among the sea-urchins West Africa's keyhole urchin *Rotula* (fig. 21) containing three species, of which two are found as far north as Cape Blanco and one as far out as Ascension, and last but not least the curious *Rhopalodina* among the sea-cucumbers with only one species (*lageniformis*, fig. 22), which forms a separate family and is known from several parts of the Guinea coast. These are the most important characteristics of the tropical fauna of West Africa.

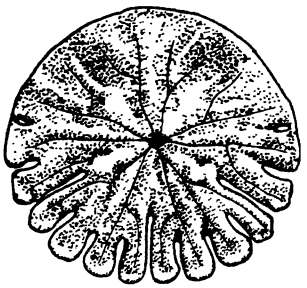


FIG. 21.—*Rotula* sp. two-thirds natural size. (After A. Agassiz, redrawn and simplified.)

The endemic species are, however, much more numerous and represent a fairly high percentage of the total number in several groups. For instance, it is 40% among decapod crustaceans, 60% among ascidians and 63% among molluscs (540 of 850),[389] but in others, as for instance in the corals, the percentage is lower. An investigation of the distribution of echinoderms,[282a etc.] has shown that roughly 50% of all species recorded in the region of the Gulf of Guinea are found exclusively there.

A scrutiny of the whole warm-water population of starfishes, brittle-stars and sea-urchins is summarized in the following table 7. It has been compiled to show whether the West African region is most closely connected with the western Atlantic or the Indian Ocean and the Indo-Malayan region. We see that the percentage of species tends very definitely towards the West Atlantic (West Indies) with 16% and only 1% for the Indo-West-Pacific, and that the genera, too, show the same bias, although not so strongly (6% and 2%). Furthermore we see how considerable a part is represented by the circumtropical or nearly circumtropical genera. If the Calculation is made with reference to the total number of stenothermal warm-water genera, the percentage is 74. Here we can still discern the after-effects of the Tethys Sea.

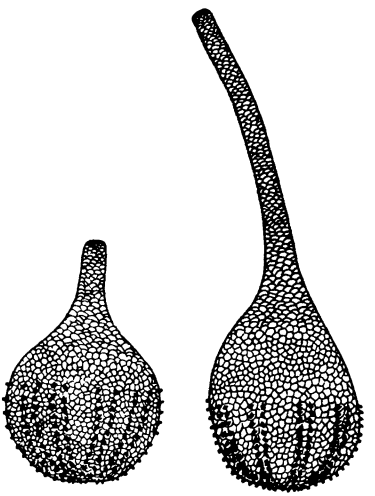


FIG. 22.—The holothurian *Rhopalodina lageniformis*, nearly double natural size. (After Panning, redrawn.)

Finally, the comparatively high number of species common to the African warm-water zone and the coastal water of South-west Europe throws some light on the very ill-defined transition between the subtropical and warm-temperate fauna in this region (cf. p. 81). The characteristic features observed in the geographical distribution of echinoderms may be representative for a large part of the remaining West African fauna.

We may now give some examples from other animal groups. Of the molluscs common to both the West African and West Indian faunas we may mention the ornamental snails or those known for other reasons such as *Dolium galea*, *Arca noæ* and *Petricola pholadiformis*. The possibilities of passive dispersal are, of course, of decisive

importance for stenothermal warm-water animals. A case in point is the genus *Astropecten* (Döderlein[128]). These starfishes have no suckers on their ambulacral feet. They are, therefore, unable to cling to seaweed and other flotsam and this has been of decisive importance for their distribution: the two coasts of the central Atlantic are inhabited not only by different species but even by different kinship groups of species within this large genus.

TABLE 7

ECHINODERMS (ASTEROIDEA, OPHIUROIDEA, ECHINOIDEA) OF THE ATLANTIC AFRICAN WARM-WATER REGION

	Species	Genera
Total number	110	70
	In percentage of the total number	
Stenothermal warm-water forms:		
Endemic to the East Atlantic warm-water region	57%	6%
Both in the East and West Atlantic but not elsewhere	16%	6%
Both in the East Atlantic and the Indo-West-Pacific but not elsewhere	1%	2%
Both in East and West Atlantic and in the Indo - West - Pacific (circumtropical partially excluding East Pacific)	1%	41%
Eurythermal forms: both in the East Atlantic warm-water and		
In the Atlantic north of Gibraltar	21%	45%
In southern temperate seas	3–4%	

There is a clear affinity also with the Indo-West-Pacific. The Atlantic is, of course, in communication with the Indian Ocean south of South Africa, so that it is not surprising that eurythermal species which are able to live both in the temperate coastal water of South-western Africa and in tropical water are to be found on both sides of Africa. But in the tropical Atlantic off Africa many stenothermal, purely tropical genera, both of echinoderms and other groups, are to be found which for the rest are present in the Indian Ocean, the Indo-Malayan archipelago etc. A smaller number now live only in the Indo-West-Pacific and East Atlantic warm-water region (West Africa, perhaps also the Mediterranean). Such genera are among the crabs *Thalamita* (many Indo-West-Pacific and one West African species), *Heteropanope* (similarly), *Matuta* and *Notopus*; Balss[27] mentions among other decapod crustaceans nine such genera. Among the molluscs we may mention many Indo-West-Pacific and one West African species. Simroth[481] gives

several similar genera whose distribution he explains by his pendulation theory (*Cynodonta*, *Persona*, *Crucibulum*, etc.). Some species, too, show the same distribution, for instance *Cassis tuberosa*, *Dolium perdix* and *Triton* species. In quoting these examples we must however point out the possibility that one or the other genus or species may be found in South-west Africa when the fauna there is better known. To the examples given we may add some from the fish fauna, such as the genera *Ephippus*, *Sparus*, *Cantharus*, *Dentex*. When we consider the Mediterranean-Atlantic fauna we shall mention other examples of genera occupying a similar position in this fauna. Probably some of them are also to be found in the West African tropical fauna although they have so far escaped attention.

Since these elements of the African marine fauna are not known from the West Indian region it is improbable that they have reached the African coast from there. We must, on the contrary, assume that their occurrence in Africa is due to historical causes; they point in fact to the existence in ancient times of a connection between the tropical and subtropical parts of the Atlantic and Indian Ocean. Such a connection did in fact exist. The tropical marine fauna of West Africa and the fauna of the Indian Ocean are both descendants of the fauna of the former Tethys Sea. This question will occupy our attention later (chapter IV).

As an appendix to the tropical-subtropical fauna of the Atlantic coastal region we may now mention the fauna of two islands situated far out in the Atlantic, namely *Ascension* (8° S.) and *St. Helena* (16° S.). According to an investigation undertaken a long time ago by E. A. Smith,[483, 484] 50% of the molluscs of both these islands are West Indian or closely related to West Indian species. The last-mentioned statement can, however, equally well mean that many of them are just as closely related to Indo-West-Pacific types. According to Smith, too, the East Indian types represent a fairly high proportion of it. See also Day[115] regarding the polychæts. The best known is the echinoderm fauna of St. Helena thanks to the investigations carried out by Mortensen.[354] Of the 26 species from the coastal waters of the island, 13 are to be found exclusively at St. Helena and the Ascension Island. Of the rest at least one, the starfish *Asterina exigua*, must have been transported there by drifting seaweed from South Africa, since it does not possess pelagic larvæ but develops directly. It is of common occurrence in South Africa and a species of seaweed which is also common there actually drifts frequently as far as St. Helena with a northerly branch of the Benguela Current which skirts the island during part of the year. Several molluscs of the genera *Mitra*, *Murex*, *Columbella* and *Gadinia* which

are endemic in South Africa have, according to Tomlin,[560] been transported to St. Helena by driftwood. Since the species in question are, as has already been stated, endemic in South Africa, their place of origin can be ascertained. This is a very interesting case of authenticated long-distance transport by an ocean current. But no permanent establishment at St. Helena of the species transported in this way seems to have resulted.

CHAPTER IV

HISTORICAL REVIEW OF THE WARM-WATER FAUNA OF THE SHELF

WE have seen that there is a faunistic resemblance between Pacific and Atlantic America and likewise between the tropical Atlantic and the Indo-West-Pacific, which is revealed in the occurrence of common families and genera and, less frequently, of common species. This is the case, although these various regions are now separated by barriers which are impassable for these animals—the Central American isthmus, the isthmus of Suez and the seas of the southern extremities of Africa and South America, which are too cold to permit stenothermal tropical animals to pass from one ocean to the other. This faunistic resemblance, which exists despite the discontinuity of distribution, obviously demands a special explanation. For the two coasts of tropical America we have already found the explanation in Tertiary geography; the problems presented by the rest of the tropical shelf fauna will find their solution along similar lines. We now enter upon a field which demands a historical treatment if we are to understand the present zoogeographical situation.

THE TETHYS SEA

Across the greater part of our planet an immense sea once stretched, mainly in an easterly and westerly direction, dividing the continents into two main groups, a southern and a northern group. It connected up the East Pacific, the Central Atlantic, the Mediterranean, the Indian Ocean and the West Pacific (fig. 23). What is to-day Central America and South-west Asia was thus covered by the sea. We propose to follow Suess and call this sea the "Tethys", the name of the wife of the god Okeanos; other names for it are Mediterranic, Mesozoic Mediterranean, Nummulite Sea, Mésogée, etc. All palæogeographers agree that this sea existed and they only differ as to its extent in time and space; it was, however, for long geological periods one of the most constant traits of the main topography of the earth. It existed already in the Lower Cambrian and continued with perhaps some brief local interruptions until the later Tertiary Period. During the whole of the Mesozoic era and

early Tertiary Period the Tethys Sea was of considerable size. Marine deposits in the Mediterranean region and in South-west Asia fully establish the existence of a former link between the Atlantic and the Indian Ocean represented by the Tethys. The Indo-West-Pacific, the Mediterranean, the tropical Atlantic and East Pacific faunas were, therefore, parts of one major unit, the Tethys fauna. Thus a knowledge of the former Tethys fauna is of the greatest importance for the understanding of the present warm-water fauna. Fortunately, we know the chief characteristics of this fauna fairly well in so far as corals, molluscs, echinoderms and fishes are concerned.

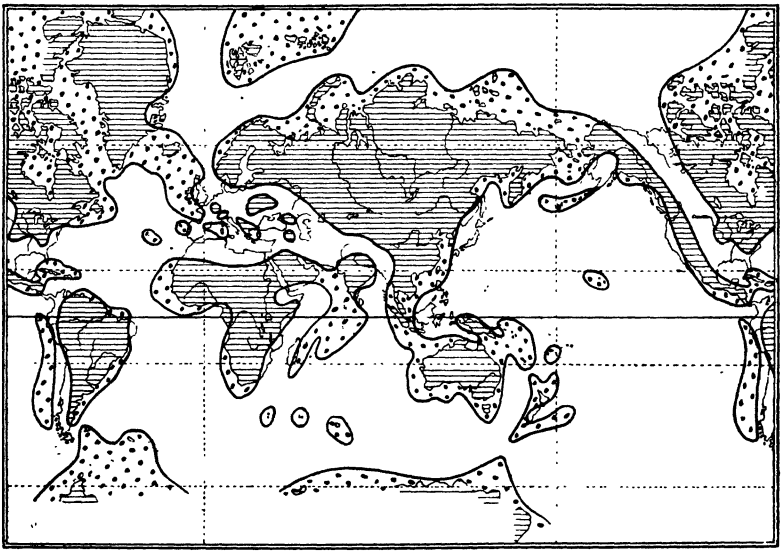


FIG. 23.—Land (lined or dotted) and sea in the middle or upper Cretaceous. Later on the Tethys Sea became directly connected with the East Asiatic coast. (After Schuchert.)

THE TROPICAL PROFUSION OF THE ATLANTIC TETHYS FAUNA

Palæontological studies give us a very vivid impression of the great multitude of species and the tropical character of this early Tertiary Atlantic fauna. In the Mediterranean region the early Tertiary reef-coral fauna was well developed; no less than 65 genera (Gerth[177]) are known, whereas the number of the present genera in the East and West Atlantic together is only 26. About 40 early Tertiary genera of reef-corals are reported from the less well-known West Atlantic region, 32 from the western Indian Ocean and at the most 35 from the Indo-Malayan archipelago. The last two regions have, however, not been so thoroughly examined for their early

Tertiary coral fauna as the Mediterranean region. Bernard[45] says of the genus *Goniopora* that it is doubtful whether this genus is so abundantly developed anywhere to-day as it was in southern Europe during the Eocene. In the later Tertiary Period, however, these circumstances were completely altered. Gerth (cf. also [156–158]) emphasizes that in the later Tertiary Period it is no longer in the Mediterranean region, but in the Malay archipelago that we find the richest development of reef-building corals. The number of late Tertiary genera here exceeds that of any other region, being 70 in number. In the Mediterranean region there are still nearly 50 genera of reef-corals in the late Tertiary Period but only the *Astræidæ* show any further development, while the *Porosa* are inhibited. This retrogression is particularly striking among the *Fungiidæ*. The reef-corals were confined to the most southern portion of the Mediterranean region, their reef-building activity finally ceasing at the end of the Tertiary Period. In the West Indies, too, a distinct, though not so great, diminution took place (Vaughan[567]; see below).

Similar findings have been reported also for other animals. All groups known to occur in the early Tertiary Period were represented by an abundance of tropical species in the Tethys Sea. Zittel in his *Handbuch der Paläozoologie* mentions the astonishing profusion of snails in the Eocene and Oligocene strata of the Paris basin. The Eocene molluscs of this basin are nowadays confined to the tropics. Not until the Miocene and especially in the Pliocene did the European fauna begin to assume its present-day character. Tropical genera disappear and their place is taken by new types immigrating from the north. We shall presently find examples of this transformation when discussing the changes in climate. The Paleocene fish fauna of Belgium was tropical or perhaps subtropical, the Eocene fauna mainly tropical.[300] For the tropical Mediterranean fish fauna of the Eocene see below, p. 69.

As examples of the abundance of the Atlantic fauna in the Mesozoic and early Tertiary Periods we quote the following figures for two groups of sea-urchins and crinoids (table 8 p. 66).

It is remarkable how rapidly the number of species decreases as we approach the present time. We mention for the sake of comparison that the Mediterranean and neighbouring parts of the Atlantic nowadays contain only two cidaroid species in coastal waters and two in the abyssal region, the Indo-Malayan archipelago only 48 species. Many of these recent species are, however, abyssal, while all fossil ones belonged to the shelf region (no fossil abyssal fauna is known). The former richness of the Atlantic is thus made all the more apparent. A comparison with the Indo-West-Pacific Mesozoic fauna which, however, is not so well explored as the European one

shows, as Mortensen[352] states, that the European cidaroid fauna was far richer in species and that Europe during the Mesozoic Period was a paradise for the cidaroids, as also for the rest of the echinoderms. This statement may be couched in this general form: in the Cretaceous and early Tertiary Period Europe's and North Africa's coastal waters housed an extremely rich fauna which has now for the most part disappeared from these regions and to a great extent also from the whole Atlantic, in some degree even from the rest of the world.

TABLE 8

NUMBER OF SPECIES OF CIDAROIDEA AND COMATULIDA (GROUPS OF SEA-URCHINS AND CRINOIDS RESP.) IN THE EAST ATLANTIC DURING THE MESOZOIC AND TERTIARY PERIODS

	Cidaroidea[352]	Comatulida[182]
Pliocene	3	2
Miocene	26	30 (38?)
Eocene	73	4 (6?)
Upper Cretaceous	95	49 (55?)
Middle Cretaceous	65	
Lower Cretaceous	68	16 (17?)
Upper Jurassic	101	37 (43?)
Middle Jurassic	193	

This superiority of the earlier periods is even more striking than it appears, since the actual number of species during that time is of course only imperfectly known. It is true that the earlier periods generally lasted longer than the late Tertiary Period, but this could not account for the facts just propounded. To give an idea of the relative, and also in rough terms of the absolute, length of the geological periods, we quote the result of the most recent investigations in the following table. This table may be of interest also in connection with other zoogeographical problems.

TABLE 9

THE LENGTH OF GEOLOGICAL PERIODS IN MILLION YEARS
(after two alternative calculations by A. Holmes, 1947)

		1 million years
Quaternary or Pleistocene		
Tertiary	Pliocene	11–14
	Miocene	14–17
	Oligocene	12–15
	Eocene	20–21
Mesozoic	Cretaceous	69–72
	Jurassic	25–27
	Triassic	30–29
Palæozoic	Permian	21–24
	Carboniferous	52–55
	Devonian	58–43
	Silurian	37–32
	Ordovician	80–80
	Cambrian	80–80
	Sum	510

In order to understand the present distribution of organisms over the earth's surface we have thus to take into account a considerable mortality which in some cases affected not only certain genera and species in the various regions, but even higher systematic groups and whole faunas. That this is well within the bounds of possibility is shown by the well-known history of the nummulites and rudists (Foraminifera and Mollusca respectively). The first mentioned, which possibly originated as early as the Jurassic period, became more common in the Cretaceous, appeared in large masses in the Eocene and subsequently died out almost completely. The rudists, which actually formed reefs in some regions, lived only in the Cretaceous Period. Both groups were tropical organisms and their distribution coincided almost exactly with the Tethys, the "Nummulite Sea". The reason for this extinction of large animal groups before the great climatic transformations of the middle and late Tertiary seems at first sight inexplicable. To one who looks on the world of nature with the philosopher's eye it makes a profound impression of the sheer squandering of life; to the student of zoogeography it stands as a warning against drawing from the absence to-day of certain animal groups from a particular region the premature conclusion that they developed exclusively in other regions.

THE INDO-WEST-PACIFIC CHARACTER OF THE LOWER TERTIARY ATLANTIC FAUNA

It is a most interesting fact that the early Tertiary Atlantic fauna had a distinct Indo-West-Pacific character. This is true especially of the Mediterranean fauna. The important paper by Gerth[177] on Tertiary reef-corals contains the following data: of the numerous Mediterranean species 12 were distributed as far as the Malay region but not as far as the West Indies, while all species found in the last-mentioned region as well as the Mediterranean also occurred in the Malay region. Among corals which were common to the Mediterranean, Indic and Malay region but were missing in America we may single out the evolutionary series *Cyclolithes-Cycloseris-Fungia.* Gerth has summarized the lower Tertiary conditions as follows. The connections of the Malay region with the Mediterranean seem to have been closer than with the West Indian region latter, but they were also closer than those between the West Indies and the Mediterranean region. The India and the Malay archipelago have a considerable number of forms in common which we fail to find in the West Indies. But in the late Tertiary Period (Neogene) the picture is much changed: the faunas of the various regions are much more specialized so that only 10 genera can be found which are distributed

through all four regions . . . In the Neogene (Miocene and Pliocene), therefore, relations between the Indic region and the Malayan are much closer than between the Indic and the Mediterranean; interchange with the latter region ceased to take place or at least became difficult. The Indic region began to form a faunistic zone in conjunction with the Malayan archipelago.

Similar changes, too, took place in other animal groups. In the Palæogene (Eocene and Oligocene) the East Atlantic fauna was much more closely related to the Indo-West-Pacific fauna than it is to-day. This relationship seems, however, to have been still closer in the Cretaceous. But in the Miocene and Pliocene this affinity disappeared for the most part.[328, 329] Views in complete agreement with these modern results had already been expressed by Zittel (1881–1885).

The following list will make clear this change of faunas. It comprises only such genera and families which are to-day exclusively Indo-West-Pacific but were formerly also to be found in the Eastern Atlantic. (The facts are taken from the relevant literature; fossil occurrence outside the East Atlantic region has not been mentioned. This is by no means a complete list but comprises only typical examples.)

Examples of Animals at Present Confined to the Indo-West-Pacific but formerly existing also in the East Atlantic.

Alcyonaria: The family *Helioporidæ* contains only one living genus with a single species, *Heliopora cærulea* which is exclusively Indo-West-Pacific. In the upper Cretaceous, however, where they were at their maximal development, *Heliopora* possessed 13, a second genus *Epiphaxum* five, a third *Ahrdorffia* two species in Europe. From the Eocene and Oligocene of Europe only three *Heliopora* species and one *Epiphaxum* species are known, from the Miocene only one species of

Madreporaria: To these belong more than 20 genera, among them *Euphyllia, Goniastræa, Cycloseris, Stylophora, Goniopora, Astreopora*, etc., from the Tertiary deposits in the Mediterranean region.[177]

Crustacea: The genus *Linuparus* which is now found in Japan is known from the Cretaceous and Eocene of Europe. Much the same is true of *Thalassina, Charybdis*, etc.

Xiphosura: This order is to-day, it is true, not restricted to the Indo-West-Pacific, but it is not found in the East Atlantic. In the Jurassic, Cretaceous and Eocene it was well represented in Europe and Palestine.

Molluscs: Many genera of molluscs may be cited as examples. We will confine ourselves here to *Nautilus*, known as the modern representative of the once prolific tetrabranchiate Cephalopods. *Nautilus* was widely distributed in Europe from the Triassic to the Eocene Period.

Echinoderms: The sea-urchin genera *Phyllacanthus, Parasalenia* and

Fibularia may be cited as examples, and moreover the order Holectypoida with the single family *Echinoneidæ*, which was formerly rich in species. "Although the circummediterranean region was formerly the centre of the echinoneids, not a single representative of the family has survived there till recent times" (Mortensen[352]). The three recent species inhabit Indo-West-Pacific, one of them also the western Atlantic.

Fishes. Thanks to the investigation of many fossil-bearing deposits within the Mediterranean region, especially the Eocene strata of Monte Bolca near Verona and Monte Postale near Vicenza, in which 154 fish species were found, the lower Tertiary fish fauna of the Mediterranean is fairly well known. Sauvage[457] classified 50% of Monte Bolca fishes as Indic, 15% as ancestral forms of modern Mediterranean species, and the rest as tropical Atlantic. The majority of the genera, families, etc., mentioned from the fossil Mediterranean fauna have now disappeared from the whole of the Atlantic Ocean and exist only in the Indo-West Pacific region.[266]

Pristiophoridæ, saw sharks. The only modern genus, *Pristiophorus*, is known also from the Würtemberg Miocene.

Gonorhynchidæ: Upper Cretaceous to Oligocene in Europe and the Lebanon; only one modern genus.

Centriscinæ: One surviving genus, *Centriscus*, is known of this little subfamily from the European Oligocene.

Solenostomidæ: One modern genus in East India and one from the Eocene in Italy.

Leiognathidæ: Two genera in Japan, the Malayan archipelago and Polynesia, one from the Miocene of Italy.

Platacidæ: A family with few species; the genus *Platax* also know from the Miocene of Italy.

Scatophagus: This genus among the butterfly-fishes represents at present a separate family; it is known from the Italian Eocene.

Siganidæ: This family is sometimes regarded as forming a separate suborder; it possesses one genus in the Tertiary deposits of Switzerland.

Mammals. The mammals, too, make an interesting contribution to the present problem because one of the families of Sirens, the *Halicoridæ*, which now occur only in the Indian Ocean and West Pacific, were formerly found in the Mediterranean region, where, in fact (according to Abel, 1914), they had their centre of development, disappearing during the later Pliocene.

The examples given here could be multiplied (see Arambourg's extensive work of 1927). The phenomenon here exemplified, namely that the Tertiary fauna of the Mediterranean and East Atlantic shows a closer relationship than the modern fauna of these regions to that of the Indo-West-Pacific, puzzled older zoogeographers and palæontologists. The discovery of a one-time continuous Tethys fauna has cleared up this mystery.

The West Indies, too, showed a closer affinity to the Indo-West-Pacific during the Eocene and Oligocene than to-day, although the divergence from the present-day state is not so striking as in the case of the East Atlantic. Several reef-corals which now have disappeared from the West Indian region contribute to this closer earlier resemblance.[567] Such were for instance *Galaxea*, *Goniastræa*, *Favites*, *Stylophora*, *Pocillopora*, *Goniopora*, *Astreopora*. The now exclusively Indo-West-Pacific sub-family *Hexapodinæ* of the crabs was represented during the Oligocene by the genus *Thaumastoplax* also in the Panama region. Among the fishes a similar history of distribution is shown by the genus *Chirocentrus* (Clupeidæ).

Finally, a considerably closer relationship existed between the eastern and western parts of the Atlantic than at present. Most genera of the various groups of animals which are now confined to the West Indies, the Indian Ocean and the Pacific were formerly also found in the East Atlantic. Other genera with a less extensive range of distribution which now only live in the West Atlantic are also known from Tertiary deposits in the Mediterranean region; for instance, to mention only a few of the better-known examples, the curious crinoid genus *Holopus* and, among the fishes, *Brevoortia* (menhadens).

The lower Tertiary (Paleogene) Tethys fauna was, therefore, more homogenous than the present tropical-subtropical shelf fauna. Within this extensive area, however, certain differences existed, of course, also in previous periods and this makes it possible to distinguish between an Indo-European and a Central American region.

THE LATE TERTIARY CLIMATIC CHANGES

The tropical character of the former central Atlantic fauna changed considerably in the later Tertiary Period. A substantial portion of the early fauna died out. That this was due mostly to the climate's becoming colder is proved by the immigration of northern forms, which took place simultaneously with the disappearance of tropical forms. A parallel development among the terrestrial fauna leaves no doubt as to the correctness of the theory of climatic change.

Let us consider the Mediterranean region. We recall the number of cidaroids in the East Atlantic: 95 in the upper Cretacean, 73 in the Eocene, 26 in the Miocene, three in the Pliocene and two coastal forms in recent times. The changes in the other echinoderms, the corals, molluscs and fishes, all point in the same direction, although in general the decline was not so steep. The northern elements of a temperate fauna immigrated especially during the Pliocene period. Cottreau says of the Mediterranean that the disappearance of the tropical genera of sea-urchins such as *Clypeaster* and *Diadema* was

simultaneous with the appearance of northern ones such as, for instance, *Echinus* (which already arrived in the Miocene) *Strongylocentrotus* and *Sphærechinus*. Arambourg[16] found only a very faint similarity between the fish fauna at the end of the Miocene and the Monte Bolca fauna; the late Miocene fauna was no longer tropical but consisted essentially of the ancestral forms of the present Mediterranean fauna and derived only to a small extent from the fauna of the Eocene. Arambourg regards even the Oligocene as subtropical and not as tropical. The Quaternary fauna of the Mediterranean will be described in Chapter V.

The fauna which was displaced from the Mediterranean withdraw partly to West Africa, which even to-day harbours some of these refugees, as for instance species of the mollusc genera *Oliva*, *Cypræa*, *Fossarus* (Dautzenberg[110, 111]). Several others, however, are no longer to be found in West Africa. One of the reasons for this is probably that the climate of West Africa was colder during the Ice Age than it is to-day. On the coast of Senegal, 55 m. above sea level, a fossil mollusc fauna of this period has been discovered which includes northern species now no longer found in these waters, as for example *Cardium edule*, *Tapes aureus*, *Bittium reticulatum*, *Hydrobia ulvæ*.[132]

On the American side, too, a change took place which was, however, not so catastrophic for the tropical fauna. Here, too, the lower Tertiary climate was entirely tropical. In the Miocene a climatic deterioration occurred which destroyed the tropical marine fauna in Florida, Georgia and the neighbouring states and it was replaced by a cold-water fauna. The disappearance of East Indian types of corals was one of the consequences of this change in climate, which has also found confirmation in the facts relating to the molluscan fauna. This revolution in the marine fauna is, according to v. Ihering,[248] the most sudden and complete which has been observed during the whole of the Tertiary Period in the south-eastern region of the United States. The upper Oliogecene molluscan fauna of the territory in question, which had 34% of its species in common with the middle Oligocene, had only 3% in common with the Miocene Period which followed upon it. The genera and species of the tropical seas had disappeared with but few exceptions and elements of the colder water fauna of the temperate zone took their place. The cold-water fauna remained in Florida and Georgia during the whole of the Miocene. In the course of the Pliocene the tropical forms which had been driven out reappeared, some of them not until the Pleistocene. In the Greater Antilles, too, signs of a climatic deterioration have been found. In the Caribbean the temperature seems to have sunk from 26–27° C. to 19–20°, a considerable fall.

Both sides of the Atlantic Ocean were thus subject to a late Tertiary climatic deterioration. There was, however, this difference that on the American side the tropical climate and the tropical fauna reappeared in the Pliocene and Quaternary period, while tropical West Africa and especially the Mediterranean received back only an insignificant part of its original fauna. North-eastern South America seems to have been a refuge for the tropical fauna during the Pliocene and early Quaternary Periods.

In the *Indo-Malayan region*, however, no climatic change of importance took place either in the Tertiary or Quaternary Periods.[123, 124, 329] The tropical fauna of the Cretaceous and Eocene could maintain itself in all its tropical abundance and developed until our own time.

THE EAST PACIFIC BARRIER AND OTHER BARRIERS

It emerged in our discussion of the Indo-West Pacific and East Pacific American fauna that the pelagic and abyssal region between outermost Polynesia and America represents a most important zoogeographical boundary. The further we go from the rich Indo-Malayan archipelago the poorer the littoral fauna becomes although its general Indo-Malayan character is unmistakable. It is particularly noteworthy that the missing Malayan types have not been replaced by American ones in Polynesia, or at least only in a very few cases. When, proceeding further east, we reach the coast of America we meet there with a fauna which, although living in the same ocean, nevertheless shows a decidedly closer relationship to the Atlantic fauna.

The explanation of this difference between East and West Pacific is not difficult to find. With this problem we enter the field of ecological geography, the ecology of distribution. In the present case we are concerned with a stenothermal warm-water fauna bound to the coastal waters which cannot migrate through the intervening abyssal region or circumvent the pelagic regions of the oceans along the curve of the northern coast, since this is situated in the temperate, and to some extent even in the arctic zone. For the members of this benthic warm-water fauna migration across the eastern expanse of the Pacific, which lacks islands, is only possible by passive transport through ocean currents, whether directly of the animal itself or with the help of flotsam to which the animal attaches itself. The longer the period of drifting, the less the likelihood of its reaching a suitable new coastal region. For in most of the animals with which we are concerned here the planktonic larval stage, where it occurs, is too short to allow transport by ocean currents from Polynesia to America. Masses of larvæ find, of course, their way out each year

into the ocean drifts, but when they reach the stage of metamorphosis and sink down into abyssal waters they die.

That the length of the larval stage is in many cases the decisive factor may be made clear by the following example: in his travels in the tropics Mortensen[357] investigated the larval stages of some 40 starfishes, ophiuroids and sea-urchins. Among the six which had the longest phase of development, the planktonic stage from fertilization to metamorphosis into the non-planktonic benthic stage takes 40 days or longer; of these six species five are distributed from East Africa or the Red Sea to Hawaii or Outer Polynesia, the sixth only as far as Western Polynesia, but one of them, *Ophiocoma scolopendrina*, reached Clipperton Island, 1000 km. off Mexico.

The tropical-subtropical shelf fauna surrounds the globe in the equatorial zone in a broad belt which, however, shows certain interruptions in its continuity. This is due partly to land bridges right across the marine faunal belt, and partly to the fact that the shelf regions are separated by pelagic regions of varying width. Of these pelagic regions in the oceanic zone the most extensive is the one between Outer Polynesia and America. Within the tropical-subtropical zone this stretch of water has no continuous coastline or even a scattered archipelago which would permit the warm-water fauna of the shelf to spread in the direction of the equator. This oceanic region, the *East Pacific Barrier*,[143, 145, 146, 148] is responsible for the most pronounced break in the circumtropical warm-water fauna of the shelf. This is particularly true of the distribution of species and genera and to a certain extent also for that of families.

Starting from the distribution of echinoderms (starfishes, sea-urchins and brittle-stars), we shall now examine more closely the effect of the East Pacific Barrier on the separation of faunas. We are here particularly concerned with the effect of this barrier on the warm-water fauna and must, therefore, confine our attention to stenothermal warm-water genera and species. This means that in the study we now propose to undertake we have to exclude those elements which are also able to live in temperate regions or in the deep sea and therefore may find it possible to migrate either along the northern coast and archipelago which runs in a curve from tropical East Asia along Japan, the Kuril Islands, and the Aleutian Islands to the west coast of North America right down to tropical Central America, or through the abyssal region. A genus with eurythermal species in addition to stenothermal warm-water species has in the course of time had the opportunity to spread along one or the other of these routes and its occurrence on both sides of the Pacific barrier does not necessarily imply that the distribution took place across it.

In the above consideration of the position of the Indo-West-

Pacific fauna compared with that of West America we have only incidentally touched on the effects of the barrier, since a substantial part of the aforementioned fauna, for instance the Indo-Malayan, did not come into contact with the barrier. If we now come to examine the direct consequences of this barrier we must confine ourselves to the faunas which border on it, namely in the west that of Hawaii and Outer Polynesia (Tuamotu, Tahiti, Fanning, Palmyra) and in the east that of the tropical-subtropical coast of America. The total number of genuine warm-water *species* of the echinoderm groups mentioned in these border regions amount to 240. Leaving aside the completely circumtropical Ophiuroid *Ophiactis savignyi*, which is found on both sides of the isthmus of Panama and may have arrived on the west coast of Central America just as well from the East Indies as from Central Pacific waters, the number of species known to be or supposed to be common to both sides of the barrier is only four, or 1·7%, including *O. savignyi* 2·1%. Therefore, roughly 2% were able to overcome the barrier while 98% of the species found it impassable. But the matter is somewhat different for the *genera*, which had a longer period at their disposal. The total number of these is a little over 80, the circumtropical genera being excluded unless particular circumstances make it possible to decide whether an amphi-Pacific distribution (across the East Pacific barrier) is acceptable or not. Amphi-Pacific distribution can be proved, or is likely, for 11–12 genera, or roughly 14%, but is unlikely for 86% of the total number of genera in the neighbourhood of the barrier.

A similar calculation as to the extent of the amphi-American (Atlanto-Pacific) communication across what is now Central America shows that the *Isthmus of Panama* represents just as much of a dividing line for the *species* as the East Pacific barrier. This is not surprising since on the whole the species do not extend as far back as the time when the Atlanto-Pacific straits existed in the Pliocene period. But the age of *genera* must be dated much further back and their distribution reflects the easy connection which once existed between the two oceans through the straits of Central America. The number of genera concerned is 80 (as in the previous case). For 37% of these amphi-American possibilities of distribution must be taken into account, while for 63% no such possibilities seem to have existed.

Roughly contemporary with the Central American landbridge another landmass which divided the faunas appeared in the Tethys, namely in South-west Asia, separating the Mediterranean from the Indian Ocean. It is interesting to compare this *South-West-Asiatic Barrier* with the two just considered. As boundary faunas of this barrier we may choose on the one hand the stenothermal warm-water

fauna of the Mediterranean and West Africa, and on the other hand that of the north-western part of the Indian Ocean, namely the Red Sea, the Persian Gulf and the Arabian Sea reaching east as far as Ceylon. The figures which refer to the same groups of echinoderms as in the previous case, must of course be only approximations in view of our incomplete knowledge of this region. They show that 35–38% of the total number of genera of this boundary fauna are common to both sides of the barrier. If we classify only the Mediterranean fauna as Atlantic boundary fauna with respect to this barrier and exclude from this classification the warm-water fauna of the East Atlantic (although such an exclusion would hardly be justifiable), the percentage would drop to 22.

Finally, we shall discuss by way of comparison a fourth obstacle to distribution which, like the East Pacific barrier, consists of a broad pelagic and abyssal region, namely the *Central Atlantic Barrier*. The stenothermal faunas bordering on this region are that of the West Indies on the one hand and the West African and Mediterranean fauna on the other. To make this obstacle to distribution fully comparable with those mentioned previously we shall examine the same echinoderm groups. As regards species, those common to both Atlantic coasts are comparatively more numerous than those common to the faunas bordering the East Pacific barrier. This is to be expected in view of the smaller width of the pelagic region of the Atlantic. An examination of the distribution of genera shows, so far as we can ascertain from our present incomplete knowledge of the fauna of West Africa and the Eastern Mediterranean, that of the combined number of stenothermal warm-water genera belonging to the two boundary faunas (60–65), roughly 45% are common to both sides of the Atlantic.

The following table shows the results of investigation of the echinoderm groups which we have just mentioned.

TABLE 10

THE INFLUENCE ON THE GENUINE WARM-WATER GENERA OF STARFISHES, BRITTLE-STARS AND SEA-URCHINS OF THE PRESENT-DAY MOST IMPORTANT OBSTACLES TO DISTRIBUTION WITHIN THE REGION OF THE FORMER TETHYS SEA

This influence is here represented by the number of genera (expressed as percentage of the total number of ascertainable genera among the border faunas of the barrier) which by their appearance on both sides of the barrier show their independence of it.

Barriers	Genera not influenced by the barrier
The East Pacific barrier . .	14% of 80
The Central Atlantic barrier .	45% of 60–65
The Central American landbridge	37% of 80
The South-west Asiatic landbridge	35–38% of 65–70

Different animal groups, however, show a different behaviour with regard to distribution. The central Atlantic warm-water fauna provides a good example of this. The flatfishes (*Heterosomata*) show a certain divergence in this respect when compared with the echinoderms, particularly as regards genera. The Eastern Atlantic warm-water genera are members of an European–African–Asiatic group, while those in the West Atlantic belong in general to an all-round American group. As representatives of the African–Mediterranean group we may instance *Bothus*, *Zeugopterus*, *Flesus* and the whole sub-family *Soleinæ* among the soles with inter alia the genera *Solea* and *Synaptura*. To the American group belong for instance the genera *Citharichthys*, *Paralichthys*, *Liopsetta* and almost the whole sub-family *Achirinæ* among the soles. Of the 35 Heterosomata genera in the tropical-subtropical and warm-temperate Atlantic region, only two to three are common to both the east and west coasts, foremost among them the circumtropical *Platophrys* and *Symphurus*, with many species. In general, the affinity between both sides of the Atlantic, as regards the fishes, is less strong than between the two sides of the central American landbridge. According to Jordan[266] the total number of fish genera in the West Indies and Mediterranean region is 373 and only 70 of them, i.e. 19%, are common to both regions, while the comparable figures for both sides of the Central American landbridge are 376 and 169 or 45%. The contrast with the distribution of crabs is almost as striking. It is therefore all the more remarkable that the marine mammals offer examples of a closer connection between the two coasts of the Atlantic. The genus *Manatus* (=*Trichecus*) among the sirens, which forms a family of its own, comprises three to four species, of which one lives in tropical West Africa and two to three in tropical Atlantic America, all of them in rivers as well as in coastal waters. They are purely littoral animals and they cannot be regarded as capable of migrating over large stretches of ocean. Whether their distribution may be explained by an exceptional age of the genus *Manatus*—the genera of mammals are in general not so old as the marine invertebrate genera—or in some other way is, for the time being, an unsolved question.

We now return to the East Pacific Barrier. The comparison we have made shows that this barrier, a pelagic region, has been a more difficult obstacle, at least for the warm-water echinoderms of the shelf, than the two landbridges. The reason lies in the fact that both landbridges have existed, geologically speaking, for a fairly short period, while the broad archipelago-free region of the Pacific with its abyssal depth is much older. This oceanic region must have existed relatively unchanged since a period before the bulk of the present echinoderm genera emerged. There are great difficulties in

determining their age not only because of the incompleteness of the palæontological records but also because the palæontological conception of genus is very often wider than that of the recent taxonomy, owing to the difficulty of distinguishing taxonomically important details in fossil material. Mortensen,[352] who stresses the incongruity between these conceptions of genus, considers however in his great monography on the sea-urchins that we may place the emergence of certain modern genera as far back as the Eocene and even the Cretaceous, for example *Stereocidaris* (Eocene, Cretaceous), *Salenia* (Cretaceous), *Glyptocidaris* (Eocene), *Cœlopleurus* (Eocene). This, and the small number of genera common to Polynesia and West America, would imply that *no more or less continuous landbridge or series of islands existed between Polynesia and West America* during the Tertiary Period. That the number of genera common to both sides of the East Pacific is higher than that of species does not contradict this statement, since the Quaternary and late Pliocene Periods, in which the species assumed their present form, were considerably shorter than the rest of the Tertiary Period (cf. table 9, p. 66). The longer the time the greater is the possibility of the occurrence of certain rare combinations of factors, such as passive distribution over exceptionally long distances by ocean currents or other circumstances which must be ascribed to chance because we are unable to trace their causal connection.

The exposition given in the previous chapters has shown that the statement now made, which is based primarily on the statistics of echinoderms, is in general true for the whole fauna of the warm-water shelf. The importance attributed to the pelagic East Pacific (and Central Atlantic) as faunal boundary regions applies only to the warm-water fauna of the shelf. It is obvious that the organisms living in the pelagic zone and in the deep-sea regions must demand quite different conditions for spreading, and in the temperate and cold regions the shelf fauna, too, shows considerably closer connections between the East and West Pacific.

THE ORIGIN OF THE ZOOGEOGRAPHICAL CONDITIONS OF THE PRESENT AGE

We have seen that in the Eocene and Oligocene the Mediterranean region and the more easterly parts of the Tethys Sea formed a fairly uniform zoogeographical province—the Indo-European—whose counterpart was the former American province. These conditions altered in the Miocene and Pliocene in two ways. In the first place geographically, by the formation of the Central American Isthmus in the west and the landbridge between Asia and Africa in the east (for the time at which this latter bridge was formed see Umbgrove[562]);

or, to express it differently, the former Tethys Sea ceased to be a single sea. Thus the fauna of the Tethys was divided into four faunas instead of two. Furthermore, climatic changes also occurred, consisting in a drastic cooling, which, however, only affected the Atlantic faunas. As a result the eastern Atlantic fauna in particular became much poorer and for the most part lost its general Indo-European character. Both the climatic and geographical changes took place more or less simultaneously. This coincidence of the appearance of land in Central America and Western Asia and the deterioration in climatic conditions in the Atlantic during the Miocene and Pliocene is the most important event in the later history of the warm-water fauna. It was this which gradually brought about modern zoogeographical conditions, i.e. the contrast between the Indo-West-Pacific and Atlanto-East-Pacific faunas. From the mid- or late-Tertiary Period on the faunas developed on different lines.

The conformity between the different sections of the great circumtropical shelf fauna, therefore, reflects the former Tethys period. The special traits of the individual sections are of different origin. In the Eocene and even earlier the Indo-European and American regions had somewhat different faunas. Since that period, too, positive features have been added by the appearance of different species in various regions, less frequently even new genera, although they always remained poor in species. But all these newly acquired characteristics cannot obscure the original connection. The most important changes are, however, mostly of a negative character, many species, genera and even families having become extinct. Because this process reached its climax in the East Atlantic, the former boundary region between the Asiatic and Atlantic fauna, the difference between the Indo-West-Pacific and the Atlanto-East-Pacific regions was intensified, with the links becoming correspondingly fewer.

The great abundance of species found in the Indo-West-Pacific, and in particular the Malay region, has often been accorded an exaggerated importance, these regions having been regarded as the main developmental centre or even as the sole centre of origin and development for many animal groups, such as for instance the Octocorallia and crinoids. The present-day quantitative and qualitative predominance of the fauna of the Indo-Malayan region as compared with any other shelf region in the world must, it is true, be regarded as established, as well as its position as the most fertile centre of development and distribution within the Indo-West-Pacific region, and, for some of the smaller groups of animals, within the whole of the tropical fauna. But it does not necessarily follow that its palæontological position, particularly as compared

with the Atlantic, was the same. It has been asserted that the Atlantic fauna represents an impoverished offspring of the Indo-Pacific fauna. The most extreme opinion held is that the Atlantic is an ancillary ocean to the Indo-Pacific and that the latter supplied it with all its fauna. But this view cannot be true in either its extreme or more general form. We must regard the question historically and consider that the Mesozoic, perhaps even the Eocene fauna of the Atlantic, was not inferior to that of present-day Malay either in quality or quantity. The present paucity of the Atlantic fauna is not caused by its position on the periphery of an Indo-Pacific centre from which it received only a small part of faunal elements radiating from there. The truth is really that it suffered from a deterioration of climate. The faunal richness of the Indo-Malayan region cannot be explained by the assumption that this region became a developmental centre for whole classes and orders of the animal kingdom to a greater degree than, for instance, the Atlantic Ocean. The explanation is rather that in contrast to the Atlantic the Indo-Malayan region has been able to preserve this inherited richness until the present time, and that in addition new forms have been able to develop continuously. The unmistakable relationship between the Atlantic and the Indo-West-Pacific fauna is undoubtedly due to long-standing communication between the two, but this is not to say that migration took place preponderantly from east to west. The relationship is due rather to the fact that both these faunas are descended from a more or less homogenous Tethys fauna. So far as the abundant animal population is concerned, the real problem is not to find an explanation for the richness of the Indo-West-Pacific region, because this was formerly a circumtropical phenomenon, but to explain the reasons for the paucity of the Atlantic fauna.

In animal geography an exaggerated importance has often been attached to the comparatively recent date of the Atlantic Ocean. That the northern parts of this ocean are comparatively recent may be regarded as very probable, whether we follow Wegener's theory of the displacement of the continents or the older theory of bridges, and the northern cold and temperate faunas consists to a great extent of late immigrants from other directions, a fact which may explain the less abundant fauna. But the central basin of the Atlantic dates from very remote geological periods. Its tropical fauna must, therefore, be of considerable age and the number of animals which immigrated from other oceans during the late Tertiary or Quaternary Periods form only a very small part of its tropical fauna. Conditions may have been different for the immigration of the pelagic and abyssal faunas, but this is not the subject of our present discussion.

CHAPTER V

THE MEDITERRANEAN-ATLANTIC FAUNA AND THE SARMATIC FAUNA

A. THE MEDITERRANEAN-ATLANTIC FAUNA

THE Straits of Gibraltar do not represent an important zoogeographical boundary and the Mediterranean is, therefore, not a distinct faunal unit but enters into a greater one which includes the neighbouring parts of the Atlantic. These neighbouring regions are the *Lusitanian region* in the north, whose northern limits, as we shall see in a moment, may be put at the western entrance to the English Channel, and a *Mauretanian region* which extends south from the Straits of Gibraltar probably at least as far as Capo Blanco. Where the boundary zone may be placed most reasonably, in other words where the most clearly defined change in fauna occurs, has not been investigated in detail. In any case it will presumably be difficult to determine since the faunal change in these regions is probably ill-defined. The Cape Verde Islands, Canaries, Madeira and the Azores, too, are usually included in the Mauretanian region. The first-mentioned seem, however, to be rather subtropical.

One might be inclined to believe that the Mediterranean, this old cradle of civilization and the field of study of Aristotle, belongs to the better-known seas in Europe, but this is by no means the case. Our knowledge of the fauna of the parts which have been investigated most, the Bay of Naples, the Adriatic, the south coast of France and other parts of the western Mediterranean, are not sufficient to permit conclusions about the Mediterranean as a whole. Our knowledge of the south and in particular the east is still very inadequate. To illustrate this point we may mention that of 63 species of fish which Steinitz (1927) mentions from Palestine, only four had previously been reported from this country or Syria. We must regard it as undecided whether the Mediterranean as a whole belongs to the region which is here called the Mediterranean-Atlantic or whether the south-eastern Mediterranean possesses rather a subtropical fauna which is in the main a relict of the Tethys fauna and thus belongs to the above-mentioned warm-water fauna. The temperature of the water is no obstacle to such an assumption. In the following account the Mediterranean fauna is, however, treated as a unit for practical reasons, because we are not yet in a position

to establish its possible subdivisions. It is, however, obvious that the greater part of this Mediterranean-Atlantic region is inhabited principally by a warm-temperate fauna.

Hydrography

In the south-eastern part of the Mediterranean the temperature of the surface water is tropical during the warmest period, the mean figure for August being 25–27° C. In the rest of the Mediterranean, the surface temperature rises in August to 20–25° C., and may therefore be called predominantly subtropical. But the annual changes are considerable, being greater than those in the East Atlantic at the same degree of latitude. In the south-eastern Mediterranean the mean surface temperature for February is between 16° and 17° C. and in the northern parts usually from 12° to 13·5° C., in patches only 10° C.[471] At medium depth these changes are levelled out so that the temperature in Monaco, for instance, is between 12·5° C. and 16° C. at 70 m. depth all the year round.

In the Atlantic, the Mauretanian coast is strongly influenced by upwelling cold water from the sea floor. Thus the surface water at Capo Blanco north of Cape Verde in August is only 3° warmer than at the western entrance to the English Channel. On the whole the eastern parts of the North Atlantic are characterized by the fact that the southern regions are abnormally cold and the northern abnormally warm, and this is clearly the main reason for the unexpected resemblance between the faunas of the Mediterranean and western European coastal regions. Salinity, as is well known, is abnormally high in the eastern Mediterranean: it may rise to more than 39‰. Whether this has any influence on the fauna is not known. The nitrate and phosphate content of the Mediterranean as a whole is, however, less than in the Atlantic and it is lower in the eastern than in the western Mediterranean.[552]

The faunistic boundaries of the region. The relationship between Mediterranean and Atlantic.

The very ill-defined transition between the various climatic belts within the eastern Atlantic north of 15°–20° N. finds its expression also in the distribution of animal species. In his faunistically important work of 1879 on Scandinavian molluscs, G. O. Sars maintains that 68% of all Scandinavian molluscs live in the Mediterranean. Later Nordgaard[381] gave similar figures also for other Scandinavian animal groups and he found that 60% of the species of the Norwegian fauna are also found in the Mediterranean.

There is, however, one coastal region which represents the northern limit of a larger number of species than any other coast: that is the

western entrance to the English Channel. We may take the decapod crustaceans as an example. Of the species living in Mediterranean coastal waters 9% stop in northern Spain, while 28% stop short at the entrance to the Channel, and the comparable figures for the genera are 14 and 27%. This behaviour is fairly typical for a number of animal groups.[279] The western entrance to the Channel and the adjacent area is also the southern limit for most of the species which are especially characteristic of the boreal region. That the Mauretanian region must be included in the Mediterranean-Atlantic region is made clear by various investigations.[27, 111, 152, 282a, 349, 522] Roughly 45% of Mediterranean molluscs have their southernmost limit at Cape Verde. But the Mauretanian fauna contains many tropical elements and so approximates fairly closely to the subtropical fauna.

Several of the species of the Mauretanian and Lusitanian regions are not found inside the Straits of Gibraltar, but the better the distribution becomes known, the more the number of these species is

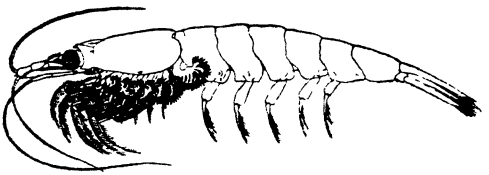


FIG. 24.—*Meganyctiphanes norvegica*, nearly twice natural size. (After Holt & Tattersall.)

reduced. Some of the intruders into the Mediterranean have not reached its eastern parts; examples of this are (according to Seurat[478]) *Patella safiana*, *Cardium hians*, *Haliotis tuberculata*, *Corallium rubrum*. Many others have been authenticated for the western but not for the eastern Mediterranean, but this is often clearly due to insufficient investigations in the eastern regions. The divergence between the western and the eastern parts is increased by other species which are confined to the eastern or south-eastern parts (see p. 85).

A number of Atlantic immigrants into the Mediterranean belong not only to the Mauretanian and Lusitanian regions of the Atlantic but extend northwards to the boreal region. Examples of such both cold- and warm-water elements are, to name only some of the best known, the amphipod *Haploops tubicola* (even arctic), the Crustacean *Meganyctiphanes norvegica* (figs. 24, 25) and many species of other animal groups (fig. 26). Such species represent a considerable proportion of the Mediterranean-Atlantic fauna. As a further elucidation of this point we mention the following relevant examples

among the fishes: *Squalus acanthias* (spiny dogfish), *Raja clavata* (thornback ray), *Clupea sprattus* (sprat), *Gadus virens* (coalfish), *G. merlangus* (whiting), *Molva molva* (ling), *Bothus maximus* (turbot), *Pleuronectes flesus* (flounder), *P. platessa* (plaice), *Ctenolabrus suillus*

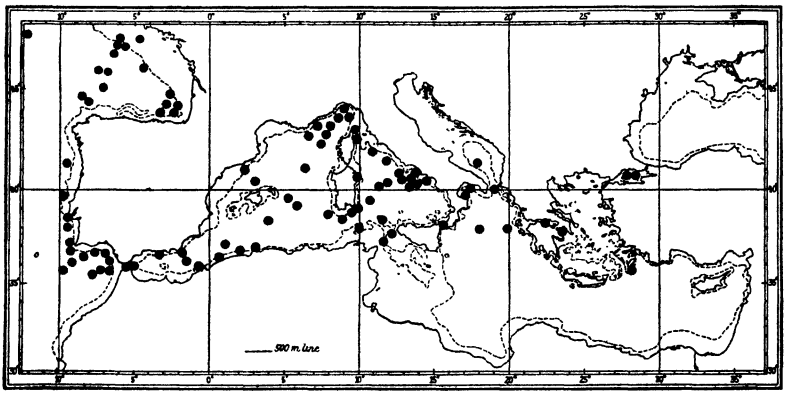


FIG. 25.—Distribution of *Meganyctiphanes norvegica* in the Mediterranean. (After Ruud.)

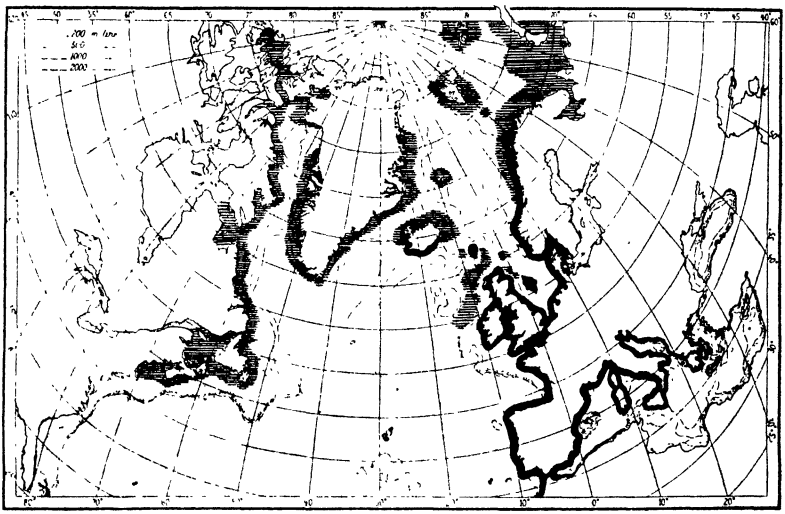


FIG. 26.—The North Atlantic distribution of two snails, the arctic *Velutina undata* (hatched) and the boreal and Mediterran-Atlantic *Lunatia nitida* (black). (After Thorson.)

(goldsinny, wrasse), *Trigla gurnardus* (grey gurnard), *Scomber scombrus* (mackrel), *Gobius minutus* (common goby). Several of these species occur only in the most northerly parts of the Mediterranean,

while others are more widely distributed. In the former case we may assume a northern origin, particularly for species which belong to genera with a mainly northern distribution, for instance *Gadus*.

A few of the more pronounced northern elements of the Mediterranean fauna have been regarded as glacial relicts, for example *Nephrops norvegicus* (Norway lobster). Later it was found that the species has in fact a fairly continuous distribution right down to the Mediterranean and that it occurs even in relatively warm water within this sea, for example off Morocco and Algeria, so that the relict hypothesis had to be abandoned.[409] But this does not mean that the relict hypothesis has to be completely given up for every constituent of the Mediterranean fauna. We know that there was a period when certain northern animals lived in the Mediterranean which are now completely excluded from it because of its climate (*Pecten islandicus*, *Cyprina islandica*, etc., see below p. 90). If we may postulate such a boreal Mediterranean fauna not only for earlier epochs of the glacial period but also for the last glacial period then it is conceivable that northern late glacial inhabitants of the Mediterranean have been able to persist until now in the cooler parts of this sea. However, no final proof of this has so far been put forward (but see Steuer[515]). It would be worth while investigating the applicability of such an explanation to *Myxine glutinosa*, which is said to occur in the Mediterranean only in the Adriatic. Perhaps *Salmo trutta macrostigma* may owe its occurrence in the inland lakes of Morocco, Algeria, Sicily, Sardinia and Corsica to the one-time presence of sea trout in the Mediterranean, where they are now extinct.

The endemic element

The Mediterranean-Atlantic region possesses a considerable number of endemic species. Here we can mention only some of the more important. Some of them are unknown outside the Mediterranean, while others are found also in the Mauretanian and Lusitanian regions. But in most cases it is not possible to say whether this picture of their distribution corresponds to the facts and whether it is distorted simply by the lack of investigations.

The widely known ornamental coral, *Corallium rubrum*, is found in the Mediterranean and Mauretanian regions down to the Cape Verde Islands and *Pennatula rubra* has in the main the same distribution. Among the molluscs we may mention *Lithodomus lithophagus*, *Pinna nobilis*, *Mytilus galloprovincialis*, *Avicula hirundo* and the largest of all Mediterranean bivalves, *Panopæa glycimeris*; here belong further *Tritonium nodiferum* and *Haliotis tuberculata*, species of *Scalaria*, *Vermetus*, *Murex* and other genera of gastropods.

Ten of the 18 members of the squid family *Sepiolidæ* which are to be found in the north-eastern region of the Atlantic are endemic in the Mediterranean-Atlantic region, most of them occurring exclusively in the Mediterranean.[441]

Pesta[409] gives nearly 30 endemic species of decapod crustaceans for the Mediterranean-Atlantic region. Among them we may mention the hermit crab *Paguristes oculatus*, and the crabs *Dromia vulgaris*, *Ilia nucleus*, *Maja verrucosa*, *M. squinado*, *Calappa granulata*, *Lambrus mediterraneus*. Among the echinoderms the number of species with a similar distribution is relatively great. Of the three echinoderm groups whose distribution is best known, the asteroids, ophiuroids and echinoids, 70 species have been collected from the Mediterranean-Atlantic shelf region, and 40% of these are endemic. Of the 60 Mediterranean shelf species, only 15–16% are endemic to this sea, while 41% occur also in the boreal region and 15–16% in the tropics. Among those endemic in the Mediterranean proper we single out the common *Ophiothrix quinquemaculata*. Among species endemic in the larger region are the starfishes *Echinaster sepositus* and *Astropecten aranciacus*, the brittle-stars *Ophiomyxa pentagona* and *Astrospartus arborescens*, as well as the sea-urchin *Paracentrotus lividus*. We may further add *Holothuria tubulosa*.

Finally, we turn now to the fairly numerous fishes which are endemic in the Mediterranean-Atlantic region and mention among those more generally known the sardine (*Sardinia pilchardus*), and anchovy (*Engraulis encrasicholus*). These, however, belong to the pelagic fauna. The genus *Gobius*, whose species have often a restricted distribution, has roughly 25 species endemic in this region, *Blennius* about 15 and *Crenilabrus* nine.

The endemic genera are, of course, relatively and absolutely speaking considerably fewer in number than the species. Such a crab genus is *Ilia*. Among the three echinoderm groups mentioned there are only three endemic genera, with four species in all, and they represent 6% of the genera which occur in the shelf region. (The same percentage of endemic genera is found among the echinoderms of the West Indian region.)

Tropical-subtropical elements

A number of the endemic elements may be called subtropical or even tropical. These include the few which are confined to the south-eastern part of the Mediterranean, for instance the gastropod *Triton* (*Epidromus*) *reticulatus* and among fishes *Sardinella aurita* and *S. granigera*, which are, however, to be regarded rather as pelagic. Others have a widespread distribution within the tropical-subtropical region, especially in the West African and West Indian

region (cf. p. 50). There are naturally very few species which go outside the Atlantic. Such an example is the fish *Ruvettus pretiosus*, unless we regard the form which occurs in the Pacific eastwards as far as Hawaii as a separate species (*R. pacificus*). The opinions of experts are divided in this matter. To older zoogeographers the great similarities observed between the Mediterranean and Japanese fauna were a source of surprise. The discovery of the former extent of the Tethys Sea has solved this riddle. In several cases, too, the similarity has proved to be not so great as was previously supposed, in that many Japanese species which were then regarded as identical with the Mediterranean and East Atlantic have now been shown to be specifically different, although closely related. An example of this is the cephalopod *Octopus macropus*, the Japanese representative of which was established as a separate species in 1929, *O. variabilis*. These are clearly a pair of twin species. But very occasionally one and the same species may occur in both regions, as for example the opisthobranch *Caloplocamus ramosus*, the crab *Actæa rufopunctata* and the ascidians *Ecteinascidia moorei* and *Botryllus magnicoecus* (Huus[246]). The species of ascidians seem to undergo change very slowly, and in these two cases the most natural assumption is that the characteristics of the species survived unchanged from the time before the Tethys Sea was divided by the south-west Asiatic land elevation. In other cases an ancient parent species has divided into two twin species. Huus mentions seven such pairs among the ascidians. Much the same is true of the Mediterranean-Atlantic prawn *Lysmata seticaudata* which occurs in the Malayan archipelago and Japan in a slightly modified form, *L. ternatensis*. Other examples are, among the Mediterranean decapods, *Paguristes oculatus* and *Xanthias granosus*; further, the common shaggy crab *Dromia vulgaris*, which is most closely related to the south-east Asiatic *D. dromia*. With the exception of a West Indian species, the whole genus occurs only in the eastern Atlantic and Indo-West-Pacific. Several other genera occur only in these two regions: for example the pennatularian *Pteroeides*, the decapod crustacean genera *Maia* and *Amphipalæmon*, the squid sub-family *Sepiolinæ*, the sea-urchin *Echinothrix*, the sea-cucumber *Pseudocucumis* (*P. mixtus* is also found in the temperate region of the Atlantic; cf. fig. 27. The same is true of the crab genus *Eurynome*) and the fish *Myrus*, *Pagrus*, *Macrorhamphosus*, *Zeus*, *Uranoscopus*, etc. In the Mauretanian region the tropical influence appears to be somewhat stronger than in the Mediterranean.

As early as 1844 the English scientist Edward Forbes propounded the rule, with special application to the Mediterranean, that the zone between 0 and 60 m. depth contains more tropical or southern

species, whereas the 60–500 m. zone contains more northern species. A. Steuer[518] has found this to be true of the fishing grounds off Alexandria; P. Volz[573], who also confirmed it, has shown that the most pronounced surface animals, i.e. those confined to the 0–30 m. layer, are even in the most northern parts of the Mediterranean distinctly warm-water species. Thanks to the subtropical surface temperatures during the summer these animals find congenial conditions for reproduction, which takes place during summer time. For this the maximal temperature is, therefore, more important than the annual mean temperature, and we find here a further example of reproductive warm-water stenothermity (cf. p. 113).

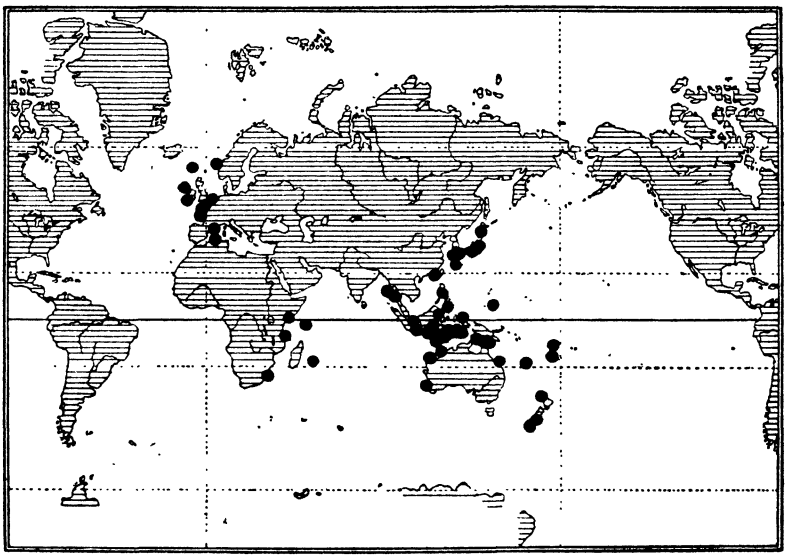


FIG. 27.—Distribution of the holothurian genus *Pseudocucumis*. Compiled from the maps and text in Engel (1933).

Several of the Mediterranean warm-water animals have been regarded as relicts from the Tertiary Tethys Sea. That they are in fact descendants of the former Tethys fauna is inescapable, seeing that no other source is apparent. Indeed, the whole of the tropical-subtropical shelf fauna in the West Indies, the East Atlantic, Mediterranean, Indian Ocean and Pacific, is derived from it. In order that the term "Tethys relict" may have a precise significance it should not be used as synonymous with "descendants of the Tethys fauna". As regards the Mediterranean, the term should imply that the organisms in question owe their presence in this sea solely to the

former extent of the Tethys Sea in the Mediterranean and that they cannot have died out there, for instance in the glacial period, and afterwards immigrated into it from the West Indies or from West Africa. Such a history can be assumed only for those organisms which are absent from the last-mentioned regions. Before this can be asserted we require accurate knowledge of their distribution. The number of real Tethys relicts may, however, be not inconsiderable.

The relation of the Mediterranean with the Red Sea. The influence of the Suez Canal fauna.

Notwithstanding the considerable similarities between the eastern Mediterranean and the Red Sea as regards water temperatures and salinity only very few animal species were common to these two seas before the opening of the Suez Canal in 1869. It is true that before this date our knowledge of the fauna on either side of the isthmus of Suez was very incomplete, but on the basis of later investigations it has been possible to confirm this slight degree of affinity (Fox,[169] O'Donoghue,[393] Steinitz[495]). The faunas of the two seas are characterized as "totally dissimilar" but with the reservation that they have a small number of circumtropical species in common and further some five other species reflecting an earlier connection between the two seas. This is true of species; the number of common genera is naturally larger.

This phenomenon is due to historical causes. In the Miocene the depression which is now occupied by the northern part of the Red Sea came into communication with the Mediterranean. It then acquired a purely Mediterranean fauna since at that time no connection existed between the Red Sea and Indian Ocean. Such a connection came about in the middle of the Pliocene whereas the connection with the Mediterranean soon ceased, at a time which has not yet been precisely determined. Even while it was still in existence its importance for the exchange of faunas was diminished by the fact that the Nile disgorged large masses of water into the gulf and thus formed a fresh-water barrier in the same way as the mouth of the Amur river in East Asia now forms a barrier between the mainland and Sakhalin.[172] At the beginning of the Quaternary Period a fresh-water lake existed in this region. As a result of these various causes, the short-lived direct communication between the Mediterranean and the Gulf of Suez has not had any great zoogeographical importance. The main connection of the Mediterranean region with the Indian Ocean in the Tertiary Period was to be found to the north, through south-west Asia. It was many times broader and it lasted longer. Thus we find that the similarity between the Mediterranean

and the Indo-West-Pacific fauna does not depend upon the neighbouring Red Sea as much as the regions further to the east.

The present Suez Canal has had earlier predecessors, since the Egyptian Pharaohs and later Darius, Xerxes, Trajan and Hadrian built or repaired canals from one sea to the other. But they took the water for their canals from the Nile. Only the modern Suez Canal, which was finished in 1869, was of importance for the distribution of marine animals. Its influence on the fauna was studied in 1924 by an expedition sent out by the University of Cambridge and these investigations were later continued by other workers.[193] Munro Fox[169] has given a résumé of the English results. Even earlier the fishes and molluscs of the Canal were objects of investigations, and Tillier[558] mentions no fewer than 80 species of fishes, a number which has not been greatly augmented since. It was shown by Munro Fox that in almost all groups of animals in the Canal most of the species have come from the Red Sea and a considerably smaller number from the Mediterranean, and that the currents are responsible for this state of affairs. At Suez there is a strong tidal current which transports organisms right up to the Bitter Lakes, whereas the northern and central parts of the Canal lack tidal currents. But because of the relative levels of the Mediterranean and Red Sea at different seasons, the planktonic organisms and others progress for 10 months of the year in a northerly and only for two months in a southerly direction. Exceptions to this last-mentioned rule of an Erythræan origin of the Canal's fauna are to be found particularly among the fishes, which have immigrated to about the same extent from both places. The fishes, because of their ability to swim, are independent of the weak currents in the Canal, in contrast to the planktonic stages of other animals. The so-called Bitter Lakes which the Canal traverses, present an effective barrier to migration for various animals owing to their high salinity. The salinity of the surface water in the Large Bitter Lake varies with the seasons between 46 and 50‰ and at 10 m. depth it is 51–55‰.

Some elements of the new fauna of the Suez Canal have reached Port Said and even spread into the Mediterranean, for instance 12 fishes and 18 decapods, which probably have become acclimatized to life in the Mediterranean.[33, 192, 301, 343, 494, 515] Since the currents in the Mediterranean run, on the whole, eastwards, these new Erythræan intruders are chiefly found on the coasts of Egypt, Palestine and Syria. The two crabs *Myra fugax* (fig. 28) and *Neptunus pelagicus* have been found as far as north-east of Cyprus. The latter, which has spread also far to the west of Port Said (approximately 500 km.), has multiplied quickly in the eastern Mediterranean. It was first observed in Port Said in 1898 and after 1930 was so common

that it was sold in the fish markets of Alexandria, Port Said and Haifa. Among these intruders into the Mediterranean is, further, the little pearl-oyster of the Red Sea, *Meleagrina albina.*

The late Pliocene and Quaternary history of the fauna

The history of the Mediterranean fauna during the Tertiary Period has been reviewed earlier in connection with the Tethys fauna. We may add that the Mediterranean was not always connected with the Atlantic Ocean by the Straits of Gibraltar, because during the middle Tertiary Period a landbridge existed between Cape Spartel and Cape Trafalgar. In the Pliocene a marine connection opened up at first across the valley of the Guadalquivir in Spain, later across the valley of Fez in Morocco and finally across the Straits of Gibraltar. It remains uncertain what influence these and other geographical changes had on the fauna of the Mediterranean basin.

The later cooling of the climate brought about considerable

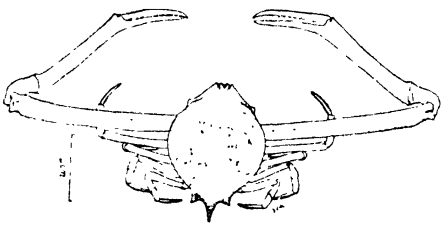


FIG. 28.—*Myra fugax* ♂, half natural size. (After Monod.)

changes in the Mediterranean fauna which in the main had already been noted by Philippi in an important treatise (1844), although they could not be correctly interpreted at that time. Later, other authors worked on this problem, in particular Gignoux.[180] In the so-called Calabrian period of the upper Pliocene (perhaps earliest Quaternary Period) a number of northern molluscs invaded the Mediterranean which they were later obliged to leave, obviously for climatic reasons. Examples are *Cyprina islandica* and *Buccinum undatum. B. humphreysianum,* which is endemic in the Mediterranean but belongs to a northern genus, may be regarded as a reminiscence of a similar but scarcely the same faunal shift. At the beginning of the Quaternary Period the northern species increased; among early Quaternary immigrants which have been found in the so-called Sicilian level and which to all appearances inhabited the Mediterranean during the glacial period, were the following molluscs which have now left this sea altogether: *Pecten (Chlamys) islandicus, P. tigrinus, Cyprina islandica, Panopœa*

norvegica and *Buccinum undatum*. Among these *Pecten islandicus* is particularly remarkable. The present distribution of this species reaches no further south than the west coast of Sweden; but fossil shells have been found not only in the Mediterranean but also in the Lusitanian region.

Still later, at a time which is considered contemporary with the last Interglacial Period, these northern species were forced to give way to southern immigrants, obviously a sign of a warmer climate. Such southern types were, for instance, *Strombus bubonius*, *Tritonium ficoides*, *Cardita senegalensis*, *Mytilus senegalensis*. These southern forms, of which fossils have been found from Spain to Greece and Cyprus, no longer live in the Mediterranean but are found now along the coast of West Africa. Their appearance in the Mediterranean would thus indicate a warmer climate at that time.

The two sturgeons *Acipenser stellatus* and *Huso huso* occur only in the Adriatic. Elsewhere they are found in the Black Sea and the Caspian. This seems to indicate that the Mediterranean contingent was derived from the Sarmatic sea during the later Tertiary Period.

Whatever history the species of the Mediterranean-Atlantic region had they all suffered change, provided the period was sufficiently long, which seems to have been the case if the isolation of the species began during the later Tertiary Period, that is to say a couple of million years ago (cf. p. 66). It is to this development of species that this region owes a large proportion of its endemic species. Other elements may have become endemic through their having died out in other regions because of climatic changes. Finally, we must take into consideration faunistic elements which have become endemic because they are relicts of the former Tethys Sea.

Appendix: The open-sea fauna of the Black Sea

The Black Sea has now an open communication with the Mediterranean, but formerly it communicated with the Caspian, with which sea it shared a very curious history. It is therefore understandable that its fauna shows two different constituents: a Mediterranean and another which we might call Sarmatic. Apart from this, the whole fauna of the Black Sea has been strongly modified by its hydrographic constitution. It seems therefore fitting to begin with a discussion of this constitution.

The Black Sea has a low salinity (fig. 29). This is, at the surface, about 18‰, but increases with depth and at 125–175 m. it varies between 19 and 21‰. At this depth the benthic fauna usually ceases to live for reasons which we shall discuss presently. In these lower strata, which by volume are about five times the amount of the inhabited strata (the greatest depth is 2104 m.), there is a lack of oxygen

and therefore an unusually large amount of hydrogen sulphide which is produced from the material of the sea floor by sulphate-reducing bacteria (*Microspira*). The upper limit for hydrogen sulphide is to be found at a depth of from 100 to 150 m. (a little lower at the mouth of the Bosphorus), somewhat higher than the lower limit for animal life. The oxygen content is here only about 5% of air saturation

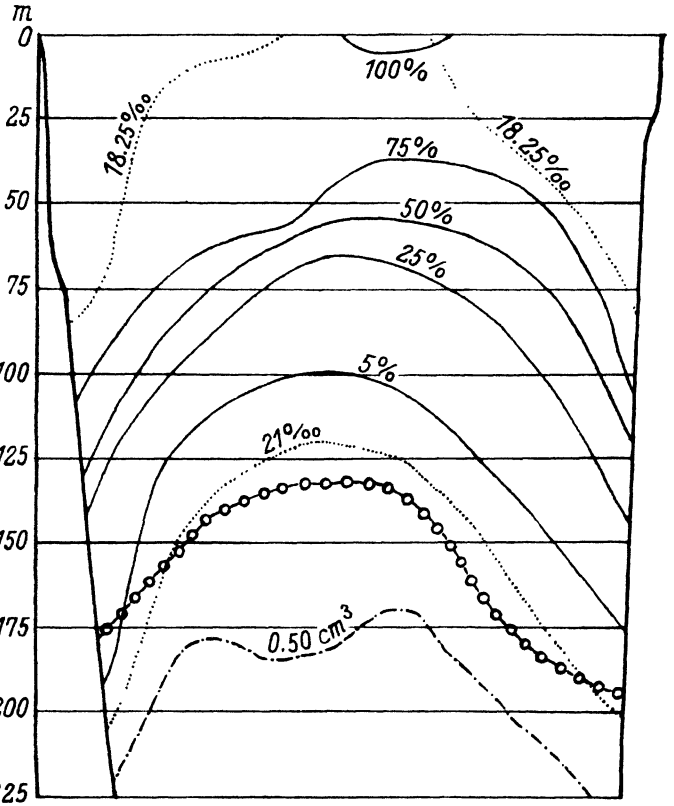


FIG. 29.—Hydrographical section through the Black Sea from the southern coast of the Crimea (left) to the Anatolian coast. ———— content of O_2 in % of saturation; · · · · · · isohalines; —·—·—· content of hydrogen sulphide per litre. o-o-o lower limit for plankton. (Modified from Nikitin.)

(Knipowitsch,[276] Nikitin[377]). That portion of the Black Sea which is inhabitable for benthic animals represents only 23% of the whole surface of the sea floor.

These peculiar hydrographic conditions have, of course, a considerable influence on the whole ecology of the sea. A great part of the planktonic organisms, among them quantities of larvæ of coastal

animals which are carried by currents out into the pelagic region, sink down to the uninhabitable region of the sea floor where they die, but only partially undergo a process of mineralization which normally makes organic substances available to plant nutrition. All the rest is lost to organic life with the exception of the sulphate-reducing bacteria. The great loss in animal food resulting from this is a special feature of the ecology of the Black Sea (Nikitin[378]).

The upper, not azoic, layers of water are by no means inhabitable for all animal species of the Mediterranean, and so the invaders from this sea are thinned out. The temperatures in the coastal waters of the Black Sea sink during the winter to 3–6° C. These low temperatures and the low salinity we have just mentioned make it possible only for eurythermal and euryhaline animals to thrive there. Thus the gorgonarians and cephalopods are completely, and the echinoderms almost completely, absent. The molluscs show the following mode of distribution (Ostroumoff[403]):

	Genera	Species
Aegean Sea	157	410
The Sea of Marmara at the Bosphorus	103	240
The northern mouth of the Bosphorus	86	151
Black Sea	56	91
Sea of Azov, outer region	20	26
Sea of Azov, inner region	13	15

The falling numbers of actinians may be seen from the following figures[407]: the Mediterranean off Naples has 45, the Adriatic 30, the Black Sea three species. As far as diminution of the number of species in the Black Sea is concerned, the animal groups mentioned are representative for the Black Sea fauna in general.

The open communication with the Mediterranean is, geologically speaking, recent. It has existed only since the beginning of the Quaternary Period, and consequently we find very few endemic species of Mediterranean origin. The flounder *Bothus mæoticus* may be regarded as an example unless it is merely a variety of *B. maximus*, as certain taxonomists suggest. Among the Cumacea the species *Iphinoë mæotica* stands in a similar relationship to the Mediterranean and Atlantic *I. trispinosa*.[597]

Although the Mediterranean species in the Black Sea are considerably fewer than in the Mediterranean itself, they nevertheless constitute the bulk of its fauna. Its most peculiar elements have, however, quite a different origin: they are derived from the ancient Sarmatic Sea, which covered a considerable area of South-east Europe in the Tertiary Period (cf. fig. 30). As an example we may mention among fishes *Lucioperca marina*, some species of *Gobius*[51a] and *Syngnathus*, *Acipenser nudiventris*, as well as the herring genera

Caspialosa and *Clupeonella* (=*Harengula*), which are both predominantly pelagic. Most of the species in question are found in the northern region of the Black Sea and also occur in other parts of the former Sarmatic Sea region, but they are missing from the Mediterranean. An invertebrate example of this is the most common hydromedusa of the Black Sea, *Thaumantias mæotica*.[545] How relatively small the Sarmatic element is in the open sea emerges from the fact that of the 19 Hydromedusæ to be found in this region of the sea, all but the above-mentioned and another one are widely distributed outside the Black Sea, several of them in cold seas. Of the eight Cumacea none seems of Sarmatic origin, and all except the previously mentioned *Iphinoë mæotica* occur also in the Mediterranean.

It is, therefore, salinity which most of all determines the open-sea fauna of the Black Sea. Its salinity of 18–21‰ is too low for a great number of true marine animals and too high for most of the Sarmatic animals, which need mesohaline or oligohaline brackish water (see p. 117).

It is clear from what has already been said that the Black Sea fauna is not an equivalent of the Mediterranean or Sarmatic fauna. It is a mixture of an impoverished Mediterranean and a no less impoverished Sarmatic fauna, the former element by far outweighing the latter as regards numbers of species. It is, therefore, a boundary, or rather transitional region.

B. THE SARMATIC FAUNA

If we enter the Sea of Azov through the narrow strait of Kertch we soon meet with a fauna in which the Sarmatic elements constitute a far more important part than in the Black Sea fauna. We are, therefore, justified in classifying the fauna of the Sea of Azov as Sarmatic, although numerically here, too, the Mediterranean species preponderate, while the Black Sea proper must be regarded both faunistically and geographically as a subsidiary sea to the Mediterranean.

A survey of the history of the South-east European marine fauna is essential for an understanding of the Sarmatic fauna in general.

History

The Eocene and Oligocene Tethys Sea comprised not only the Mediterranean region but extended over vast stretches of central and South-eastern Europe, North Africa and West Asia. In the middle Eocene period there still existed an inland sea, the Danubian-Pontic basin, stretching from the mouth of the Rhône across Switzerland, South Germany, Hungary, Galicia and Roumania to the

territories of the Black and Caspian Seas. In the upper Miocene the sea diminished, its western portion becoming shallow and the eastern part increasingly more brackish. This caused an impoverishment in species but an increase in the number of individuals within the fauna, a common occurrence in extreme biocœnoses. Stenohaline marine animals such as corals, echinoderms, brachiopods, cephalopods and dogfishes died out, but animals which thrive in brackish water preponderated, for instance among the molluscs species of the genera *Cardium*, *Mactra*, *Tapes*, *Trochus*, *Rissoa*, *Congeria*. This extensive East-European and West-Asiatic portion of the former Tethys Sea

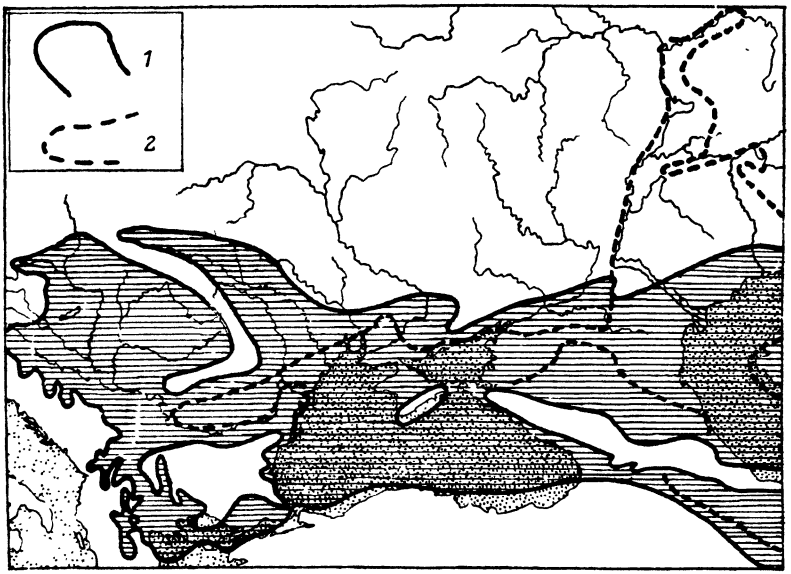


FIG. 30.—The Sarmatic Sea: 1, maximal extent in the Sarmatic epoch; 2, the Pontic in the Mæotic epoch; dotted: sea at the present time. (Modified from Arldt.)

became separated from the Mediterranean in the upper Miocene and is known as the *Sarmatic Inland Sea* (fig. 30). At the time of its greatest extent it covered nearly the whole of Hungary, large parts of the Balkan peninsula and Southern Russia, the Black and Caspian Seas, which at that time were still joined together, reaching as far as Transcaspia in the east. In the Lower Pliocene a considerable regression took place in the west while in the north a long arm of the sea flooded the valley of the Volga as far as Kazan, the middle reaches of the Kama river and the Ural river as far as Uralsk. The water became more and more brackish. In the west, a connection with the Mediterranean was opened up during the Lower Quaternary

Period. In the east, the Caspian became separated from the Black Sea during the middle Pliocene, but it extended its territory towards the east and made contact with Lake Aral. The thus newly formed *Aralo-Caspian Sea* reached its peak during the second glacial period. Its water level lay 80 m. above the present surface of the Caspian Sea. For some time it was once again connected with the Black Sea.

We must also mention another part of the ocean which possibly influenced the present Caspian fauna. In the Jurassic, Cretaceous and Tertiary Periods there existed an open, though probably temporarily interrupted, connection between the Arctic Ocean and the Tethys Sea in the shape of a broad arm which has been called *Obik* because of its position. It seemed to have ceased to exist in the Oligocene, at any rate its existence during the Miocene seems very problematical. (On the transport of arctic animals through the blocking of former ocean bays by glaciers, see p. 99.)

The fauna of the Sarmatic and Aralo-Caspian basin was a brackish one mixed to a fairly considerable extent with fresh-water species. This was the richest known brackish-water fauna in the world. Today only remnants are left, which, although seeming modest if compared with the older parent fauna, constitute a considerable number of species. They are now scattered in isolated regions which we shall proceed to describe.

The Sea of Azov and the Black Sea estuaries and lagoons

When the salt water of the Mediterranean intruded through the Bosphorus at the beginning of the Quaternary Period it destroyed in the open part of the Black Sea the largest part of its Sarmatic brackish fauna. But in the Sea of Azov, especially in the Gulf of Taganrog, which is made very brackish by the Don, at river mouths along the coast of the Black Sea and in the neighbouring fresh waters of the rivers and inland lakes, survivors of the Sarmatic fauna are still to be found.

The whole of the Sea of Azov is particularly shallow in comparison with its extensive surface; the maximal depth is only 13 m. and the temperature of the water is consequently unusually changeable. The mean temperature may be as much as 25° C. in July and the extreme limits are 30° C. and −0·6° C. This naturally makes great demands on the adaptability of the animal species. We may mention among the Azov Sea species[275, 276] the Cladocera *Evadne hircus* and *Cercopagis pengoi* (fig. 31), the copepods *Eurytemora affinis*, *E. velox* and *Heterocope caspia*, the cumacean family *Pseudocumidæ* (fig. 32, cf. p. 98); among the molluscs we find the well-known *Dreissensia polymorpha* as well as species of the genera *Adacna* and *Monodacna*, and among fishes the three sturgeons *Acipenser güldenstädti*, *A.*

stellatus and *A. nudiventris*, three species of the herring genus *Caspialosa*, with *Bothus torosus* and *Percarina mœotica*.

The estuaries of the Black Sea have been investigated in Bulgaria by Valkanov[565] and in Roumania by Bacesco.[24] The Sarmatic fauna of this region closely resembles the last-mentioned fauna. The hydroid family *Mœrisiidæ* is especially to be noted, since all its five genera are confined to brackish water. The copepod *Calanipeda aquæ-dulcis* (also known as *Popella guernei*) seems to be the most generally



FIG. 31.—The cladoceran *Cercopagis tenera*, 10 × natural size. (Modified from G. O. Sars.)

distributed brackish-water animal in these regions. The abundance of Mysidacea (*Diamysis*, *Mesomysis*, *Limnomysis*, etc.) in Roumania is also noteworthy, since this country possesses a greater number (21 species) of fresh-water or brackish-water representatives of this group of animals than any other country.

The Caspian Sea

Here, too, as in the Black Sea, the lower strata are contaminated by hydrogen sulphide, but the upper limit of this deep-water layer



FIG. 32.—*Pseudocuma pectinata* Distribution: Caspian Sea and the Sea of Azov. (After G. O. Sars.)

lies lower than in the Black Sea, in the middle region at about 600 m., in the southern region at about 730 m. depth. The benthos descends here to 400 m. and the zooplankton to 400–500 m. depth.[276] Here, too, we find then an immense azooic region, since the depth of this sea is 945 m. In the animate zone the salinity fluctuates greatly. In the north a region nearly half the size of the North Sea is only 20 m. in depth and is made very brackish by the great rivers Volga and Ural.

In the middle and southern regions the salinity of the surface water is, however, about 14‰ and in the larger shallow bay of Karabugas, which is almost completely separated from the rest of the sea, the salinity may be as high as 170‰ because of intense evaporation. The percentage of saline constituents in the Caspian is not the same as in the ocean, common salt is a little less abundant, magnesium and calcium sulphate more common.

The Caspian fauna is practically a pure Sarmatic fauna. Among crustaceans, which are very well known since G. O. Sars' work,[452] the endemic Sarmatic species represent more than 90% and the genera more than 30% of the total number of 160 species and 65 genera. Characteristic genera are *Cercopagis* (fig. 31) among the Cladocera, *Niphargoides* among the amphipods; *Paramysis* with many species among the Mysidacea, and the previously mentioned cumacean family *Pesudocumidæ*.[597] With the exception of four species, the whole of this family, containing 23 species, is confined to the Sarmatic region. Among molluscs the characteristic genera are *Adacna*, *Monodacna* and *Didacna*, which are closely related to the common *Cardium*. The fairly numerous fish species belong for the most part to purely Sarmatic genera, for example *Caspiomyzon* (Petromyzontidæ), *Caspialosa* with 10 Caspian species, *Clupeonella* (=*Harengula*). Here we must add the Sarmatic species of genera with a distribution otherwise in fresh water, for instance *Lucioperca marina*, and the economically important "wobla" (*Rutilus rutilus caspicus*).

Formerly, almost all Caspian species were regarded as endemic in the Caspian itself, but as the coastal regions of the Black Sea became better known it was found that several species and genera were common to both regions. Several Sarmatic species penetrate a considerable distance into the South Russian rivers, especially the Volga.

The Caspian has had little in common with the Mediterranean. The communication between the two seas lay across the Black Sea. At the time this communicating strait was best developed communication with the Mediterranean was interrupted, and when it started again at the beginning of the Quaternary Period, the Black Sea-Caspian Strait was much diminished and seems to have allowed only purely brackish-water animals to pass. The very few species common to both the Caspian and the Mediterranean are also brackish species and are probably of Sarmatic origin. The Caspian fauna has been exempt from the levelling influence of the marine fauna proper because of its isolation from the world's oceans for about 30 million years (see p. 66), and this is why it has preserved its highly individual character.

But the Caspian fauna also contains species which cannot be explained by Sarmatic ancestry but are of arctic origin, since their nearest relatives live in the Polar Sea and the Siberian estuaries. These are a seal (*Phoca hispida caspica*), a migratory fish (*Stenodus leucichthys*), some Mysidacea, an isopod, as well as amphipods and copepods. Some of them must be regarded only as varieties of arctic species, namely *Mesidothea entomon caspia*, *Gammaracanthus loricatus caspius*, *Pontoporeia affinis microphthalma* and the variety of *Phoca* already mentioned; *Limnocalanus grimaldii* occurs in identical form in both regions and most of the rest can be referred back to certain arctic species as parent species. The Caspian forms are thus comparatively little changed, and in some cases less changed than relict forms of the Swedish and Norwegian inland lakes which arise from the same parent forms.[141] In these cases their glacial origin would seem to be of no very remote date. Högbom[241] has therefore assumed a late-glacial migration from the Baltic as a consequence of a forward move of the land ice damming up certain northern relict lakes and thus causing an overflow of water to the south through the Volga into the Caspian Sea. This theory has found some support in that geological researches in northern Russia suggest the existence of extensive late-glacial and interglacial bays in the region of the sources of the Volga. Sars[454] on the other hand has rightly pointed out that the Baltic-Caspian connection could not have been the only route of migration, since the Caspian Sea contains two species of the arctic amphipod genus *Pseudalibrotus* which are missing in the Baltic region (see map on p. 171). The same holds good for the above-mentioned fish, *Stenodus leucichthys*. We may thus entertain another theory,[415] if its geological basis proves secure, namely that another ice-lake in the southern part of the Kara Sea was dammed up by the confluence of glaciers from the Taimyr peninsula and the Ural mountains. Water from this lake possibly flowed out in a south-westerly direction into the Aralo-Caspian region and brought with it the animals in question.

CHAPTER VI

THE BOREAL FAUNA OF THE NORTH ATLANTIC

In the last chapter we surveyed the warm-temperate European and African Atlantic shelf fauna. We now turn our attention to the cold-temperate Atlantic fauna, commonly called boreal fauna. Although the European boreal fauna in its essentials forms a single unit with the American fauna, we propose, partly for practical reasons, to treat them separately.

A. THE BOREAL FAUNA OF THE EUROPEAN ATLANTIC

This fauna is in some respects perhaps the best known in the world. But still, how recent is our knowledge! When the 18-year-old Georges Cuvier travelled in 1788 to the coast of Normandy to study its fauna, it was the more than 2000-year-old writings of Aristotle which he used as his reference book.

1. THE FAUNA OF THE SEAWATER OF ORDINARY SALINITY

The recognition of a separate boreal region dates from the very beginning of systematic zoogeographical investigations into the world of the North Atlantic. These were first undertaken by Milne-Edwards (1838), Lovén (1846), Schmarda (1853), Woodward (1856), Michael Sars (1851), Forbes (1859) and G. O. Sars (1879). Lovén was the first to group the species correctly according to arctic, boreal and Lusitanian-Mediterranean constituents, although he did not yet employ these terms. Later investigators have considerably enriched our knowledge. Probably no oceanic region has been investigated more intensively than the boreal-Atlantic region, the centre of which is represented by the North Sea. It sounds, therefore, paradoxical to state that the task of delimiting the boreal faunal region is more difficult than that of some other faunal zones. And yet such a statement is in the main true. The difficulties do not arise from lack of investigations but are inherent in the natural conditions.

Boundaries

We have already seen that for a relatively large number of animals of Mediterranean-Atlantic coastal waters the south-western entrance to the English Channel represents the northern boundary, but quite

a number of others are to be found also further north. Similarly, species with a mainly arctic distribution penetrate more or less deeply into the boreal region. In the earlier period of zoogeographical investigations scientists were inclined to draw the boundaries of the regions at the point where a certain number of species of neighbouring regions ceased to occur, thus choosing a negative characteristic. More important, however, are the positive characteristics, in this case the occurrence of endemic boreal elements and the limits of the distribution of these elements. It has been shown that the boreal region possesses many endemic elements and that most of them have their centre of distribution in the North Sea. No effective barrier to distribution is to be found along the European coast and we therefore obviously cannot expect sharply defined limits. The boreal region is bounded by intermediate zones with representatives from both the neighbouring faunas.

The southern intermediate zone lies to the south-west of Great Britain and north-west of France. The northern boundary was placed by older zoogeographers at the arctic circle, a quite arbitrary use of an astronomical-geographical line as a zoogeographical boundary. This mistake recurs sometimes even in our time. Michael Sars, on the other hand, pointed out as early as 1851 (in a very modest publication), and his son G. O. Sars in 1879, that a more pronounced northern fauna starts at the region of the North Cape and that the region east of the North Cape forms a transition to the arctic zone. Grieg[190] and Oestergren[402] point out that, as far as the echinoderms are concerned, the arctic fauna is first met with north and east of Norway, and Apellöf[12] regards East Finmark, the south-western part of the Barents Sea, the shallow parts of the White Sea, north and east Iceland, the most south-western part of Greenland together with the submarine ridge between the Shetlands, Faroe Islands and Iceland as forming the boreal-arctic, or, as we prefer to call it, the *subarctic transitional zone*. As v. Hofsten[237] pointed out, this region is almost entirely lacking in endemic species and is therefore only an intermediate zone. However, the well-known mussel *Pecten islandicus* may be regarded as a predominantly subarctic (low-arctic and high-boreal) species. Iceland partly belongs to the boreal zone, namely in its southern and western regions, and partly to the subarctic zone. Its fauna has lately been analysed by several authors in a collective work entitled The Zoology of Iceland (Copenhagen, 1937, *sequ.*).

Hydrography and climate

The temperature of the surface water in the boundary regions thus delimited may be seen from the following survey of the mean

temperatures for the coldest and warmest months and for the year as a whole.

TABLE 11

MEAN SURFACE TEMPERATURES IN THE COLDEST AND WARMEST MONTHS AND THE ANNUAL MEAN AT THE BOUNDARIES OF THE ATLANTIC BOREAL REGION

	February	August	Annual Mean
Murman coast, Kola peninsula . .	1° C.	9–10° C.	4° C.
Northern Iceland	0–1	8–10	3–4
Bear Island (between Spitsbergen and Norway)	0–1	5	2–3
Southern tip of Greenland . . .	1	5	3
English Channel, south-western entrance.	9	17	12–13

The ill-defined nature of the faunistic boundaries is due not only to the gradual change of water temperature in a north–southerly direction but also to the fact that the annual variation in temperature is greater in the boreal region than in any other coastal Atlantic region. Appellöf[13] and Reibisch[431] were the first to point out the zoogeographical importance of this variation. On the Norwegian coast, between the Lofoten Islands and 63° N., it amounts to 10–12° in the surface water, in the south-eastern half of the North Sea likewise to more than 10°, whereas in the Kattegat it rises to 15° and in the Baltic to 16°. This means that an arctic animal which is cold-stenothermal while propagating but is otherwise eurythermal (animals of this type do occur, as we shall see below) is able to live in the same region of the boreal zone as a normally eurythermal southern animal which becomes warm-stenothermal during propagation. But both animals propagate at different seasons, the northern animal during the cold, the southern during the warm season. This must, of course, contribute to the blurring of the faunistic boundaries (cf. also p. 113). In the tropical and cold seas conditions are quite different. Large tracts of the tropical Atlantic Ocean show a yearly variation of surface temperature of at the most 2° C.; the same is true of the high arctic and antarctic regions.

Even at a medium depth conditions differ greatly from the surface as may be seen from the following table.

At 100 m. depth the annual variation is thus insignificant and at 300 to 350 m. it is almost nil, while at the same time there is a shift in the seasons since at 100 m. to 200 m. depths the highest temperatures occur towards the winter.

The whole of the boreal region of Europe is, as is well known, dominated by the European Gulf Stream or North Atlantic Current,

TABLE 12

THE TEMPERATURE OF THE WATER OFF WESTERN NORWAY AT 61° N.[218]

Depth	February	May	August	November	Annual variation
0 m.	4·83° C.	7·30° C.	13·78° C.	8·70° C.	roughly 9° C.
100 m.	6·80	6·37	6·87	9·30	,, 3
200 m.	7·91	7·00	6·71	7·94	,, 1·3
350 m.	6·25	—	6·38	6·29	,, 0·2



FIG. 33.—The surface currents of the Norwegian Sea and adjacent seas. (After Murray & Hjort.)

an expression preferred by oceanographers, since it consists only partly of water from the Gulf Stream proper (fig. 33). After this current has reached the most northerly part of Norway it gives off a branch at the North Cape which penetrates into the southern part of the Barents Sea and there bars the way for the arctic fauna, while

another branch goes straight north. The water flowing from the open sea to the coasts is therefore of mid-Atlantic origin. Arctic water never reaches the coasts unmixed. It might be supposed that the arctic deep water of the Norwegian Sea between Norway and Greenland, which in the southern regions of this sea has a temperature constantly below zero at depths beginning with 550–600 m., would penetrate into the deepest regions of the Skagerak and the

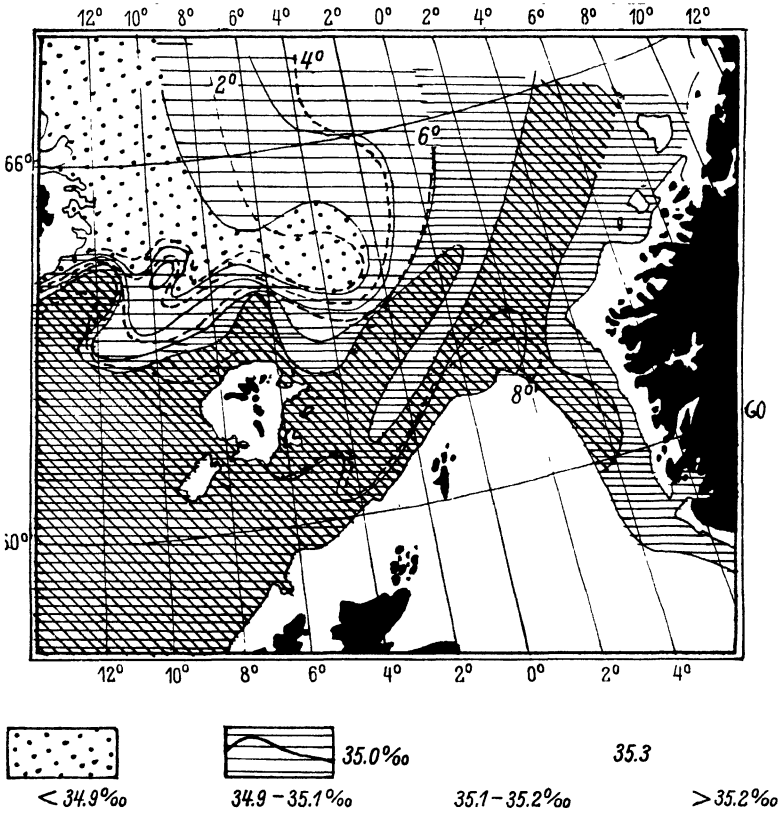


FIG. 34—Salinity and temperature at 200 m. depth in the sea between Norway, Scotland and Iceland. (After Helland-Hansen & Nansen.)

west Norwegian fjords, since these fjords are often much deeper than 600 m. This is, however, not the case. Firstly, the deep parts of the fjords are divided from the deep water of the Norwegian Sea by high sills at their entrances, and secondly the whole region of the shelf between the coast and the deep parts of the Norwegian Sea is covered by the Gulf Stream which thus acts as a flowing wall

(fig. 34). Hydrographical measurements have also shown that the water of the fjords at 600 to 700 m. depth has a considerably higher temperature than the water of the Norwegian Sea at a similar depth, for instance in the south-west Norwegian fjords it is 6·25–7° C. Neither the water nor the fauna of these fjords or of the Skagerak is arctic. Even at a depth of more than 1200 m. the Sogne-

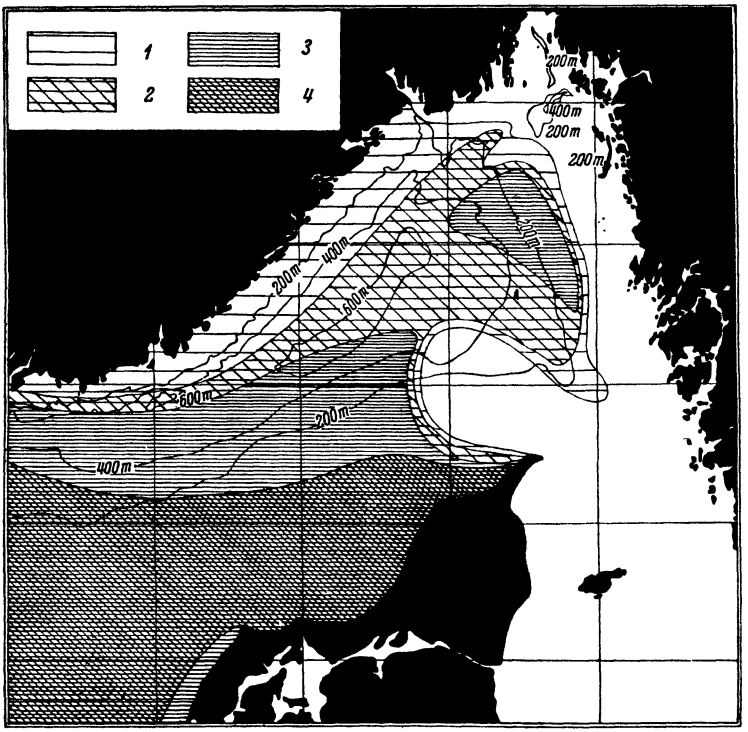


FIG. 35.—Salinity of the surface water of the Skagerak and the Kattegat in February 1890. Without designation=less than 30‰; 1=30–32‰; 2=32–33‰; 3=33–34‰; 4=34–35‰. Isobaths are inscribed. (After Pettersson & Ekman.)

fjord, for instance, contains Atlantic water of a temperature of 6–7° C.

The complicated and interesting hydrography of the Skagerak and Kattegat merits a special discussion (fig. 35). A surface current derived from the North Sea and possessing a high salinity (30 to 34‰) flows along the coast of Jutland. It turns towards the Swedish

coast but gives off a branch at Skagen (Skaw) into the Kattegat. Off the coast of Sweden it meets with the Baltic current which, originating in the Baltic Sea, has a salinity of between only 10 and 15‰ in the Belts and Oeresund during the late summer. Both currents flow along the coast, the Baltic closer inshore. Its salinity gradually increases through mixing with more saline water. But even off the south-east coast of Norway it is only 25 to 30‰ among the outer archipelago and 32‰ off the south-west coast of Norway. Off Bohuslän this Jutland-Baltic Current reaches sometimes (probably infrequently) a speed of 65 km. in 24 hrs. The surface water thus forms a great whirlpool. Exceptions from the usual conditions of flow are not infrequent. The lower strata are more saline than the upper and they often move, particularly in the Kattegat, in one direction while the surface water moves in the opposite one. In the open sea of the Skagerak the lowest stratum is a large mass of water which originates in the open Atlantic and has a salinity of at least 35‰. In the middle of the Skagerak it reaches up to about 40 m. below the surface, but off the coasts the upper limit is lower (at a depth of about 100–150 m.) because here the less saline water intrudes between the Atlantic water and the coast. Water of 34 to 35‰ salinity which covers water of 35‰ salinity is in the middle of the Skagerak sharply divided from the surface water which has a salinity of 30 to 32‰. The difference in temperature between the cold deep water and the warmer surface water from the Baltic is very considerable during summer.

Both currents, the Jutland and Baltic, dominate the coastal fauna of the Skagerak region. The Baltic current is the home of the coastal fauna within the archipelago, a fauna consisting mainly of euryhaline and eurythermal species. Only in the outermost archipelago and particularly in the deep water of the fjords and the slope towards the depth of the Skagerak do we find a stenohaline salt-water fauna.

In the west, too, the influence of the Gulf Stream is noticeable. One branch flows along the west coast of Iceland, the Irminger Current, which partly turns towards Greenland, where it flows south below the Polar Stream, and at the southern tip of Greenland turns north for some distance. Its temperature of 4–6° C. makes it possible for some non-arctic animals to live in the deeper coastal water near south Greenland, for instance the fish *Sebastes marinus*, *Hippoglossus hippoglossus*, *Gadus morrhua*, and the decapods *Pontophilus norvegicus* and *Pandalus propinquus*, and so on.

The endemic fauna

The European boreal fauna exhibits quite a number of similarities with the neighbouring faunas. It has a large number of species in

common with the Mediterranean fauna. These Mediterranean-boreal elements are stronger within certain taxonomic groups and, presumably in most of them, stronger than the arctic-boreal. This is not very surprising because the warm-temperate fauna is considerably richer in species than the arctic and can, therefore, supply more to the boreal region which is situated between them. It is more surprising, however, that the arctic-boreal element is sometimes equal to the Mediterranean-boreal, as in the case of the polychæts,[171] and that it may even be stronger, as for example among ostracods.[149] That the boreal fauna occupies a relatively independent position in spite of this mixture of faunas is due to the occurrence of an endemic element which is fairly rich in species for certain groups; in other groups, however, it is less pronounced, for instance among the polychæts.

Since we are here concerned with the European boreal fauna we shall only consider those animals as endemic elements which exclusively belong to it. In the following collection of examples, however, we have included species which occur in the American boreal region, too, and which are therefore amphi-Atlantic† boreal. To keep the two groups apart the exclusively European species are marked with an asterisk. * A slight transgression of the above sketched boundaries of the boreal region, that is an occurrence in the northern or southern intermediate zone, does not prevent a species from being here considered as endemic. Endemic boreal species are fairly numerous; we can, of course, only quote a few examples.

Among the Octocorallia we may mention the well-known *Alcyonium digitatum* (dead men's fingers) and **Stenogorgia rosea* and among decapods **Crangon allmani*. Some of the molluscs in question are very well known, among them *Mya arenaria*, which however now is also to be found in the Pacific, although not spontaneously but as a result of the transplanting of oysters from the Atlantic‡; further *Ziphaea crispata* and *Cyprina islandica*. This last-mentioned species which played an important part in zoogeographical and palæontological literature has often been considered as mainly arctic. This is not correct. It is distinctly boreal[253] since it occurs in Europe between south-west France, the White Sea (in its "warmer area") and Iceland, and in America between Cape Hatteras and Newfoundland.

† This term as well as the corresponding "amphi-Pacific" is at times wrongly used to denote only *discontinuous* amphi-Atlantic and *discontinuous* amphi-Pacific elements respectively.

‡ *Mya arenaria* is recorded also from Japan and Alaska. In the Pliocene it still occurred in California, that is in the same water into which it has now been artificially transplanted. But it should be noted that this species has often been confused with the fairly similar *M. truncata ovata*.[252]

Most echinoderms of this region are eurythermal and live both in the upper and lower water layers, that is they are eurybathic. The following may be called endemic: **Ophiura affinis*, **Ludwigia* (=*Cucumaria*) *lactea*, *Antedon petasus*, and to some extent the boreal and Lusitanian **Echinus esculentus*.

A considerable number of fishes belong to the endemic elements, about 25% of the fish fauna of the whole region. We mention the following examples: **Centrolabrus exoletus*, **Cottus* (*Acanthocottus*) *bubalis* (long-spined sea scorpion), **Agonus cataphractus*, **Gobius niger* (black goby), *Pholis gunellus* (butterfish), **Zoarces viviparus* (eelpout), **Ammodytes lanceolatus* (greater sand eel), **Zeugopterus punctatus*, **Scophthalmus norvegicus*, **Microstomus kitt* (smear dab), **Pleuronectes* (*Limanda*) *limanda* (dab), *Spinachia spinachia* (fifteen-spined stickleback), **Syngnathus rostellatus* (lesser pipe fish), *Gadus morrhua* (cod), *G.* (*Melanogrammus*) *æglefinus* (haddock), *G.* (*Pollachius*) *virens* (coalfish), **G. esmarki*, *Molva molva* (ling), **Raniceps raninus* and *Clupea harengus* (herring). A few species of *Gadus*, for instance the cod and coalfish, which have pelagic eggs and in the adult stage, too, are not strictly confined to the sea floor verge on the pelagic. The herring is pelagic between the spawning periods but it lays its sticky eggs either on the sea floor or on seaweed and the like within the upper zone of the shelf.

Thanks to the careful investigations which have lately been undertaken into the biological conditions of economically important fish we now know fairly well the environmental requirements of many boreal fishes. It has been shown on the one hand that the sensitivity to temperature and salinity differ during the spawning period from other times, and further, that the pelagic eggs and young are often transported by currents very far from the spawning grounds. The young fishes may therefore appear fairly far outside the spawning grounds of the species. In such cases only the latter should be regarded as the real home of the species.

Figure 36 represents the East Atlantic spawning grounds of the cod. In Europe they stretch from the North Cape and western Iceland to the English Channel and south Ireland. In America the cod spawns from Newfoundland to Cape Cod. We must however mention that the cod, like other boreal marine animals, for instance the herring, has shifted its distribution to the north during the last decades so that it now has its spawning grounds as far north as the west coast of central Greenland, where a flourishing cod-fishing industry has developed, and also off south-east Greenland.[255] This is clearly due to the improvement in climate which has taken place simultaneously in this and other arctic regions both with regard to seawater and air. The boreal region itself has extended

northwards. While spawning the cod and several other fishes are considerably more particular as regards environmental conditions than during the non-breeding period of their lives. Thus the Atlantic cod spawns only in water of 4–6° C. and 34–35‰ salinity, in greatest numbers at depths of 40–80 m. It is therefore during the spawning period stenothermal and stenohaline, a fact which determines its zoogeographical position (cf. p. 114). In the Baltic, however, the cod spawns at a considerably lower salinity.

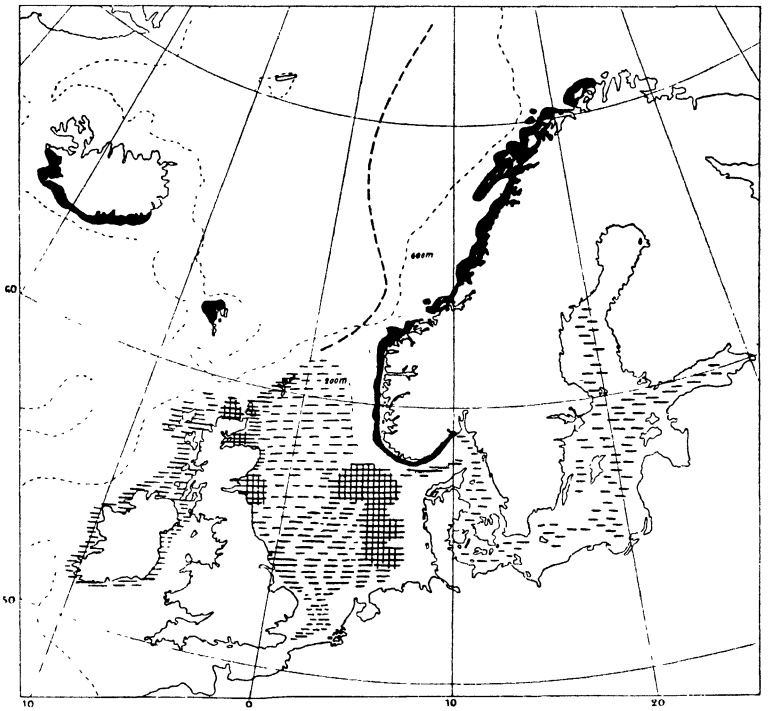


FIG. 36.—The European spawning grounds of the cod. The shading (black, unbroken lines, broken lines) varies according to the numbers of spawning fish. The broken line in the Norwegian Sea marks the western boundary for the larvæ. (After Hjort & Damas, with additions.)

The haddock is more sensitive to salinity than the cod, it demands a salinity of 35–35·2‰ and a temperature of 6–7° C. and it does not spawn in the Baltic. The most frequented spawning grounds in Europe are in the northern North Sea at a depth of about 80–150 m. A still higher salinity is required by the coalfish which spawns only in water of at least 35·2‰ and at a temperature of 7–8° C. The spawning coalfishes find water of this composition at the outer edge

of the shelf at a depth of about 200 (100–400) m. This fish may be regarded as archibenthic as far as its reproductive habits are concerned, but during its non-breeding life the species wanders further afield, even into the coastal region. Almost the same may be said of the ling whose spawning regions are given in fig. 37.

Certain fish *genera*, too, are endemic boreal, namely **Crystallogobius*, **Chirolophis*, **Zeugopterus*, **Scophthalmus* and **Raniceps*. Among these *Raniceps* is particularly noteworthy because of its isolated systematic position which, according to some ichthyologists, justifies the setting up of a special family. To these five genera which

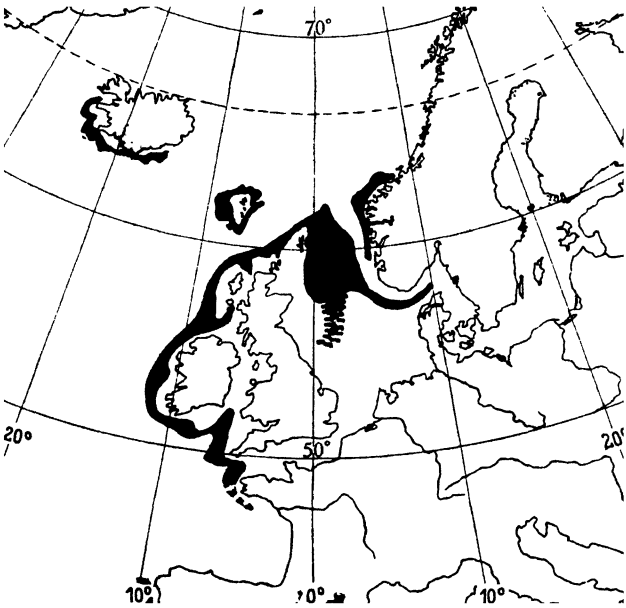


FIG. 37.—Spawning grounds of the ling, *Molva molva*.

are confined to the European boreal region, we must add *Cyclopterus* (Atlanto-arctic-boreal) and *Spinachia* which also occur in the American zone. None of these seven genera contains more than one species.

The Mediterranean-Boreal and Lusitanian-Boreal Elements

Of those decapods, mussels and fishes which are not preponderantly northern or endemic, most (at least 90%) reach as far as the Mediterranean or North-west Africa. Thus the warm-temperate (Mediterranean) element in Europe's boreal fauna is considerable. Among the crustaceans, all but two of the crabs (*Hyas araneus* and *H. coarctatus*) belong to it, and of the remaining Reptantia also

all but two (*Eupagurus pubescens* and *Anapagurus hyndmani*, the latter being only found in Great Britain and France). Examples of southern and boreal mussels are *Isocardia cor*, *Pecten varius*, *Arca tetragona*, *Tapes decussatus* and the oyster, *Ostrea edulis*. Among the echinoderms we may mention *Psammechinus miliaris*, (not in the Mediterranean but off Morocco), *Amphiura chiajei*, *A. filiformis*, *Ophiocomina nigra*, *Trachythyone elongata* (syn. *Cucumaria*). Both species of *Amphiura* belong also to the deep-water zone. A large number of species of other invertebrate groups could be added.

A corresponding distribution is shown among the fishes by the members of the family *Labridæ* (with the exception of the endemic species *Centrolabrus exoletus*), the species in the boreal region of *Pagellus*, *Mullus*, *Trigla*, *Trachinus*, *Bothus* and *Solea*, the gadid species *Gadus minutus*, *G. luscus*, *G.* (*Pollachius*) *pollachius* and *Merlucius merlucius* (hake); *Pleuronectes platessa* (plaice) and several others.

During their post-glacial expansion into the North Sea most species which have not reached western Norway, and thus are of a pronounced western or south-western character within the boreal region, seem to have migrated through the English Channel. Others, however, to judge from their present-day distribution, have come from the Atlantic around northern Scotland and reached the western North Sea in this way. *Siriella armata*[596] is such a species among the group Mysidacea. The southern immigrants which have reached the Scandinavian peninsula, like the species of the lower shelf zone, have probably used this northern immigrant route to a large extent.

The Arctic-Boreal Element

Of this group the echinoderms, decapods and fishes has been analysed mainly by N. von Hofsten.[237, 239, 240] Several of its members are eurybathic. Of the commoner species we mention the polychæts *Arenicola marina* and *Pomatoceros triqueter*, the crustaceans *Hyas coarctatus*, *Spirontocaris gaimardi*, and the common barnacle in the tidal zone *Balanus balanoides*, the molluscs *Mytilus edulis*, *Leda pernula*, *Buccinum undatum*, and *Dendronotus frondosus* (syn. *D. arborescens*), the echinoderms *Solaster* (*Crossaster*) *papposus*, *Ophiopholis aculeata* (also abyssal), *Ophiura sarsi* (also abyssal), *Strongylocentrotus drœbachiensis* (also abyssal). Fishes of this kind are *Cottus* (*Acanthocottus*) *scorpius* (Greenland bullhead), *Liparis liparis* (common sea snail), *Lumpenus lampetriformis* (snake blenny), *Cyclopterus lumpus* (lumpsucker) and *Anarrhichas lupus* (wolf fish). To these must be added the hermit crab *Eupagurus pubescens* and the echinoderms *Solaster endeca* (fig. 38), *Psolus phantapus* and *Cucumaria frondosa* which avoid the shallow southern North Sea;

this is also true of some ascidians (Hartmeyer[215]) and many amphipods (Enequist,[150] Stephensen[504]).

The peculiarity which we have just mentioned is a special case of a more general phenomenon. It is quite common for cold-water animals which in the northern regions inhabit the surface water to occur mainly or exclusively in deeper zones in the southern seas. This phenomenon is called *submergence*, a term introduced by V. Häcker.[202] This is of course clearly a result of the animal's sensitivity to temperature.

To this arctic-boreal group belong in addition various originally arctic species which occur as relicts within the boreal region. These will be discussed later.

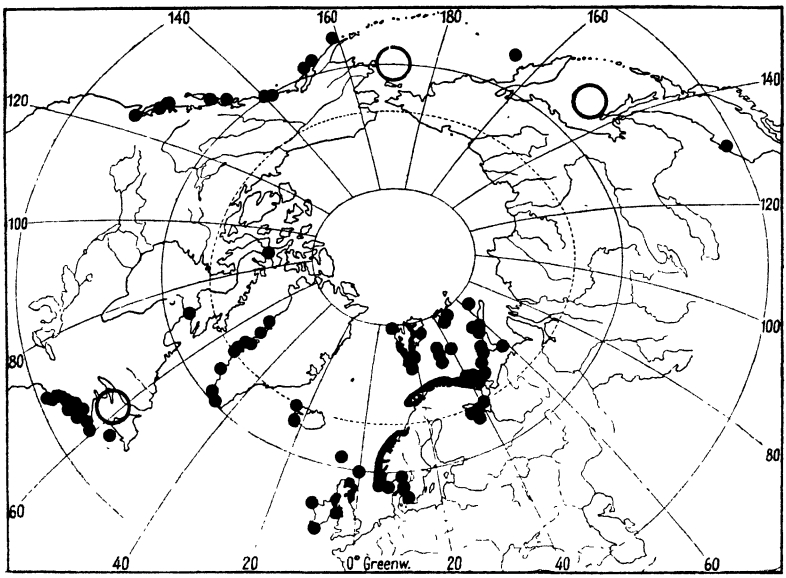


FIG. 38.—Distribution of the starfish *Solaster endeca*. The large open circles denote not precisely indicated finds. (Principally after v. Hofsten.)

The boreal fauna contains further cosmopolitan or at least widespread species which, however, are only of minor zoogeographical interest and may therefore be passed over.

Temperature at the reproduction period as a factor in distribution

As is well known, animals are divided into eurythermal, cold-stenothermal and warm-stenothermal. The concept "stenothermal" requires, however, a more profound analysis. An animal may be stenothermal or eurythermal during the whole of its life but it may

also be stenothermal or eurythermal to different degrees at different periods of its life. In particular, stenothermy is often more pronounced during the reproductive periods. The careful investigations of the last decades into the economically important fishes and other animals have provided so many examples of this physiological peculiarity that we may ask whether such a periodically increased stenothermy is not rather the rule than the exception. That each animal species as a rule choses a certain locality and a certain spawning season is a fact due not only to the periodicity of environmental conditions but also to a periodicity with regard to temperature requirements in the animal itself. The same is true for salinity.

We may therefore distinguish between a *reproductive* eurythermy or stenothermy which occurs during the reproductive period and a *vegetative* eurythermy and stenothermy at other times of life; we can similarly distinguish between reproductive and vegetative eurihalinity and stenohalinity. Reproductive stenothermy does not always coincide with the spawning period proper but it is possible that increased sensitivity to temperature is most marked at some other time, for instance during the ripening of the gonads in the parent generation, which is probably the rule in amphipods,[150] or in the young during the embryonic or larval stage. An animal which is eurythermal during the vegetative but stenothermal during the reproductive period, regardless of whether it is cold or warm stenothermal, may possibly find favourable conditions in boreal waters since the difference in temperature is greater here than in any other region. This may be responsible for the fact that the boreal fauna is a distinctly mixed one. Animals which are stenothermal during the whole of their life, however, do not find favourable conditions in the boreal region because of the great variation in temperature. Such species are thus barred from the region.

Pelseneer,[408] Appellöf,[13] Orton[400] and in particular S. Runnström[444] have investigated these conditions experimentally. They have been able to show that the arctic-boreal species, whose temperature requirements during the reproductive period lie between $-1°$ and 11° C., spawn in the winter in the boreal region, while the boreal species whose corresponding temperature requirements lie between 4° and 16° C. spawn during the greater part of the year and the Mediterranean-boreal species with a reproductive temperature of between 8° and 23° C. spawn during the summer. In the boreal region the annual temperature in the surface layer varies generally between 5° and 13° C. or 3° and 17° C. Originally subarctic or Mediterranean-Atlantic species are thus well able to find a suitable temperature for reproduction. In this way we can explain

the occurrence in the upper layers of boreal waters of *Cucumaria frondosa* and *Spirontocaris gaimardi*, which occur otherwise only in the arctic, since in winter it is, of course, the surface water which cools down most.[13]

Investigations into the spawning conditions of certain fish species in the open sea have confirmed the result obtained experimentally. The table below, which also includes several deep-water fish, illustrates this matter. That other factors than the temperature and salinity during the spawning periods may be concerned is seen from the fact that *Gadus* (*Micromesistius*) *poutassou* and the pelagic *Gadiculus argenteus* have a different distribution from *Molva byrkelange* and *Brosmius brosme*, although they spawn in water of the same temperature and salinity.

TABLE 13

TEMPERATURE, SALINITY AND DEPTH OF THE SPAWNING GROUNDS OF SOME GADID FISHES.[105]

	Temperature in ° C.	Salinity in ‰	Depth in m.
I. Mediterranean - Atlantic and boreal species			
Gadus minutus	more than 10	32 to 35·35	less than 100
Gadus luscus			
Gadus pollachius			
Merlucius merlucius (syn. *M. vulgaris*)	about 10	35·2 and more	100 to 200
Gadus poutassou	6 to 9	more than 35·3	1000 and more
Gadiculus argenteus			400 to 1000
II. Southern boreal species			
Gadus esmarkii	about 6	35 to 35·2	60 to 200
III. General boreal species			
Gadus morrhua	4 to 6	34 to 35	40 to 100
Gadus æglefinus	6	35 to 35·2	60 to 200
Gadus virens	7	35·2 and more	100 to 200
IV. Northern and western boreal species			
Molva molva	more than 7	35·2 and more	100 to 200
Molva byrkelange	6 to 9	more than 35·3	400 to 1000
Brosmius brosme			200 to 1000

2. THE FAUNA OF THE BALTIC AND OTHER BRACKISH REGIONS

The Baltic, which has a surface of 422,000 square kilometres, is the largest of the world's brackish-water basins at the present time. The Black Sea is, of course, almost as large (420,000 square kilometres) and of a much reduced salinity, but it is only partly of a truly brackish nature. As a subsidiary of the North Sea, the Baltic

has a fauna which is to a large extent derived from Atlantic species, but their number decreases progressively the further one penetrates into the interior regions. Here we find also euryhaline fresh water species. The Baltic possesses, moreover, two elements which characterize it positively, namely the genuine brackish-water animals and the glacial marine relicts.

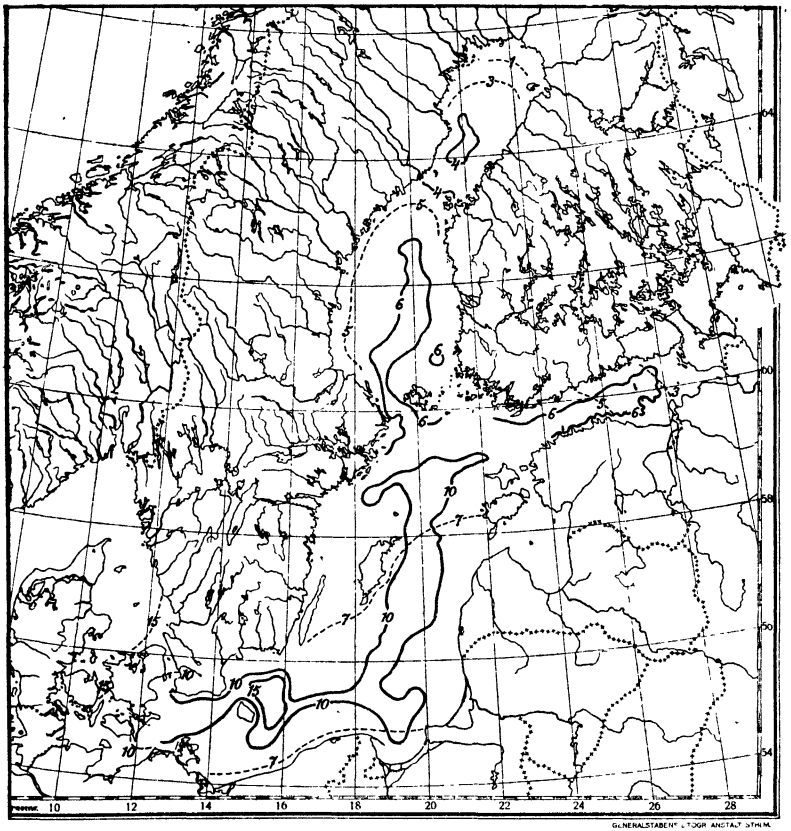


FIG. 39.—Isohalines (in ‰) of the Baltic at the surface (broken lines), and at the bottom (full-drawn lines). (After Deutsche Seewarte, Hamburg.)

Hydrography

The special character of the Baltic fauna is determined by the hydrographical peculiarities and the history of the Baltic Sea.

This sea is hydrographically over its full extent a brackish region, but its salinity varies greatly in its different parts. In the transitional region between the Kattegat and the Baltic proper, in the so-called

Belt-sea† the salinity is 15, and even 20, to 10‰. It steadily decreases towards the interior, and at the northern end of the Gulf of Bothnia it sinks to about 2‰. The figures for the deeper layers of water are higher than for the surface (fig. 39). Because it is renewed comparatively slowly, the deeper water contains a considerable amount of carbon dioxide and in certain hollows even hydrogen sulphide, but it is often poor in oxygen. By far the largest part of the Baltic and the whole of the Baltic proper belong to the mesohaline region (cf. p. 117).

It is clear, therefore, that marine animals will decrease in number in the interior of the Baltic and fresh water animals will increase.

The temperature of the water naturally decreases towards the north; in the most northern parts of the Gulf of Bothnia the surface water during August has a temperature of only 12–14° C. The mean period for the freezing-over of the innermost part of the Gulf of Finland is generally five to six months, in that of the Gulf of Bothnia more than six months. The conditions with regard to temperature may be seen from the following table.

TABLE 14

TEMPERATURE IN THE BALTIC FROM MAY TO JULY (MEAN OF SEVERAL YEARS)

Depth in m.	Baltic E. of Gotland, 57° 11′ N.		Gulf of Bothnia 62° N.		Gulf of Bothnia 64° 20′ N.	
	May 15th	July 17th	May 23rd	July 20th	May 23rd	July 22nd
0	4·3° C.	15·7° C.	2·7° C.	13·7° C.	1·1° C.	14·1° C.
10	4·0	14·1	2·5	12·2	1·0	10·9
20	3·8	9·3	2·3	7·2	1·0	5·4
40	2·9	3·6	2·1	3·6	0·9	3·2
80	3·4	0·9	1·8	2·0	0·8	0·8

The temperature is thus at 30–40 m. depth continually arctic and therefore favourable for the arctic relics which live there. The glacial conditions which we have mentioned are important for one arctic relict, the seal *Phoca hispida*, which gives birth to its young on the ice.

As we have seen, the salinity of the water is very different in different regions and various brackish regions have therefore been distinguished. Redeke,[427] who put forward the first system, took the chlorine content (chlorinity) as basis for his divisions and his system referred to the Zuider Sea. Since it is more practical to base a system on the total amount of dissolved substances, i.e. its salinity,

† The boundary between the Belt-sea and the Baltic proper is the threshold of Darss and the southern end of the Oeresund. The region south of the Danish islands, which in German literature is inappropriately called "Western Baltic" (Westliche Ostsee), will here be called "German Belt-sea".

Välikangas[564] devised a system which took due consideration of the distribution of animal species in so far as it is known, which on the whole agrees fairly closely with Redeke's, but is specially applicable to the Baltic. With a minor alteration of Välikangas' system and an addition referring to marine waters the system takes the following form†:

Fresh water	Salinity 0–0·5‰
Oligohaline brackish water	,, 0·5–3‰
Mesohaline ,,	3–10‰
Polyhaline ,,	10–17 (20?)‰
Oligohaline seawater	17 (20?)–30‰
Mesohaline ,,	30–34 (?)‰
Polyhaline ,,	>34 (?)‰

Genuine brackish-water animals

In brackish water, and especially in the mesohaline region just mentioned, animals occur which find here more or less optimal conditions. Several of them occur both in the Baltic and in other brackish-water regions, for instance in the estuaries of the North Sea, in the Zuider Sea and even in arctic estuaries. In the latter live some Baltic glacial marine relicts (which we shall neglect for the moment since we shall treat them in a later connection). The Baltic in spite of its size, possesses no endemic brackish-water animals. It is obviously too recent to have been able to evolve new species. We shall give here some examples of brackish-water species, and to complete the picture we shall also include the plankton.

The cœlenterates are represented here by the primitive *Protohydra leuckarti* which is recorded from several localities from Kiel Bay to the region of Stockholm and south-west Finland and further off Ostend and Kamchatka; and *Cordylophora caspia* (occasionally found also in fresh water); further the turbellarian *Promesostoma baltica*; the nemertine *Prostoma obscurum*; the polychætes *Alcmaria*

† Välikangas includes also water which above is called oligohaline seawater, in brackish water and calls it polyhaline brackish water. The brackish water, which above is called polyhaline, he calls pleiomesohaline. One must, however, agree with Remane (1940, p. 31), in spite of Dahl's[97] criticism, that "polyhaline brackish water" (above called oligohaline seawater) is not brackish as far as its fauna and flora are concerned. It is a mixed zone with a predominating element of euryhaline sea animals. Välikangas and Brattström[51] strongly emphasize the fact that the most important boundary in the Baltic is to be found at 8–10‰ salinity, that is between Darsser Ort and Gjedser which represents the south-western boundary of the Baltic proper. The change proposed above gives the term "polyhaline brackish water" a new meaning of course, but we are thus able to avoid the division of the mesohaline fauna into two subdivisions, which Välikangas' system entails, i.e. meio- and pleiomesohaline. This division is logically unsatisfactory since the subdivisions show more marked differences between themselves than the main divisions mesohaline and polyhaline. To call, as sometimes happens, polyhaline brackish water simply "polyhaline water" is not correct since ordinary seawater is naturally more polyhaline than polyhaline brackish water.

romijni (from an estuary near Greifswald, Holland, and Ringköbing fjord in Denmark), and *Manayunkia æstuarina* (estuaries in England and Ireland, Holland, the Ringköbing fjord in Denmark, south-west Baltic); the rotifer *Synchæta fennica*; the copepods *Eurytemora affinis* (also as a relict in inland lakes) and *E. hirundoides*; the cladoceran *Podon polyphemoides*; the ostracods *Cyprideis litoralis*, *Cytheromorpha fuscata*, and *Cytherura gibba* (only known from the East Atlantic region); the amphipods *Gammarus duebeni* and *Corophium lacustre*; the prawn *Palæmonetes varians* which occurs only as a brackish-water animal in northern Europe but is found both in brackish and fresh water in Mediterranean countries; further the bryozoan *Membranipora crustulenta* which also occurs in the Arctic Sea and is widely distributed in the North Sea region and the Baltic, and the rare *Victorella pavida*; the snail *Hydrobia jenkinsi* (Great Britain, Holland, Denmark, the Baltic), which arrived at a late date in Europe from America and the mussel *Congeria cochleata*.[574]

A fairly substantial number of genuine brackish-water animals from the north European coasts also occur in the brackish-water region of South-east Europe (the Black Sea's estuaries, etc.). These include, among the above-mentioned forms, *Cordylophora caspia*, *Cyprideis litoralis*, *Podon polyphemoides* and *Victorella pavida*.[565] Several others could be added. This probably means that a considerable number of the north and west European species of the brackish-water fauna are derived from the prehistoric Sarmatic brackish-water fauna.

Apart from the Zuider Sea and the Baltic, other boreal regions, too, contain a brackish-water fauna. Several investigations on this subject have been undertaken, for instance in the Ringköbing fjord in western Denmark,[285, 492] in estuaries in England[37, 92] and the German Haffs, which in certain respects differ from the brackish water of the rest of the Baltic.[373, 580]

The dependence of these animals on a more or less strictly defined salinity is, of course, due to physiological reasons, mainly to the mechanism of osmoregulation (cf. the survey of Gessner[178]). It has been demonstrated that bony fishes and fresh-water animals in general are homoio-osmotic, i.e. they possess the faculty to retain their body fluid at a fairly constant level of salinity irrespective of the surrounding medium. In contrast to this the marine invertebrates were until recently considered to be poikilo-osmotic. But it has been proved that these animals, too, which do not need to employ osmotic regulation in normal seawater since the molar concentration of both body fluids and seawater tally, are able to live in brackish water only if either they reduce the molar concentration of their body fluids accordingly (and then they may be regarded as truly

poikilo-osmotic) or if they are able to maintain the molar concentration of their body fluids at the necessary level above the concentration of the environment with the help of osmoregulatory mechanisms. In the latter event they will be only in a few cases completely homoio-osmotic since the concentration of body fluids may vary within certain limits. The degree of variation differs greatly for the various species and this brings about a gradual transition between homoio-osmotic and poikilo-osmotic animals.

Euryhaline marine animals

The genuine marine animals in brackish water have of course migrated from the more saline regions of the sea and represent the most euryhaline group of the marine fauna. In the Baltic it may be seen quite clearly how the diminishing salinity influences the selective immigration of marine animals. Taxonomic groups such as the Madreporaria, Octocorallia, Scaphopoda, Pteropoda, Cephalopoda do not penetrate at all into the Baltic, or perhaps only by chance; others show a greatly diminished number of species with decreasing salinity. Among the sponges 27 species are known from the Kattegat, 16 from the sea south of the Danish islands (the German Belt Sea), but none from the southern part of the Baltic proper between Darsser Ort-Gjedser and Bornholm. Likewise there are none in the Gulf of Bothnia and the Gulf of Finland. The figures for sea-anemones in the regions mentioned are 18, 4, 2 and 0, for polychæts 150–175, 70, 15 and 4, for amphipods 132, 36, 13 and 5, for decapods 64, 13, 5 and 2, for lamellibranchs 87, 34, 24 and 5, and for echinoderms 35, 8, 2 and 0. For completeness' sake we mention that *Campanularia flexuosa*, *Aurelia aurita*, *Nereis diversicolor*, *Harmothoë sarsi*, *Acartia longiremis*, *Balanus improvisus*, *Idothea baltica*, *Jæra albifrons*, *Gammarus locusta*, *Corophium volulator*, *Leander adsperus*, *Crangon crangon*, *Mytilus edulis*, *Cardium edule*, *Mya arenaria*, *Macoma baltica* and others less well known occur as far as the outer regions of the Gulfs of Finland and Bothnia, and a few penetrate also into the interior parts. Other species again do not penetrate so far into the brackish regions, for instance *Scoloplos armiger*, *Terebellides stroemi* and *Priapulus caudatus* whose northern limit is the region of Gotland, and *Nereis pelagica*, *Arenicola marina*, *Balanus balanus*, *Ophiura albida* and the common starfish *Asterias rubens* which do not penetrate further than the region of Bornholm. It has been shown that several of the euryhaline animals mentioned are incapable of breeding at the furthest points of penetration and so cannot be granted full domiciliary status there. The sea-anemones *Metridium dianthus* and *Sagartia viduata* and a large number of others come to a halt even sooner, in fact south of the Danish islands,

and at the southern entrance to the Oeresund, that is at the thresholds of the Baltic proper. The number of species of invertebrates in the Baltic has been calculated as between 200 and 300.

Many fishes of the North Sea are distributed as far as the Gulfs of Bothnia and Finland. First of all we mention the brackish race of herring, *Clupea harengus membras*, a fish which economically is of great importance for the whole of the Baltic region, then the cod (*Gadus morrhua*) whose northernmost Baltic breeding ground is the deep trough off the Swedish province of Ångermanland; the same holds good for *Lumpenus lampetriformis*. Because of hydrographical conditions, the cod and several other fishes are mainly restricted to the deeper troughs where the water is more saline than at the surface. In contrast to the cod of the Atlantic, the Baltic cod is a stationary fish which only occasionally travels as far as 20 km., as has been proved by some marking experiments. The following fishes are regularly to be found in the Gulf of Bothnia: *Cottus* (*Acanthocottus*) *scorpius* (Greenland bullhead), *Liparis liparis* (common sea snail), *Cyclopterus lumpus* (lumpsucker), *Lumpenus lampetriformis* (snake blenny), *Pholis gunellus* (butterfish), *Zoarces viviparus* (eelpout), *Spinachia spinachia* (fifteen-spined sticklebass), *Nerophis ophidion* (straight-nosed pipe fish), *Syngnathus* (*Siphostoma*) *typhle* (broad-nosed pipe fish), *Ammodytes lanceolatus* (greater sand eel), *A. tobianus* (lesser sand eel), *Gadus morrhua* (cod), *Pleuronectes flesus* (flounder), *Bothus maximus* (turbot), *Clupea harengus membras* (small Baltic herring, "strömming") and *C. sprattus* (sprat). *Pleuronectes platessa* (plaice) and *P.* (*Limanda*) *limanda* (dab), which in the area round Gotland reach the northern limit of their regular appearance, are the subjects of lucrative fishing in the southern Baltic, e.g. round Bornholm.

The region of distribution in the Baltic of euryhaline marine animals commonly lies at a greater depth than is the case for the purely marine habitat of the species. Such a submergence in brackish water is easily explained by the fact that a layer of greater salinity lies beneath the less saline because of its higher specific gravity.

Euryhaline fresh-water animals

In contrast to marine animals, the species which are really fresh-water animals and have only secondarily migrated into brackish water are naturally most numerous in the most brackish water in the Baltic, in the Gulfs of Bothnia and Finland. Several of them, however, live also in the archipelagoes of the Baltic proper, and in its most southerly estuaries. The southern limit of distribution can, therefore, hardly be given for any but the plankton animals of the open sea, for instance the rotifers *Keratella* (=*Anuræa*) *cochlearis*,

Notholca longispina and *Asplanchna priodonta*, which occur widely in the Gulfs of Bothnia and Finland as well as in the northern part of the Baltic proper but are missing or rare in its south-western regions. One of the most euryhaline plankton fresh-water species is the cladoceran *Bosmina obtusirostris* whose variety *maritima* (sometimes regarded as an independent species) can be found as far out as the northern entrance to the Oeresund. As examples of euryhaline benthic species we may mention the sponges *Spongilla lacustris* and *Ephydatia fluviatilis*, further the oligochæte *Tubifex tubifex*, several snails (*Lymnæa ovata, Theodoxus fluviatilis*), the isopod *Asellus aquaticus*, etc. Of moderately euryhaline fishes we find *Coregonus lavaretus* (whitefish), *Abramis brama* (bream), *Esox lucius* (pike), *Lota lota* (turbot) and *Perca fluviatilis* (perch). Most euryhaline are *Salmo salar* and *Anguilla anguilla*, as well as the stickleback (*Gasterosteus aculeatus*).

3. HISTORY OF THE ATLANTIC BOREAL FAUNA

Palæontological and geological data

The Late Tertiary connection with the North Pacific. As we shall see later on, the ancient connections between the North Pacific and the North Atlantic had a profound influence on the fauna of the latter. Such connections seem to have existed in the late Tertiary Period. This emerges mainly from the investigations into the Crag deposits of eastern England which F. W. Harmer[208] published in an extensive and important work. The formation mentioned belongs to the Pliocene, partly even to the early Quaternary Period (Pleistocene) and it shows quite clearly a gradual lowering of temperature before the advent of the glacial period. The Pliocene fauna of western Europe and North America has also been studied by other workers.[462, 540] From their results we shall mention here only that the climate of the North Atlantic coasts varied in the late Tertiary Period between warm-temperate and subarctic and that we may assume a fairly comprehensive faunistic connection during the late Pliocene between the cold-temperate faunas of the Atlantic and Pacific. These palæontological investigations also throw light on the mortality of species, which seems inseparable from the biological development of the geological periods. The following table may serve to illustrate this point (p. 122).

Last inter-glacial period. On the North Sea coast of Denmark, in Schleswig-Holstein and the southern region of the Baltic fossils from the so-called Eeemian Sea have been found which belonged to the last inter-glacial period. These fossils seem to indicate that the climate of this region was very little warmer than at present.[321, 383]

In the Eemian Sea lived, among other forms, *Cyprina islandica*, *Macoma baltica* and the now extinct *Tapes senescens*. After some slight climatic variations a cooling of the climate occurred towards the last Ice Age. During a boring undertaken in North Jutland beneath 57 m. of deposits of the last Ice Age, inter-glacial strata were found, and the bore passed through a further 123 m. of these strata. Here was found at the lowest level the boreal *Turritella terebra* zone and above this a zone containing *Portlandia arctica*, which was deposited in the glacial sea existing there. These inter-glacial deposits are called after the hamlet where the borings were executed the *Skærumhede* series.

TABLE 15

MOLLUSCS WHICH LIVED DURING THE LATE TERTIARY PERIOD IN THE NORTH ATLANTIC BUT ARE NOW TO BE FOUND EXCLUSIVELY IN THE NORTH PACIFIC OR *vice versa*

Species	Present Period	Late Pliocene or Early Quaternary Period
Liomesus canaliculatus .	Bering Sea, Alaska, Arctic Sea	England, Iceland
Neptunea castanea .	Bering Sea and south of Alaska	England
Sipho herendeeni . .	Bering Sea, Aleutian Islands	England
Trichotropis insignis .	Bering Sea, North Japan	England
Serripes laperousii .	Bering Sea	New England
Littorina palliata . .	New England to White Sea	Bering Strait

As is well known, there was a considerable shifting of boundaries between land and sea during the Quaternary Period. This shift was due to two causes: partly an isostatic one, since the weight of the ice during the glacial period brought about a depression of the earth's crust throughout the glaciated regions while the lightening of the burden during the inter-glacial and post-glacial periods caused an elevation; and partly to an eustatic cause, due to the variation of the amount of water in the oceans. During the glacial periods a considerable amount of atmospheric water was accumulated in the shape of inland ice and thus withdrawn from the oceans, while the opposite process took place during the warmer periods when the inland ice melted. It has been calculated that during the peak period of the last Ice Age, that is for about 40,000 years, the surface of the world's oceans was roughly 90 m. below the present one (cf. the "glacial control theory" regarding coral reefs, p. 9).

Ancient zoogeographical and physico-geographical circumstances are, of course, of paramount importance for the present-day composition and distribution of faunas, but our knowledge of the

times before the late glacial period is very sketchy. The natural history of the late and post-glacial periods on the other hand has been studied from many angles.

The late-glacial and post-glacial periods in eastern North America

Fossil-bearing marine deposits of the late glacial time were already described by Dawson (1893) from the valley of the St. Lawrence River. They contain an arctic fauna with *Leda glacialis*, etc. But on Prince Edward Island and in Maine several species, for instance *Venus mercenaria* and *Ostrea virginiana borealis*, have been found which belong to a non-arctic fauna. In the region of Fundy Bay the faunas indicate, according to Matthew,[330] a late glacial climate, similar to the present conditions in southern Labrador, followed by increased temperatures which in time exceeded those prevailing today; subsequently there was a slight fall which brought about present-day conditions; thus we have the same climatic changes as took place in North-west Europe.

The late-glacial and post-glacial periods on the British coasts

Formerly the Scottish coast was 30 m., in the Hebrides as much as 60 m., higher than at present, at a time when the Highlands were still under ice. The so-called 100-foot terrace thus formed contains a marine fauna which may be characterized as arctic or subarctic,[587] while on the west coast of Scotland, which has a position opening on the warmer Atlantic water, a boreal fauna seems to have lived even during the glacial period. In the northern North Sea there lived at that time *Portlandia arctica*, which points to high-arctic sea temperatures, and the Lusitanian-boreal-subarctic *Cardium edule* and *Tellimya ferruginosa*, which could, however, not have lived there at the same time as *Portlandia*, but may belong to a later period. Further to the south the land during the glacial and late glacial periods was, however, higher than it is now (Reid[433]), the maximal difference between the glacial and the present-day coast line being at least 55 m. Thus the southern half of the North Sea was for the most part land and the English Channel did not yet exist (fig. 40). The late glacial and the earliest post-glacial fauna of the North Sea immigrated therefore not through the English Channel but from the north.

The late-glacial and post-glacial periods on the west coast of Scandinavia

The elevation of the land which started at the end of the last Ice Age, was more pronounced in the central parts of Scandinavia than on the periphery. Thus there was no elevation in southern

Scania, while in North Germany and western Denmark the land was actually higher than it is now. In several regions periods of transgression of the sea alternated with periods of regression. The whole process seems like a race between isostatic land elevation and eustatic rise of the level of the sea, in which the land elevation

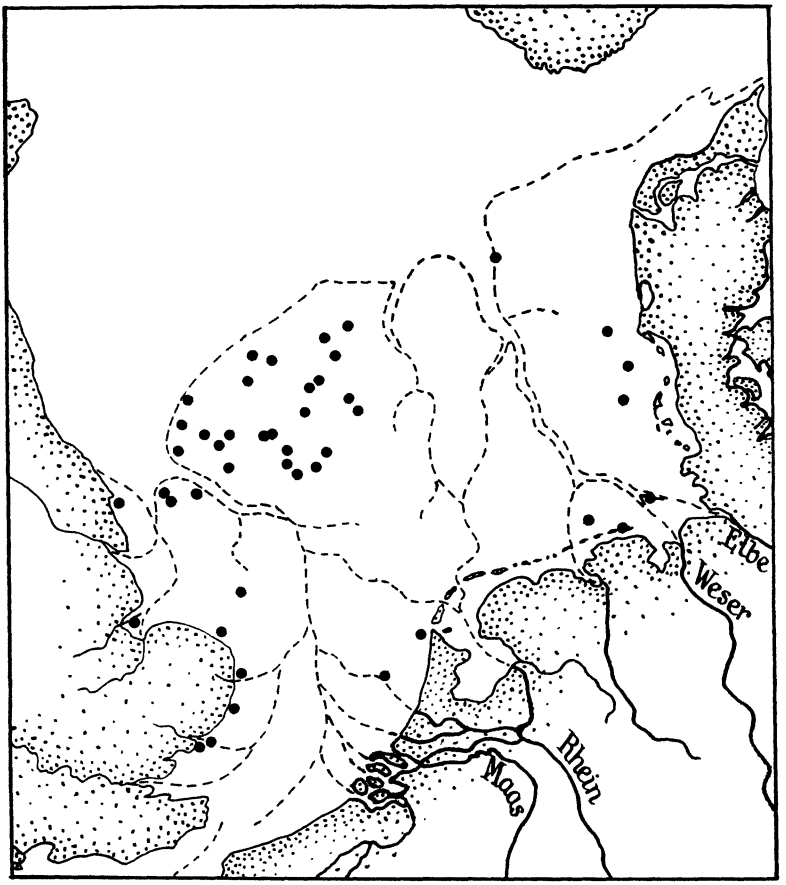


FIG. 40.—Coast-line and river-beds of the southern North Sea in the so-called continental age. (After Reid.) The black spots in the sea mark submarine moorlog finds (after J. G. D. Clark, 1936).

in the centre gained an advantage which was greater the nearer the region in question was to the former centre of the inland ice. The maximum elevation was 280 m. near the town of Oernsköldsvik.

More than a hundred years have passed since J. Smith (1839) in Scotland, and S. Lovén (1846) in Sweden, discovered a fossil arctic

marine fauna, and soon afterwards Michael Sars published his epoch-making investigations in Norway. Since then there have been many finds. Along the coast of Scandinavia, a great number of fossil-bearing clay deposits and shell beds at various heights above sea level have been examined and it has been proved that the faunas change through the ages. An early high-arctic fauna was followed by a low-arctic, and this in its turn by a boreal fauna.

The oldest fauna, which was arctic, is characterized chiefly by the mussels *Portlandica* (=*Yoldia*) *arctica*, *Macoma torelli* and *M. loveni*, which nowadays lives only in high-arctic waters. At the time when the margin of the land ice retreated as far as the region of Göteborg the fauna was, however, no longer high-arctic but low-arctic or subarctic. *Portlandia arctica* is however a characteristic species for the Baltic Yoldia Sea, which came into being when the land ice receded further and no longer acted as barrier between the Baltic and the western sea; thus a high-arctic fauna once again prevailed. A cooling of the climate is also indicated by the fact that the margin of the ice during the early period of the Yoldia Sea deposited larger marginal moraines (oses) than before, since for a long period it did not recede but stood still or possibly even advanced. Many finds of *Portlandia* have been made somewhat to the north of the great central Swedish marginal "oses" both in west and east Sweden. The oscillations of the sea-climate which we have just referred to thus accord well with the developments of the land-climate. At the time when the ice receded from the most southern part of Sweden an arctic flora existed, which later, in the so-called Alleröd period, was followed by a completely temperate flora. The Alleröd period was succeeded by a colder period which is considered to have been contemporary with the appearance of the great marginal "oses".

The time during which the ice receded from southern Sweden as far as these moraines is called the Gotiglacial Period. Apart from the mussels already mentioned, the following animals are among the constituents of the west Swedish marine fauna of that time: *Gadus* (*Boreogadus*) *saida* (polar cod), *Balæna mysticetus* (Greenland whale), *Delphinapterus leucas* (white whale), *Monodon monoceros* (narwhal), *Odobænus rosmarus* (walrus), further *Phoca hispida*, *P. barbata* and *P. grænlandica*, as well as *Thalarctos maritimus* (polar bear). In the Finiglacial Period which followed, the marine fauna was no longer arctic but a subarctic mixed fauna which was almost identical with that which lives at present on the north coast of the Kola Peninsula or along the coast of the Norwegian Finmark. Of purely northern species we find in this fauna *Pecten islandicus* and *Macoma calcarea*, and to these are added species which in the main have a more

southerly distribution, such as, for instance, *Mytilus edulis*, *Littorina litorea* and the barnacle *Verruca stroemia*. This fauna has been found in Denmark as well as in Sweden and Norway.

The deposits of the faunas which we have just discussed consist of clay layers with scattered fossils. The origin of the numerous shell beds which have been investigated along the whole of the west coast of Scandinavia originated, however, in the next period, which had a boreal fauna. In central Bohuslän are situated the most extensive shell beds in Scandinavia and probably in the whole of Europe; some of them (unfortunately now largely destroyed) are near the town of Uddevalla. They may reach 13 m. in depth and are in the main formed by white shells and shell fragments which were deposited there when the water level was higher. Among mussels we find particularly frequently a thick-shelled large form of *Saxicava arctica* with *Mya truncata uddevallensis*, *Pecten islandicus*, *Astarte borealis* and *Mytilus edulis*, among snails *Trophon clathratus* and among barnacles *Verruca stroemia* and *Balanus hammeri*. This combination of animals shows that the fauna was northern-boreal or possibly subarctic.

The Uddevalla-beds owe their great size probably to local conditions.[390] During the Yoldia Period and the early Ancylus Period (cf. p. 128), that is about 9000–7000 years B.C., enormous masses of water poured through the straits which at that time connected the Wänern basin and hence the great Baltic Sea with the Skagerak. These straits were situated east of Uddevalla. The strong superficial brackish-water current caused a deeper current of more saline water to flow in a contrary direction. Thus there was a very active circulation of water bringing a great amount of food with it, conditions which produced a particularly rich fauna. When the Baltic water could not longer use the Wänern basin because of the central Swedish land elevation, but had to take the route through the Oeresund and the Belts to the ocean, the favourable conditions for a mass production of molluscs in the region of Uddevalla disappeared.

The origin and history of the shell beds in northern Bohuslän have been carefully investigated by Hessland[233] who has shown *inter alia* that already in the late-glacial period, that is about 9000–8000 years B.C., boreal-Lusitanian species began to immigrate in considerable numbers into this region, and this immigration of relatively southern species about 6000–5500 B.C. had reached such proportions that nearly 80% of the animals of the shell beds were boreal-Lusitanian (and Lusitanian) species.

About the end of the Ancylus Period (cf. p. 128) the seawater on the coast of western Sweden seems to have had the same temperature as at present. Later, however, the temperature rose, and thus, in the

period which followed, the climate was milder than it is at present. That was the so-called *Post-Glacial Warm Period* (about 5000–2000 B.C.). It is indicated in the marine deposits of western Sweden and Norway by the mussel *Tapes decussatus*, in those of the Baltic by the snail *Littorina litorea* (the Littorina Sea); this period is, therefore, also known as the Tapes Period, the Tapes-Littorina Period or the Littorina Period. *Tapes* is now still to be found in some localities of western Norway, but has disappeared from south-west Norway and Sweden, where it was by no means rare during the warm period. Other mussels which are Lusitanian-boreal, for instance *Isocardia cor* and *Ostrea edulis*, were evidently more common formerly and found further to the north than they are now. The oyster lived in the Lofoten Islands, several degrees further north than at present. True oyster beds are now no longer found north of the Limfjord in northern Jutland and even here their present abundance dates only from about 1850, being due to the well-known break-through to the west caused by a storm flood in the year 1825, when the Limfjord, which formerly communicated only with the Kattegat, also became connected with the North Sea. In the Tapes Period oysters were common in many places in Denmark: they form the main constituent of the shells found in the kitchen middens and they also occurred profusely in several parts of the Swedish and Norwegian coasts where today they are either very scarce or not to be found at all. The more profuse occurrence in the Danish islands was also made possible by the higher salinity of the Baltic (cf. p. 129). The difference between sea temperature during the warm period and at present was probably about 2°. It fits in well with these Scandinavian data that some molluscs, for instance *Mytilus edulis*, *Cyprina islandica* and *Littorina litorea*, formerly lived near Spitsbergen and other arctic localities which lie at present outside their habitat.[257]

Faunistic shifts have taken place also in later periods. So far as Europe is concerned the most remarkable one concerns the immigration of the soft-shell bivalve *Mya arenaria*, which is now a characteristic animal for the sandy bottoms of shallow coastal waters in most parts of North-west Europe, including the Baltic. Hessland[234] has described in detail the history of the distribution of the species. In the later part of the Pliocene it was found in Great Britain but died out during the Ice Age and was thereafter confined to the Atlantic coast of North America until it re-entered Europe in quite recent times, most probably with the aid of ships after America was discovered. There is no proof of an earlier occurrence in Europe during the post-glacial period and the pelagic life of the larva is too short to make a distribution with the aid of the Gulf Stream across

the Atlantic possible. On the Pacific coast of America, too, *Mya arenaria* has spread quickly and far since it was introduced in 1874 in connection with the planting of *Ostrea virginica*. It has, however, to be explained why *Mya arenaria* was not only exterminated in Great Britain by the Quaternary Ice Age but was also at the same time prevented from gaining a foothold on south-west European coasts and afterwards, in the early post-glacial period, from re-immigrating from there, to North-west Europe. Such may have been the history of the main part of the present British coastal fauna as well as of that of the other European coasts.

The late-glacial and post-glacial periods in the Baltic [363]

After the great mass of inland ice had retreated from the North German land ridge to the north, water was hemmed in between the ice and the southern watershed. Thus the *Baltic Ice-dammed Lake* originated, which increased continually with the melting of the ice masses until it overflowed through a low pass in central Sweden and thus was reduced to sea level. Some of the glacial relicts which will be mentioned below apparently reached the highest inland lakes only with the help of this Ice Lake, and according to Munthe[363] it is probable for other reasons that the Ice Lake incorporated a marine predecessor in the south-west and thus received a marine cold-water fauna which was, however, poor in species. With the continued retreat of the ice margin, it was possible for seawater to penetrate into the Baltic basin and so the *Yoldia Sea* was formed. This is called after the mussel *Portlandia arctica* (formerly *Yoldia arctica*) which we have mentioned before; it covered wide stretches which are now dry land, while in the South Baltic the opposite was the case. The connection with the ocean went across what is now the central Swedish lowland; an earlier assumption of a connection with the White Sea across Ladoga and Onega is now considered by the geologists to be wrong. Because of its narrow connection with the ocean and the strong influx of fresh water from rivers and melting ice, the fauna of the Yoldia Sea was not a true marine fauna but was a brackish, or oligohaline marine fauna. *Portlandia* itself has not been found east of Stockholm. We shall discuss the most important of the other species when treating the relicts. After a short time (according to the present view of Sauramo and Munthe after 500–700 years) the central Swedish strait became elevated and thus transformed the Yoldia Sea into a gigantic fresh-water lake, the *Ancylus Lake*, so called after the gasteropod *Ancylus fluviatilis*. The brackish fauna was replaced by a fresh-water fauna. The first outflow, the Sveaälv (Svea River), occurred across the lowest pass in central Sweden, but because of the isostatic movement of the

earth's crust a southern outflow between the Great Belt and the Danish islands came into being later on. Through continuous lowering to the south the Belts and the Oeresund were formed. They were once even deeper than at the present time and to this was added possibly an eustatic rise of the level of the sea because of the melting of polar ice during the post-glacial warm period; thus saline water was able to penetrate in larger amounts than today. In this way the Baltic entered a new stage called the *Littorina Sea* after the common periwinkle, *Littorina litorea*, which together with several other molluscs penetrated further into the Baltic than they do today. The salinity at its maximum in this sea was about twice as high as at present. This is indicated by certain molluscs. *Littorina rudis*, now only found as far as Bornholm, lived then near Kalix at the northern end of the Gulf of Bothnia; *Littorina litorea* which does not now occur east of Ruegen and the southern entrance to the Oeresund, was found as far as Sundsvall (62° 20′ N.); the oyster, *Ostrea edulis*, then lived (cf. p. 127) in the most south-western parts of the Baltic (the Belt-sea) and so on. The greater salinity also influenced the size of the molluscs. The cockle, *Cardium edule*, and the common mussel, *Mytilus edulis*, were larger than they are now in the same region of the sea (this may be partly also due to the food conditions then prevailing).

Among the animal species of the Littorina Sea the Greenland seal, *Phoca grœnlandica*, deserves special mention. It is a genuinely pelagic sea animal which bears its young on the ice and is also in other respects completely independent of dry land. It is furthermore an arctic animal which normally only appears south of the arctic sea region in connection with the great drifting ice packs. It is therefore peculiar that this seal occurred profusely in the Baltic during the warm Littorina Period. Such finds have been made in the larger part of the Baltic and on the coast of the Kattegat in Denmark. Particularly in Gotland and Åland the numerous fossil finds in archæological prehistoric dwelling places shows that this species was hunted by the men of this period in considerably greater numbers than other seals and that this seal had a firm foothold in the Littorina Sea. As far as we can judge it was a relict from the Yoldia Sea. It is not at all impossible that the ice formation in the Littorina Sea was greater than in the present Baltic. If the more saline water of the Littorina Sea was closer to the surface and the surface fresh-water layer was therefore thinner than it is at present, this would mean that the vertical currents which are caused by cooling (the convection currents) and the horizontal currents caused by the wind had a much thinner layer to work on (because the heavier salt water was relatively unaffected) and freezing was facilitated.

Between 1000 and 2000 B.C. the Oeresund and the Belts became shallower and thus the Littorina Sea changed to the conditions which now characterize the Baltic.

The relicts of the European boreal fauna

The geographical, climatic and faunistic changes which we have just described may partly be gathered from the distribution of the present fauna and its constitution. When the arctic fauna retreated towards the north it left behind in certain regions populations of isolated species which were able to survive in isolation right up to the present time. Certain such survivors of a prehistoric fauna or flora are termed relicts.

Not all survivors from an ancient fauna do, however, merit the name relicts. It would be senseless to regard for instance *Saxicava arctica* or *Hyas coarctatus* as glacial relicts in the North Sea simply for the reason that they have lived there since the Ice Age. For the North Sea and the Arctic Ocean are still in communication with each other, and the two species mentioned would presumably be found in the North Sea even if it had not gone through an arctic stage. The concept "relict" may be defined in the following way:[140] a species (or genus, etc.) is a relict in a region if it occurs there in isolation from its main centre of distribution and if its presence can only be explained by the fact that it or its ancestral form was left behind there under different natural conditions than exist at present.

The first condition for a relict hypothesis is the isolation mentioned, and this must be so complete that the species in question cannot be presumed to have been passively transported under present conditions into the assumed relict area, for example as planktonic larvæ. Relict hypotheses can therefore be well founded only for regions which have been thoroughly examined.

Almost all certainly established relicts within the marine boreal zone are *glacial relicts* which remained when the arctic region shifted to the north during the late-glacial and post-glacial periods. It is further noteworthy that no great occurrence of relicts has been demonstrated for polyhaline or mesohaline seawater, and that only a few outposts of one or two relicts have been found even in oligohaline seawater. All glacial relicts within the marine boreal region possess their main distribution in the brackish water of the Baltic.

According to their attitude towards salinity the relicts may be divided into various groups. Several of them are originally brackish species which in the Arctic Ocean, too, are not to be found in normal salt water. Here belongs the isopod *Mesidothea entomon* (cf. fig. 67).

Its distribution may be seen from the map in fig. 59. In the Baltic it is rare in the south-west but very common in the central and northern parts. As the parental form of the species we may regard *M. sibirica* (fig. 67), which lives in large numbers in the more saline water of the Siberian Arctic. The amphipod *Pontoporeia affinis* is also, in the Arctic Ocean, a purely brackish species which is found in several estuaries. Its Baltic distribution (fig. 41). closely tallies

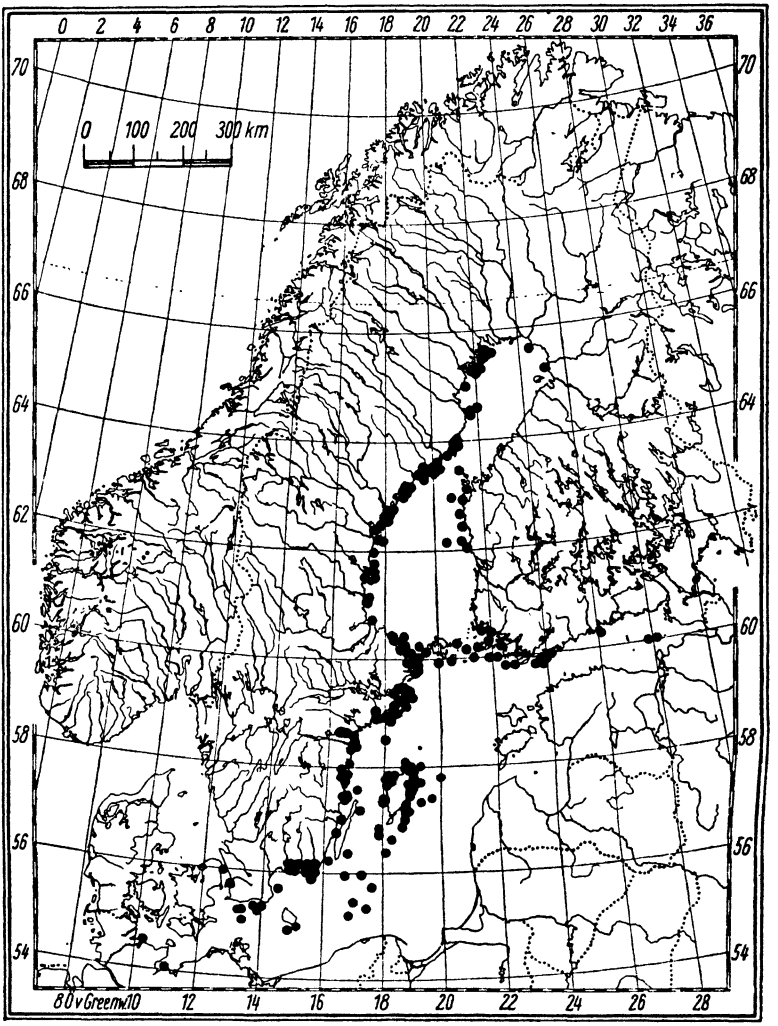


FIG. 41.—The European marine occurrency of the amphipod *Pontoporeia affinis*. (After S. Ekman, 1933.)

with that of *M. entomon*. The same is also true of the copepod *Limnocalanus grimaldii* (fig. 42).

Another group is composed of extreme euryhaline species which flourish in the fully saline water of the Arctic Ocean as well as in the fresh water of the inland lakes. Here we find the fish *Cottus*

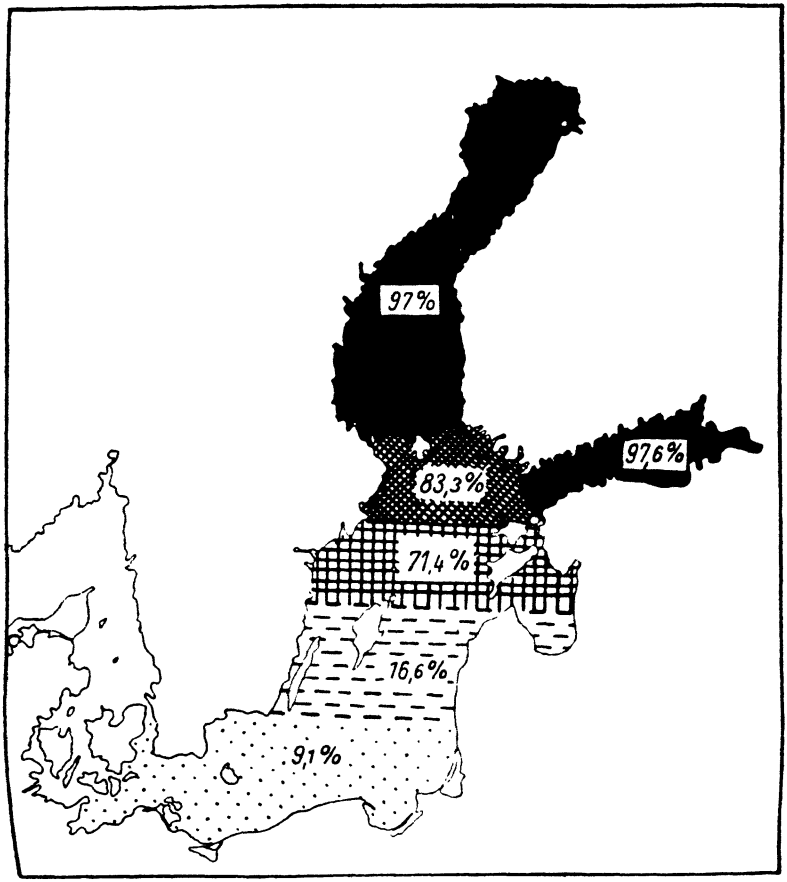


FIG. 42.—Occurrence of the glacial relict copepod *Limnocalanus grimaldii* in the Baltic. The figures represent the number of hauls containing *Limnocalanus* as a percentage of the total number of hauls. (After S. Ekman, 1914.)

(*Myoxocephalus*) *quadricornis* (fig. 60). It is circumpolar in the Arctic Ocean and common in the northern parts of the Baltic, but rare south of Kalmar and to the west of the deep water in the Gulf of Danzig. Another generally known relict is *Mysis oculata*, also circumpolar in the Arctic (fig. 43).

A third group consists of salt and brackish-water species. As typical for this group we may regard the amphipod *Pontoporeia femorata* (fig. 44). Its requirements with regard to salinity may be seen from the fact that its distribution in the Baltic does not extend north of the Åland Islands or into the outer parts of the Gulf of Finland, that is not into water with a salinity of less than 6‰; but it includes on the other hand certain parts of the Kattegat and the fjords of Bohuslän, where the considerable differences in the annual temperature may offer this species a sufficiently low temperature at the stage when it is most sensitive to temperature. A few finds from western Norway need not modify our conception with

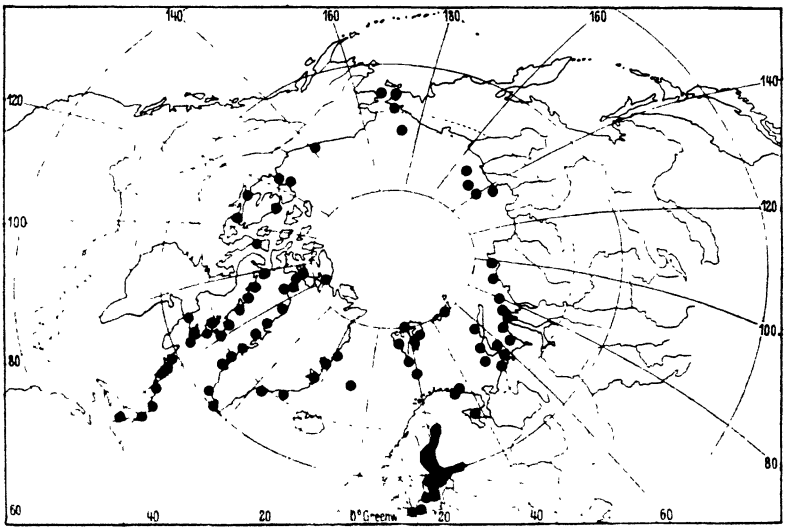


FIG. 43.—Distribution of *Mysis oculata* (omitting the relict occurrence in inland lakes). (Principally after K. Stephensen, 1933.)

regard to the relict nature of the Baltic and south Swedish populations. The distribution in the Arctic Ocean is presumably circumpolar and it also includes southern Iceland.

The distribution of *P. femorata* holds good also for the priapulid *Halicryptus spinulosus*, as well as for *Mysis mixta*, which however occurs in the whole of the Gulf of Finland and a large part of the Gulf of Bothnia and is not altogether absent from the North Sea. The hydroid *Halitholus cirratus* also belongs to this group, likewise the ostracod *Paracyprideis fennica*[149] whose distribution in the Arctic Ocean is little known (it possibly lives in brackish water even there). Notwithstanding a few find in the North Sea, the mussel

Astarte borealis may also be considered as a relict in the Baltic and the Belt Sea (between the Baltic and the Kattegat). It is interesting that the animal community in which this mussel occurs in the relict region shows an astonishing similarity in its composition with the community in which the species lives in eastern Greenland;[555] this, however, does not mean that the whole community, the rest of

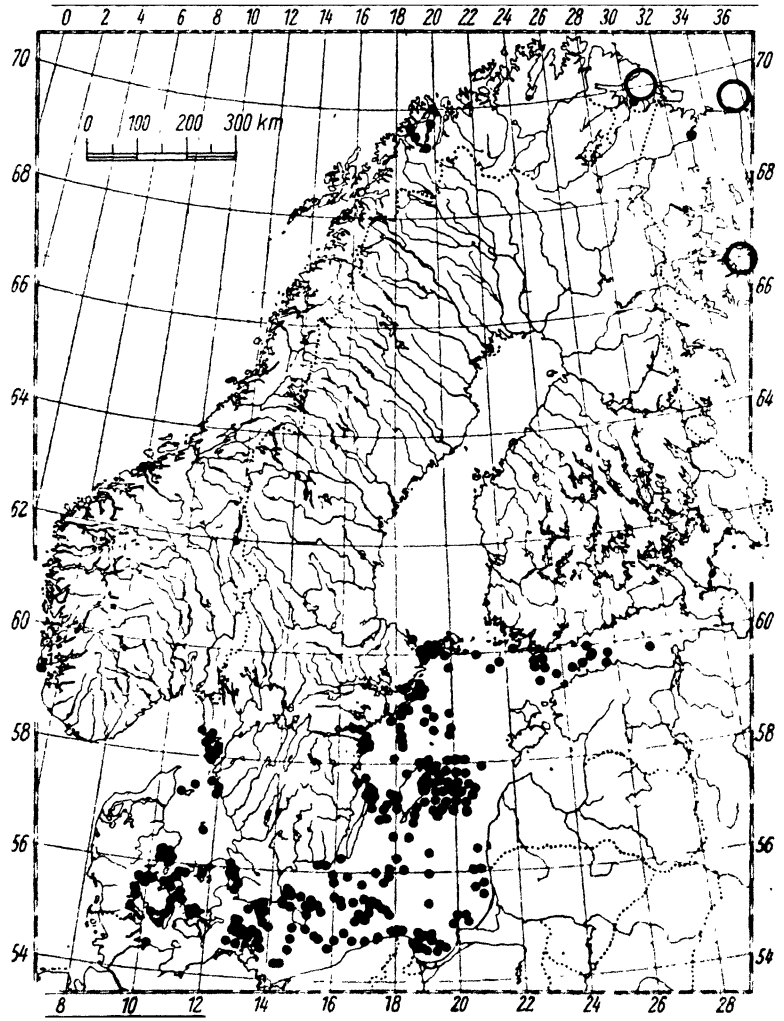


FIG. 44.—Distribution of the amphipod *Pontoporeia femorata*. The large circles mark not precisely indicated finds. (After S. Ekman, 1935.)

whose species are not relicts, should be regarded as a relict community.

Since the species in this third group cannot tolerate fresh water, it cannot be supposed that they were able to live in the Ancylus Sea, and their present-day area of distribution in the Kattegat was for the most part dry land during the Ancylus Period. Probably they were at that time mainly to be found in the Wänern basin, which was an inlet of the Skagerak and considerably larger than the present lake Wänern, while its character was affected by the larger volume of fresh water it received from the Ancylus Sea which flowed into it. For the same reason the sounds connecting the Wänern basin and the Skagerak also contained brackish water. In the extensive brackish-water region which thus existed these animals will have found favourable conditions.

The Baltic is not only by its history and its climate but also by its shape exceptionally well suited to the development of a glacial relict brackish-water fauna. The connection with the ocean is transferred to narrow channels in the south, thus allowing only a very restricted inflow of Atlantic warm-water. In the gulfs of Bothnia and Finland the way to the far north is barred, which further obstructs this inflow and makes the hydroclimate colder.

B. THE TEMPERATE REGION OF THE NORTH AMERICAN ATLANTIC

We have already found that it is possible to draw an approximate boundary for the tropic-subtropical warm-water fauna at Cape Hatteras, with the reservation that the region between this Cape and Florida represents a transitional or mixed zone. Certain American zoologists consider Cape Canaveral on the east coast of Florida to be a zoogeographical boundary, although at the same time they point out that south of Cape Hatteras Caribbean species appear in considerable numbers.[265] As for the northern boundary with the arctic fauna, this is very difficult to define since the hydrographical conditions are very complicated, much more so than on the European side. It is therefore necessary to begin with a hydrographic survey.

Hydrography

As is the case on the west coast of the North Pacific, the west coast of the North Atlantic, too, has a warm current, the Gulf Stream, which comes from the south, and a cold current, the Labrador Current, coming from the north. And just as the warm

Kuroshio Current is deflected by the bend of the coast in the centre of Japan's main island Hondo from the land out into the ocean, the Gulf Stream, which in its beginning is called the *Florida Current*, is similarly deflected at Cape Hatteras from the North American coast and leaves a space for the colder water from the north. The Florida Current possesses a speed of more than 5·76 km. per hour in the centre of the current, which is quite extraordinary for an ocean current (Sverdrup and others 1946). The great force of this current seems to be mainly due to the fact that the water level in the eastern part of the Caribbean is raised by the influx of the equatorial current so that it is 19 cm. higher at the south-western tip of Florida than at St. Augustine on the east coast of northern Florida. Near Cuba the sea level is still further raised, being here 45 cm. higher than off the mainland of America, thus explaining the extraordinary power of this current which is of such great importance for the climate of the whole North Atlantic and its animal geography. The Florida Current and its continuation, the Gulf Stream proper, which is formed by the union of the Florida Current and the *Antillean Current*, skirts the outer edge of the shelf and therefore influences the shallower coastal water only to an inconsiderable extent. The temperature of this coastal water is determined by the mixture of the marginal ramifications of the Gulf Stream and the cold coastal water from the north. The boundary line between the coastal water and the deep blue Florida Current is often clearly visible.

The *Labrador Current*, which originates in the coastal water north of Labrador and from there flows towards the south-east past Newfoundland, afterwards follows the coastline in a south-westerly direction. It lies in a broad mass, "the cold wall", between the coast and the Gulf Stream, so that the upper zone of the shelf has a lower temperature than the outer, deeper part. Both currents mix with each other in the region where they come into contact and thus the coastal water gets progressively warmer towards the south. The conditions with regard to temperature are, however, very involved. A consequence of the two main currents flowing side by side in opposite directions is the fact that the isotherms converge with one another to an unusual degree near the coast of North America (fig. 19 p. 57), so that for the annual isotherms the coast between Cape Cod and Cape Hatteras corresponds on the East Atlantic side to a five times longer stretch between south-western Norway and the Canary Islands.

Cape Cod was regarded by older American scientists, for instance Packard and Verrill, as an important zoogeographical boundary. Even in the most recent publications this cape is regarded as the southern boundary of the arctic region. This cannot, however, be correct.

The cod, for instance, which is a typical boreal fish, has not the northern limit but the southern limit of its breeding grounds in the neighbourhood of Cape Cod. The same is true for many other animals; for instance, in the St. Lawrence Bay which is further to the north the amphipod fauna is mainly boreal.[480a] However, the question is complicated by the fact that many animal species with a mainly arctic-subarctic distribution descend as far as Cape Cod. This is bound up with the complicated conditions of temperature, among other things with the considerable seasonal variations. The table below, which gives the mean temperature of the surface water at different seasons compared with the corresponding temperature on the European coast, illustrates this point:

TABLE 16

TEMPERATURE OF THE SURFACE WATER OFF CAPE COD (42° N.) COMPARED TO EUROPEAN OCEANIC REGIONS[471]

Off Cape Cod	Corresponds to the mean of the same period at:
Mean Annual temp. 8° C.	South-west Norway and the Skagerak (60° to 58° N.)
Mean for February 3° C.	South-west Norway and in the south-eastern North Sea (58° to 54° N.)
,, ,, May 5° C.	Arctic circle off Norway and near the Lofoten Islands (66° to 69° N.)
,, ,, August 19° C.	Southern Portugal (38° N.)
,, ,, November 8° C.	South-western Norway (59° N.)

Cape Cod, therefore, does not lie at the southern boundary of the arctic region. The impossibility of an exact climatic and faunistic homologization is shown by the fact that this cape at one season (August) corresponds in its maritime climate to southern Portugal, and at another (May) to the Lofoten Islands. Add to this the great vertical differences which are much greater at Cape Cod than on the European side, because off Europe the Gulf Stream affects the deeper water, while off America it is the Labrador Current. At a depth of 50 m. the temperature off Cape Cod is only 4–5° C., i.e. the water is as cold as off the southern tip of Greenland, northern Iceland and in the sea between the North Cape and Spitsbergen. It must further be noted that the isotherms of the deeper strata run more or less parallel to the American coast. Thus it is possible to find at a depth of 100 m. off Cape Cod temperatures from 3° to 15° C. according as the measurements have been taken closer to or further from the coast; this means that the whole scale of temperatures between the Davis Strait off western Greenland and the north-west of Africa is to be found. The bare fact of a find of an animal species near Cape

Cod does therefore not say anything about its zoogeographical position. The North Atlantic testifies even more clearly than other parts of the ocean that marine zoogeography must primarily be the zoogeography of the various waters, and only secondarily a zoogeography of the various coastal regions. As far as the northern boundary of the boreal region is concerned the situation may also be expressed by saying that the boundary between the arctic and boreal water changes its position according to the season and the ocean currents and thus influences the mobile part of the fauna.

The sea north of Cape Cod around Nova Scotia, Newfoundland and the St. Lawrence Bay is similarly characterized by complicated conditions of temperature. The Newfoundland bank is, of course, one of the main spawning grounds for the cod in the Atlantic, a fish which is of marked boreal character and which in the Atlantic demands a temperature of 4–6° C. for spawning. The bottom water of the bank of Newfoundland at a depth of 75–100 m. is even in July only 0–4° C. and therefore of arctic type; it is part of the Labrador Current. But nearer the surface the water is of a more favourable temperature for the cod. The yearly temperature changes can be seen from the table below (table 17).

TABLE 17

THE MEAN TEMPERATURE OF THE SURFACE WATER DURING VARIOUS SEASONS IN LOCALITIES ALONG THE NORTH-EAST COAST OF NORTH AMERICA

	February	August	Annual
Halifax, Nova Scotia . . .	<0° C.	16° C.	6–7° C.
Newfoundland bank . . .	0	13–15	3–6
St. Johns, East Newfoundland .	<0	12	2–3
South-west Newfoundland . .	<0	14–15	<5
St. Lawrence Bay, interior . .	<0	8–10	5

These summer temperatures indicate a boreal rather than arctic marine climate.

The temperatures in the North American coastal waters a little further to the south down to a depth of about 20 m. have been closely studied by Parr.[406] He states that a warm-water barrier is established in the region of Cape Hatteras during the winter, while a cold-water barrier develops in the region of Cape Cod during the summer; but in neither locality are such barriers found to be a permanent feature during all seasons. The shallow-water belt along the Middle Atlantic coast between these two points is in open communication with the waters south of Cape Hatteras in the summer and with the waters north of Cape Cod in the winter. That this exercises an influence on the migratory components of the fauna, has been proved, for instance

for the fish. At certain times the temperatures fluctuate greatly at both these capes, namely during the summer at Cape Cod and during the winter at Cape Hatteras. These fluctuations often reach 11–13° within 2–5 days, and oscillate in both localities around a mean temperature of 15–16° C.; they are the same at Cape Cod in summer as at Cape Hatteras in winter. These great changes of temperature make great demands on the eurythermy of non-migratory organisms.

The fauna

Owing to the difficulties discussed above it is at present not possible to delimit accurately a boreal American marine region. But it would be wrong to deny the presence of a boreal fauna because of this. If one wanted to find out whether there is in America a boreal fauna corresponding to the European one, the following method could be employed.

There are several animals to be found along the American coasts which in Europe with its more surveyable climatic conditions are pronounced boreal species. These may therefore be regarded as indicators of boreal conditions in America. In the American territory of these species, other purely American species have their centre of distribution, and they can also be therefore termed boreal. According to this method the following list of endemic-boreal or at least mainly boreal species has been compiled; it is confined to fishes, and even among them the less important ones have been omitted. Species which are endemic to America have been marked with an asterisk: **Tautogolabrus adspersus* (cunner), **Cottus* (*Acanthocottus*) *octodecimspinosus* (common sculpin), **Hemitripterus americanus* (sea raven), *Cyclopterus lumpus* (lumpsucker), *Pholis gunellus* (butterfish), **Zoarces* (*Macrozoarces*) *americanus* (eelpout), *Hippoglossus hippoglossus* (halibut), **Liopsetta putnami* (eelback flounder), *Gadus* (*Microgadus*) *tomcod* (tomcod), *Gadus morrhua* (cod), *G.* (*Melanogrammus*) *æglefinus* (haddock), *G.* (*Pollachius*) *virens* (coalfish), *Clupea herengus* (herring).

In America, too, the region with boreal fishes contains, of course, a number of arctic-boreal species. As example for these we may mention among fishes *Aspidophoroides monopterygius*, *Stichæus punctatus*, *Anarrhichas lupus* and *Gymnelis viridis*. On the other hand several animals live in this region, either permanently or at certain seasons, which have their main centre of distribution further south.

In the region between Cape Cod and Cape Hatteras lives moreover a fauna which may be described as warm-temperate. Among the fishes which belong to it we mention several which are more

generally known and are characteristic for the region even though not strictly confined to it: *Pomolobus mediocris* (hickory shad), *Sphyræna borealis* (barracuda), *Centropristes striatus* (black sea-bass), *Prionotus strigatus* (northern striped gurnard), *Tautoga onitis* (tautog), *Paralichthys dentatus* (summer flounder) and *Lophopsetta maculata* (windowpane).

Other species are characteristic for the whole of the temperate region as for example the fishes *Pomolobus pseudoharengus* (alewife), *Alosa sapidissima* (common shad) and *Pseudopleuronectes americanus* (winter flounder).

Whether the fauna between Cape Hatteras and Florida (Cape Canaveral) must be considered, as we have done, as a mixed fauna between the subtropical and the warm-temperate fauna, or whether it should be more closely linked with the latter, must for the present be left open. According to one view the whole fauna between Cape Cod and Cape Canaveral is a single unit (which is given the curious name Transatlantic province) and is divided into two subdivisions, a Virginian to the north and a Carolinian to the south of Cape Hatteras. A closer analysis of this question, taking into consideration not only species which are economically important or well known for some other reasons, but the fauna in general, both with regard to species and genera, seems not yet to have been made.

The relations of the American Atlantic fauna to the European

As early as 1846 the Swedish zoologist Lovén pointed out that the purely boreal fauna in Europe is very much more specifically European than the arctic-boreal, which Europe has to a great extent in common with North America. He illustrated this with a list of the northern molluscs known at that time, which showed that of the arctic-boreal bivalves and gastropods of Europe 75% lived also in America, but only 8% of the purely boreal species. After the century which has passed since then the figures are naturally no longer exact, but the rule is firmly established and may well apply also to most other animal groups within the shallower coastal waters. A similar investigation made into the American fauna leads to the same result. Of the fishes which regularly occur north of Cape Cod, 60% live also on the European side; but of fishes which do not go further north than the cape mentioned, only 7–8% are also European, Other animal groups, too, show the same behaviour (Ascidiacea, Crustacea Decapoda, Cumacea, Scaphopoda, Foraminifera, etc.). The figures for ascidians are characteristic (Huus[246]). Of 28 arctic-boreal European species of this group 24 occur also in America but of 46 purely boreal or Lusitanian-boreal species only four are also American.

This state of affairs is not difficult to explain. It is clearly connected with the fact that the possibilities for active or passive distribution are for purely geographical reasons much greater in the most northern parts of the Atlantic than further to the south. Even today the distance between Europe and North America is divided up into smaller stages by the islands and the under-water ridges between Scotland, Iceland, Greenland and America, and this was the case even more during the earlier periods of the Quaternary. Those species, however, whose northern limit lies more to the south than these islands and under-water ridges are generally prevented from a spreading across the Atlantic, since the time during which their planktonic larvæ can be passively transported by ocean currents is many times too short to allow a transport across the Atlantic. The central Atlantic barrier is, therefore, effective also within the warm-temperate region (cf. p. 50 and 75). There are, however in several animal groups, isolated species with a discontinuous amphi-Atlantic distribution, for example the above-mentioned four ascidians, among them *Styela partita* and the generally known *Botryllus schlosseri*. It might be suspected that the latter's habit of attaching itself to algæ may have had a hand in its passive transport by means of drifting seaweed.

CHAPTER VII

THE TEMPERATE FAUNA OF THE NORTH PACIFIC

NORTH of central Japan on the Asian side and the middle part of Lower California on the American side where we have found the approximate northern limits for the warm-water fauna, we meet with another fauna. The great coastal arch from north-western North America to North-east Asia is uninterrupted within the upper region of the shelf since the Bering Strait consists only of shallow water. But within the temperate marine region the coastline in the north is formed by the Aleutian Islands, and between their western tip and Kamchatka lies a deep-water region. Here, too, we find a faunistic boundary. It is possible, therefore, to distinguish within the temperate Pacific fauna between an American and an Asian region.

A. THE TEMPERATE FAUNA OF NORTH-WEST AMERICA

Hydrography

Along the whole stretch of coast from the middle of Lower California to the Gulf of Alaska the marine surface temperature is extraordinarily uniform. In August it is only 15° C. on the oceanic coast of Lower California (30° N.), at San Francisco 13–16° C., in the inside passages north of Seattle, Washington (49–51° N.) 16° C., a little to the north (51–53° 30′ N.) 14·7° C. and from there right up to southern Alaska 14° C. In the open sea the temperature is, however, 1–2° C. lower. Only at the Alaskan peninsula at the base of the Aleutian Islands does it fall to 10–12° C. The table below, which also contains some figures from the Atlantic to serve as comparison, illustrates this point; cf. also fig. 45.

The North American Pacific coast receives in its northern part a warm oceanic current while in its southern parts it is cooled down by upwelling cold water from the bottom. The warm current gets a great deal of its water from the Japanese Kuroshio Current, but as its water is more and more mingled with the influx from other quarters, its eastern portion is called the North Pacific Current (less ambiguously the North Pacific Warm Current; cf. the North Atlantic Warm Current of the Gulf Stream). This current meets the

coast roughly off Oregon and Washington, and from then turns partly to the south and partly to the north. The southern branch is called the California Current, the northern the Alaska Current. This latter thus supplies the Gulf of Alaska with relatively warm water, turns off in the direction of the coast to the west and south-west on the south side of the Aleutian Islands and partly finds its way between them into the Bering Sea. The cold upwellings mentioned above are, with some interruptions as to place and time, to be found along the stretch of coast from the southern part of Lower California to about 45′ N. The warm temperatures which might have been expected for instance in the coastal waters of California because of its southerly position, thus do not occur. The cooling process goes so far that the water temperature in August at Cape Mendocino in northern California is actually hardly 11° C., lower

TABLE 18

SURFACE TEMPERATURES IN FEBRUARY AND AUGUST IN THE NORTH-EASTERN PACIFIC AND THE EASTERN BERING SEA COMPARED WITH THOSE IN NORTH-EASTERN ATLANTIC

North-eastern Pacific and Bering Sea			North-eastern Atlantic		
	February	August		February	August
Bering Strait, Alaskan coast, 65°–66° N.		7–12° C.	Between Bear Isl. and North Cape, 72° 40′ N.		7° C.
Nunivak Island, 60° N.		6–9·5	Murman coast, Kola peninsula, 68°–70° N.	1° C.	9–10
			Northern Iceland, 66° N.	0–1	8–10
Alaska peninsula, S. coast, 55°–58° N.	2–3° C	10–12	Lofoten Isl., N. Norway, 68° N.	3	12
Sitka, S. Alaska, 57° N.	3	13–14			
Cape Mendocino, 40° N.	10	11			
San Francisco, 37° N.	11	13–16			
Lower California, ocean coast, 30° N.	16	15	English Channel, S.-W. mouth, 48°–50° N.	9	17
Lower California, ocean coast, 28° N.	17–18	19	Cape Blanco, W. Africa, 21° N.	18–19	20
Lower California, Cape San Lucas, 23° N.	21	27	Cape Verde, W. Africa, 15° N.	19–20	25

therefore than on the whole coast right up to southern Alaska and about as low as in the Aleutians. Outside San Francisco Bay the annual surface temperature varies between 14·6° and 11·3° C. (monthly mean values). As far as its marine climate is concerned, California is not nearly as mild as is commonly assumed.

The last-mentioned part of the Alaska Current, which finds its way between the Aleutian Islands into the eastern part of the Bering Sea, brings about a rise in temperature here too, so that the coastal water on the northern side of the Aleutians cannot be called arctic but rather cold-temperate (high-boreal or subarctic). Even right up north, on the American side of the Bering Strait, the marine climate lies between cold-temperate and arctic temperatures. Figures illustrating this will be quoted later when the southern limit of the arctic region in these parts is discussed (p. 169). The American side of the

Bering Sea is warmer than the Asian. For the moment we merely note that the sea in this part is very shallow. The Bering Strait and a large tract north and south of it do not reach a greater depth than 50 m. (fig. 46). A great deal of the fauna which is recorded from the eastern Bering Sea has lived in shallow water with a summer temperature of 7° C. or more. This accords fairly well with the view that the region between 58° N. and 62° N. is a transitional region between

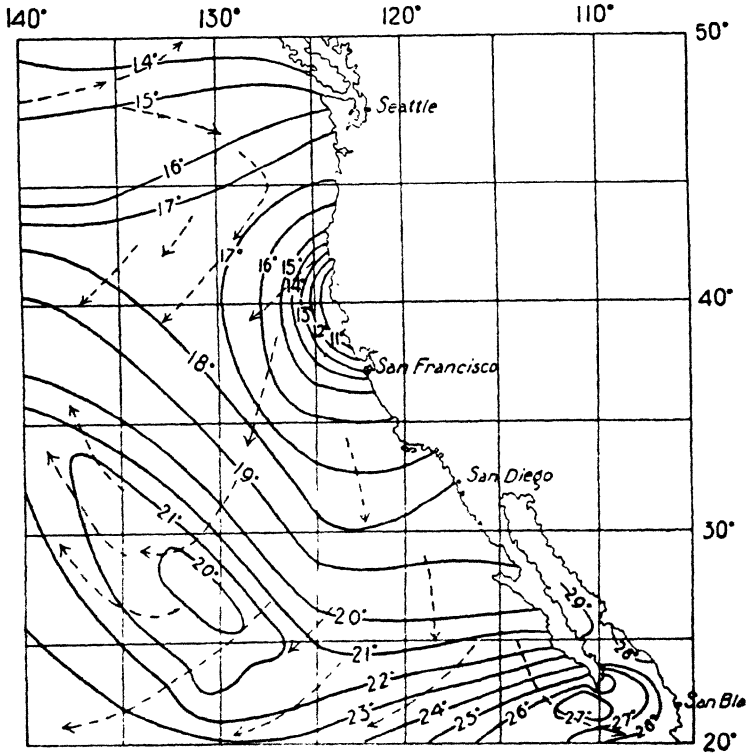


FIG. 45.—Surface isotherms for August off the west coast of North America. Arrows indicate the main surface currents. (After McEwen, 1912.)

the Aleutian and the Arctic province (see p. 169). To judge from the temperatures the boundary with the Arctic province could be shifted still further north, namely into the Bering Strait (65° N.).

The table on p. 143 shows also another interesting fact. Climatically similar tracts of the Pacific and Atlantic are printed on the same line in the table. It may thus be seen that the whole of the North American coast from and including the northern part of Lower California and northwards corresponds on the Atlantic side to the

boreal region, the southern boundary of which the south-western entrance to the English Channel corresponds, as regards surface temperatures, to this part of Lower California. Thus there is practically no room for a warm-temperate fauna on the Pacific coast of North America, to judge from the marine climate, if "warm-temperate" is taken to mean the same as far as America is concerned as it does

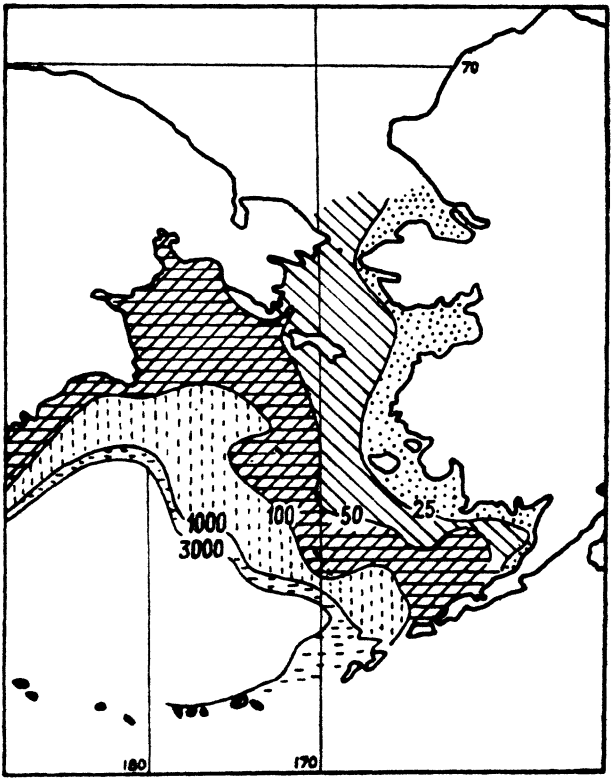


FIG. 46.—Bottom topography of the Bering Sea. (After Barnes & Thompson, 1938.)

in Europe. We shall return to this question in our survey of the fauna.

The endemic element of the fauna

The endemic element in the temperate fauna of the North American Pacific is well developed. First, as regards the species, the endemic species constitute by and large half of the whole number of species of the various animal groups, while in the European boreal region

they represent only a quarter at the most. Endemic genera, too, and even families play a much more important part in the North Pacific fauna than in the North Atlantic. This will now be demonstrated in greater detail by examples from a few animal groups.

Decapod crustaceans. Here we find in particular the family *Lithodidæ* (fig. 47), which in this region consists of 13 genera and 26 species. No species enters the warm-water zone; two genera are however represented with one species each also in the anti-boreal region of South America. The other endemic decapod genera are very poor in species. A member of such a genus is for instance the common *Oregonia gracilis* (fig. 48). The distribution of the crab genus *Fabia* is of interest. It is, of course, not wholly confined to

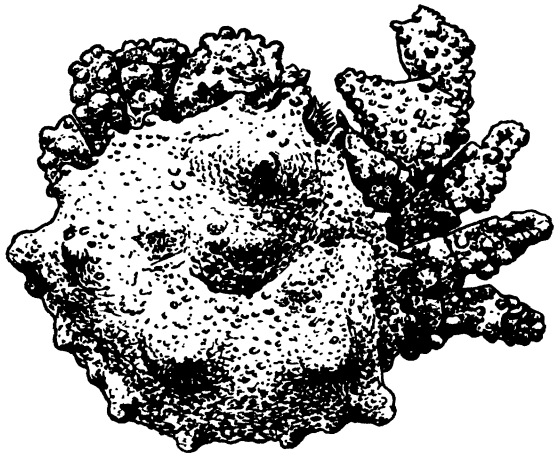


FIG. 47.—*Lopholithodes mandtii*, ♂ (family *Lithodidæ*). Distribution: southern Alaska to California. (After W. Schmitt, redrawn.)

this region: for one of its species lives in the Gulf of Mexico. But it is probable that the genus originated in the temperate North-east Pacific and that the Atlantic species, *F. byssomiæ* (which, according to Rathbun, is a twin-species of the Californian *F. canfieldi*) has reached its present distribution via the Tertiary central American marine straits. Thus it is an example showing that these trans-American oceanic connections, which played such an important part in the warm-water fauna, had also a certain importance for the temperate fauna, probably at the time of the Tertiary climatic changes in central America.

More important than the purely endemic genera are certain genera, richer in species, which, while they are also to be found in other regions, have developed most profusely within the north-west

American coastal region. Among these we find, for instance, *Pandalus* with about 10 species, *Spirontocaris* (fig. p. 153) with more than 40 species and *Crangon* with approximately 17 species. A small number of these species also live in the arctic region.

Molluscs. Among families which have developed more species in the North Pacific than in any other sea we mention the Buccinidæ, Chitonidæ and the octopod cephalopods.

Starfishes. Thanks to the two great monographs by Verrill (1914) and Fisher (1911 to 1930) the starfishes are one of the best-known groups. The first author stresses that in no other region in the world are there near so many species, genera and families, or such a great number of individuals as here; neither the Panama region nor the West Indies, not even the richest parts of the East Indies can compete with the temperate East Pacific with regard to this animal group.

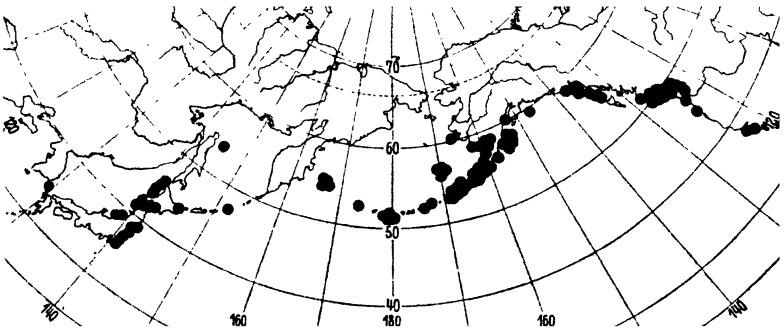


FIG. 48.—Distribution of the crab *Oregonia gracilis* (more than 200 finds); many Japanese localities are not to be found in the relevant maps. (After S. Ekman, 1935.)

Fisher mentions 92 species and 10 subspecies for this region, of which approximately 60% are endemic, while 31% also occur in the arctic or subarctic regions, but only 8% in more southerly regions. The affinity with the north is, therefore, closer than with the south. The same is true for certain other animal groups. Among the starfishes, too, the endemic genera are usually poor in species. As against 11 monotypical genera there is only one (*Pisaster*) with three species and one (*Mediaster*) with two. Several of the species of the monotypical genera are particularly characteristic for the whole of this region as for example the big multibrachiate *Pycnopodia helianthoides* (fig. 49). Apart from these endemic genera other genera, which have here the main number of their species, are also characteristic for this region, as for example *Dipsacaster*, *Henricia*, *Solaster*, *Pteraster*. The last three are to a lesser extent also represented in the northern Atlantic.

Fishes. Among the fishes there are not only a large number of species and genera but even several families characteristic for this region, since they are either wholly or for the most part endemic here. The family *Embiotocidæ*, the surf-fishes, which on their own form the order Holconoti and are known because of their viviparous species, contain 21 species divided among 20 genera. Two genera with one species each are Japanese, but the remaining 18 genera are endemic to north-western America between Lower California and southern Alaska (fig. 50). Most of the 17 marine genera live in the region between Vancouver Island and San Diego. *Cymatogaster aggregatus*, depicted in fig. 51, lives in the whole of this region up to the northern limit for the family. Characteristic for both the Asian and American coasts of the North Pacific is the family *Hexagrammidæ*, the greenlings, among whose species is *Hexagrammos decagrammus*, a well-known edible fish (fig. 52). The same is true of the closely related, purely North American *Anoplopoma fimbria* and *Ophiodon elongatus*, each of which is regarded by certain ichthyologists as the sole representative of its monotypical family. The great

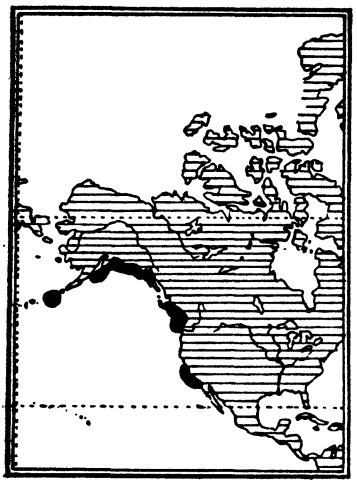


FIG. 49.—Distribution of *Pycnopodia helianthoides*, the largest of all known starfishes. (After S. Ekman, 1935, compiled from the text in W. K. Fisher, 1928.)

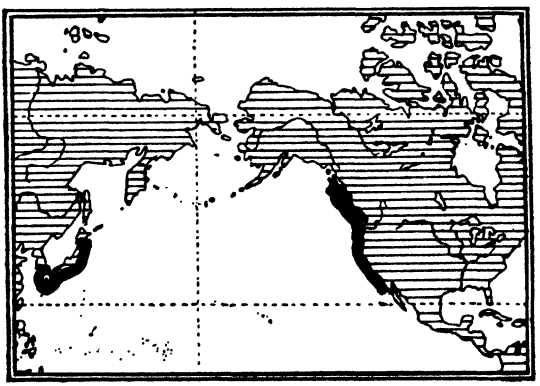


FIG. 50.—Distribution of the surf-fishes, family *Embiotocidæ*. (After S. Ekman, 1925.)

family Scorpænidæ may also be mentioned in this connection. For geographical reasons it may be divided into two groups, a warm-water group with the genus *Scorpæna* as the most important type, and a cold-water group with approximately 60 species in north-western America and roughly 25 in north-eastern Asia. The species of the cold-water group were formerly united in the great genus *Sebastodes*, but they are now divided into 15, a division which is, however, for the moment only provisional. This group of species is very characteristic for the North Pacific and particularly

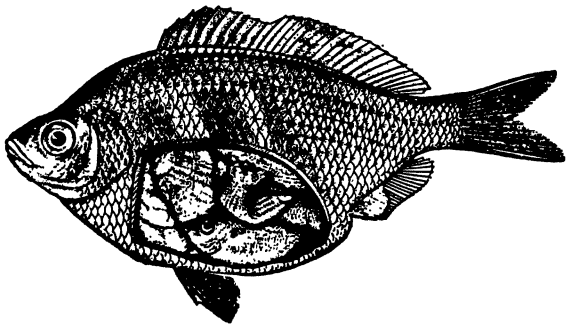


FIG. 51.—The surf-fish *Cymatogaster aggregatus*, dissected. All species of the family *Embiotocidæ* are viviparous. (After Jordan.)

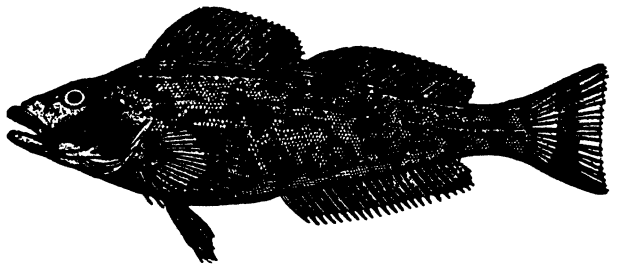


FIG. 52.—*Hexagrammos decagrammus*. (After Jordan.)

so for the American side; only a few species are to be found outside it on the west coast of South America. The families *Cottidæ* (including the Icelidæ), *Agonidæ* and *Liparididæ* are very characteristic for the northern seas and contain more than 100 species which are representative for north-western America. Many of them are endemic there, some of them also occur in the north-eastern part of Asia, others also in the arctic region. A number of the genera, and also some closely related families which are poor in species, are endemic in this region. A survey of the whole order Cataphracti,

to which belong, apart from the four families just mentioned, the Hexagrammidæ and Scorpænidæ which we discussed earlier, shows that this great order is represented by 22 families† in the western North American coastal waters, and that a number of these families have here or at any rate in the North Pacific their main area of distribution, in certain cases their sole habitat. The order has a little more than 100 genera and approximately 180 species (apart from deep-water species) in this region. The representation of this order in the warm-water region of the American Pacific is in comparison very meagre, being confined to six species of the group Scorpæna and eight species of the family Triglidæ. Of the 180 species, according to present data as to their distribution, approximately 90% are endemic, a figure which might possibly have to be slightly reduced when the distribution is more fully known. Among other endemic species we might mention the economically important Californian sardine or pilchard, *Sardinia coerulea.*

The arctic-temperate element

Species and (particularly) genera which are common to the arctic and temperate regions are of considerable importance in the Northwest American coastal fauna. Often such genera are also found in the northern Atlantic, although the main mass of their species belongs to the Pacific. Among decapod crustaceans we find here the previously mentioned genera *Pandalus*, *Crangon* and *Spirontocaris* (fig. 55), among other prawns also the specifically northern *Sclerocrangon* and *Nectocrangon*, among the crabs *Chionoecetes* with four species, of which the large *C. opilio* also occurs in the north-western Atlantic (figs. 53, 54). Several genera among the echinoderms are pronounced arctic-temperate, as for example the starfishes *Henricia*, with many species, and *Leptasterias*, the brittle-stars *Ophiopholis*, the sea-urchins *Strongylocentrotus*. Among the molluscs we find here the genus *Buccinum*; among the fishes the already mentioned families Cottidæ, Icelidæ, Agonidæ and Liparididæ and many of their genera.

A good number of these families and genera are distributed along the whole of the North American coast from Bering Sea down to southern California. Of the species, naturally, only a smaller number have such a wide distribution. *Oregonia gracilis* (fig. 48) has already been mentioned. A fish of this type is the starry flounder, *Platichthys stellatus*, which provides about half of the West American catch in flatfishes. On the Asian side the same species is found as far as middle Japan.

† Here, as in other cases where North and Central American fishes are concerned, I have followed the check-list of Jordan, Everman & Clark of 1930, who are, however, very much more liberal than older taxonomists as far as the number of genera and families are concerned.

Within the North Pacific fauna, too, a southern submergence is commonly found by which is meant that a species or genus which in the northern parts lives in shallow water, occurs at a greater depth further to the south, for example in southern California. This phenomenon involves a direct adaptation to the conditions of temperature.

Faunistic subdivisions

Various investigators have subdivided the extensive temperate region of North-west America in various ways and with varying expressions for the subdivisions, for instance Californian, Oregonian, Aleutian and so on, while others maintain that the whole region is so uniform that it can hardly be subdivided. A rational attempt at subdivision, which has the advantage of being founded on a very

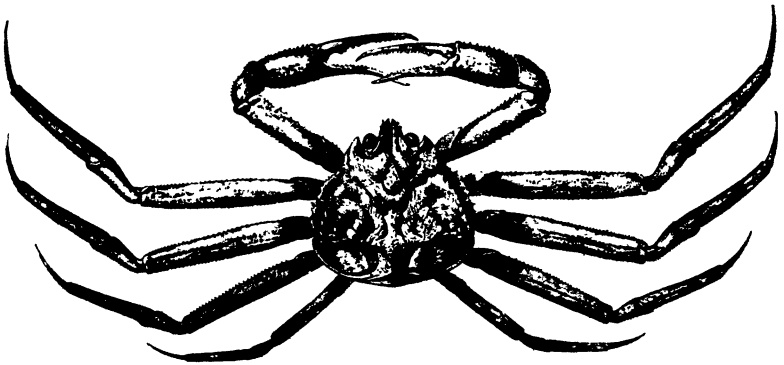


FIG. 53.—*Chionoecetes opilio*, half natural size. (After Stuxberg.)

large material and takes proper account of endemic and characteristic ("unique") elements, has been made by Schenk & Keen (1936, etc.). On the basis of the distribution of nearly 200 molluscs, they distinguish two provinces, namely a Californian province reaching to 42° N. (north of Cape Mendocino), followed by a transitional region with a mixed fauna reaching as far as 48° N, (Seattle and Puget Sound), where an Aleutian province takes over, reaching as far as 58° N. (north of the Pribilof Islands), followed again by a transitional zone until the arctic region at 62° N. (south of the estuary of the Yukon River). It remains still to be decided whether the arctic region really has its southern limit at that point. The temperature does not suggest this; the great Norton sound, which lies round 64° N. south-east of Nome, and also the region between Nome and the Bering Strait has actually higher summer temperatures than the water of the coastal region between 62° N.

and the Alaska peninsula (see table 18, p. 143). But we must admit that the actual distribution of animal species must take precedence over the temperature. Methodologically, Schenk & Keen's division is a pioneer work. A provisional examination of the data with regard to the distribution of the approximately 180 North-west American fish species of the order Cataphracti indicates that these also show two peaks of species frequency, namely one in California and another in southern Alaska and the Aleutians. This phenomenon

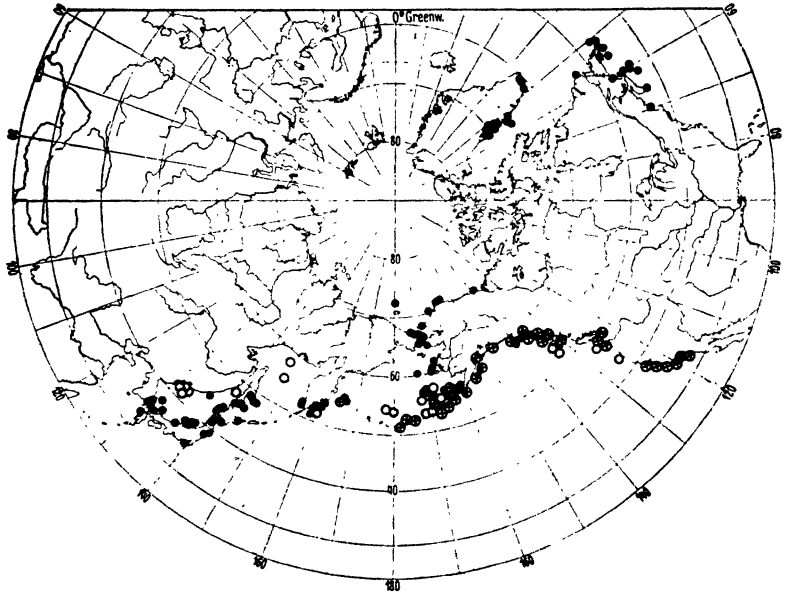


FIG. 54.—Distribution of the crab genus *Chionoecetes*. Entirely black circles *C. opilio*; open circles *C. angulatus* (90–2900 m. depth); circles with cross: north of 50° N. *C. bairdi* (littoral), south of 50° N. and at the Bering Island *C. tanneri* (usually 600–1900 m). (After S. Ekman, 1935.)

is possibly common to the larger part of the temperate coastal fauna of North-west America. In this case, however, the faunas of the two subdivisions, with regard to climate, do not wholly correspond to the warm-temperate and cold-temperate faunas of the eastern Atlantic, since, as we have already found in the hydrographical survey on p. 145, the transition from subtropical to the colder marine climate occurs so suddenly on the West American coast that the boreal climate in the European sense follows on almost abruptly north of the subtropical one. Keeping this in mind one may possibly term Schenk & Keen's Californian province low-boreal and their Aleutian province as high-boreal.

B. THE TEMPERATE MARINE FAUNA OF NORTH-EAST ASIA

In the North Pacific roughly the same differences obtain between east and west as in the Atlantic. The warm Kuroshio Current leaves the coast of Japan at 36° N. at the point where it makes a sharp bend almost precisely at the same degree of latitude as Cape Hatteras, where the Gulf Stream leaves eastern America. From the north

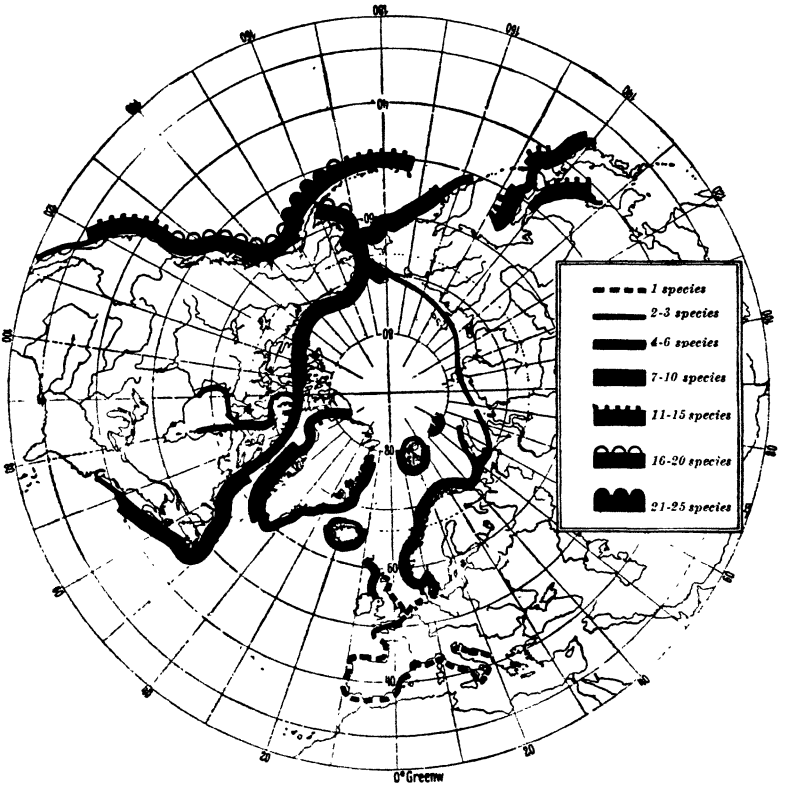


FIG. 55.—The prawn genus *Spirontocaris*: map of the distribution and number of species in the particular regions. (After S. Ekman, 1935.)

comes the cold Oyashio Current which originates in the Bering Sea and the Okhotsk Sea and makes the coastal waters of northern Japan considerably colder than those of southern Japan. The limit of temperature is sharply defined at 36° N. From the Okhotsk Sea a cold current also flows in a southerly direction towards the continental coast of the Sea of Japan. This is called Liman Current and it makes the north-western continental part of the Sea of Japan

considerably colder than its south-eastern part and considerably lowers its winter temperature, to which the low temperature of the air also contributes. Both the Oyashio and Liman Currents flow further south along the western Pacific coast than the cold-water reaches on the east coast, just as the Labrador Current on the west coast of the Atlantic goes further south than the cold water on the east coast.

If we come to determine the northern limit of the temperate faunal region in these tracts, we have to rely more on temperature in view of our, as yet, imperfect knowledge of the distribution of animal species. The main features of the conditions with regard to temperature in the seas in question may be seen from the following tables (19 and 20). To illustrate the contrast between the north-western and south-eastern parts of the Sea of Japan the figures for the same latitude are given for both these marine regions.

TABLE 19

THE TEMPERATURE OF THE SURFACE WATER IN THE ASIATIC PARTS OF THE NORTH PACIFIC. MEAN VALUES FOR THE COLDEST AND WARMEST MONTHS OF THE YEAR (MAINLY AFTER SCHOTT, 1935.)

	February	August
North Hondo, east coast	0(?)–10° C.	21–25° C.
,, ,, west coast	5–9	24–25
Hokkaido (Yezo), south-west coast	<0	15–18
,, ,, west coast	2–5	17–20
The sea at Vladivostock	−1·8	20–21
Southern Kurile Islands	−1	8–13
Northern Kurile Islands	−1	7
Exterior part of Okhotsk Sea (50° N., 150° E.)	−1·6	11·5
Petropavlovsk, South-east Kamchatka	<0	10

TABLE 20

SUMMER TEMPERATURES IN THE JAPAN SEA, THE SOUTHERN OKHOTSK SEA AND THE PACIFIC EAST OF THE KURILE ISLANDS[472]

Depth	Sea of Japan, Japanese coast 41° N., August	Sea of Japan, mainland coast 41° N., August	Okhotsk Sea, southern part 47° N., September	E. of the middle Kurile Islands 45° N., 160° E., July
0 m.	27·00° C.	19·30° C.	13·4° C.	6·91° C.
25	22·04	5·35	2·0	6·00
50	17·73	2·58	0·6	3·00
100	12·45	1·23	−1·1	1·60
200	6·54	0·50	−0·4	3·15
deeper		0·16		
than 200	800 m. 0·16	3300 m. bottom	400 m. 1·1	1000 m. 2·50

It must be emphasized that the relatively high summer temperatures on the surface are by no means representative for the whole of the upper shelf zone. Within the cold currents the temperature sinks quickly with increased depth, as is shown by table 20. This table also shows the remarkable fact that the water in the continental part of the Sea of Japan, in the Okhotsk Sea's southern part and among the northern islands of the Kurile group, is characterized by arctic temperatures during the whole year at a depth below 25–30 m. A considerable part of the zoological collections made in these regions undoubtedly comes from this layer and therefore consists of purely arctic or arctic-boreal species. To what extent one or the other of these categories predominates is at present not possible to determine since the general reports are too summary and detailed data are not easily accessible through being written in Russian. Several of the authors in question evidently mean by "arctic elements" only those which belong in the main to the Polar Sea but not those which live in the Okhotsk Sea or the arctic waters of the Bering Sea, which considerably complicates the exploitation of these results. P. J. Schmidt,[466] however, regards the greater part of the Okhotsk Sea as arctic.

The great difference in temperature between the surface water and the layers below 25–50 m. which we have just mentioned underlines the need for basing the divisions of regional animal geography on the relationship of animals to certain hydrographical factors and not primarily on the geographical position of the areas of distribution with reference to land regions. For at present it seems hardly possible to determine with any certainty whether the Sea of Japan and the regions immediately adjoining it house a temperate fauna of some independence, i.e. characterized by an appreciable endemic element, though this seems quite probable. Still less can we designate certain elements as warm-temperate and others as cold-temperate.

That the fauna off the mainland coast of the Sea of Japan, apart from possible endemic elements, consists of a mixture of southern and northern species may be gathered from reports on a number of animal groups. This mixture is to some extent temporary. The difference between the highest and lowest annual water temperatures is approximately 24° C., and Lindberg[302] points out that consequently 32 species of fish appear in the sea off Vladivostok during the period July–October although they are not to be found there during the rest of the year.

A number of the species which live in the north-west American region near the Aleutian Islands are also found in the temperate north Asiatic region. But these species are comparatively few. The

reason for this is, as far as we can judge, that the arctic water along the east coast of Kamchatka represents a barrier for animals which demand a temperate marine climate, and that the broad and deep stretch of sea between the western Aleutian and the Kurile Islands does not allow passive distribution of the larvæ of benthic species. Among the approximately 1950 species of molluscs which live near western North America there are, according to M. Keen,[273] only 24–32 species (1·2–1·6%) which possess such a continuous amphi-Pacific distribution reaching from Japan to Alaska, and only five to seven species which reach from Japan along the coast as far as California. Among fishes certain of the North Pacific species (for instance *Icelus spiniger*, family Cottidæ) vary in such a way that on the American side of the Bering Sea we find one race, another in the Sea of Japan and yet another in the Okhotsk Sea which represents morphologically an intermediate position between the other two.[8] As far as the isopods are concerned, Gurjanova[198] reports that five species which are in common for both the American and Asiatic side of the extreme northern region of the Pacific are all parasitic on fishes and therefore are easily distributed passively.

Comparatively few species of an almost warm-temperate nature have a discontinuous amphi-Pacific distribution; they occur off Japan and western North America but not, however, in the northern regions of the great coastal arches. There are only two to four such molluscs (0·1–0·2% of the total number of American species; earlier reports of several times this number were due to wrong determination of species). Other examples are to be found among decapod crustaceans, for instance *Cancer amphioetus*.[28] Among the opisthobranch molluscs we find two species[23] and among fish the very common Californian sardine, *Sardinia coerulea*, which occurs from the Puget Sound to Magdalena Bay in Lower California and is very closely related to the Japanese *S. melanosticta*. This discontinuity must be due to an earlier continuity in distribution which may have occurred at a time when the Bering Strait was dry land and the cold water could, therefore, not penetrate from the Polar Sea. The draining of the Bering Strait through an elevation of the land is considered to have taken place at various periods during both the Quaternary and Tertiary Periods.

Similar geographical changes in the Tertiary Period may have been the reason for the fact that the family Embiotocidæ, which otherwise is purely West American, has two monotypical genera in Japan, namely *Ditrema*, which is closely related to the American *Embiotoca jacksoni*, and *Neoditrema* which is also closely related to the Californian genus *Hypocritichthys* (fig. 50, p. 148).

C. THE RELATIONSHIP OF THE NORTH PACIFIC FAUNA TO THE NORTH ATLANTIC FAUNA

A quantitative and qualitative comparison

The cold-water fauna is considerably richer in the North Pacific than in the North Atlantic. To illustrate this fact we begin with the representation of fishes within the two oceanic regions since the fishes are better known as regards distribution than any other group of animals. In the following table species and genera which are mainly found in warm-water regions or in the deep sea or the pelagic regions are excluded. On the other hand it includes not only the temperate but also the arctic fishes of the shelf region, since we are chiefly concerned here with the whole of the North Pacific with the adjoining Polar Sea as compared with the whole North Atlantic including its arctic regions in the Polar Sea.

TABLE 21

DISTRIBUTION OF THE ARCTIC AND TEMPERATE SHELF FISHES OF THE NORTHERN HEMISPHERE

	Species	Genera
Total number	725	335
Characteristic for the North Pacific including the neighbouring parts of the Polar Sea .	550=76%	230=69%
Characteristic for the North Atlantic including the neighbouring parts of the Polar Sea .	150=20–21%	51=15%
Common to both regions	25=3–4%	54=16%

These figures are naturally only approximate since it is not possible to draw the exact limits between species and subspecies, between shelf and deep-water zone, between coastal water and pelagic regions and so on, and we must also take into account the difficulty of access to certain primary data. But from the material available it is fairly clear that the fish fauna of the North Pacific shelf region is many times more prolific in species than the North Atlantic. Several other animal groups agree with the fishes in this respect.

As regards the genera common to both regions it should be pointed out that most of them possess more species in the Pacific than in the Atlantic. As an example we quote several of the more generally known genera of crustaceans, echinoderms and fishes:

TABLE 22

THE REPRESENTATION OF SOME GENERA OF CRUSTACEANS, ECHINODERMS AND FISHES WHICH ARE COMMON TO BOTH THE NORTH PACIFIC AND NORTH ATLANTIC SHELF REGION.

	Purely North Pacific species	Purely North Atlantic species	Species common to both
Crustaceans:			
Pandalus	12	2	3
Spirontocaris	51	3	10
Crangon	25	1	1
Cancer	6	1	—
Lithodes	7	1	—
Echinoderms:			
Solaster	6	1	2
Henrica	12–14	2	2
Leptasterias	27	7	5
Strongylocentrotus	8	—	1
Ophiopholis	3	—	1
Fishes:			
Raja	16	8	—
Icelus	7–8	—	1
Artediellus	6	1	—
Careproctus	17	3	—
Pholis	5	1	1
Gadus (sensu lat.)	5	5	1
Limanda	4	2	—

Finally it should also be noted that the North Pacific contains a number of endemic families and other taxonomic groups of a higher order. While the North Atlantic does not contain a single endemic fish family, the North Pacific has a not inconsiderable number of these. According to the system employed by Jordan, Evermann & Clark in their check list of 1930 the number is no less than 21. Eleven of the 21 families mentioned contain only one species but these, too, throw light on the importance of the North Pacific as a centre for the creation of new types. Among families less poor in species we instance the *Embiotocidæ* (surf-fishes, viviparous perches) with 18 genera of which two, however, are to be found in southern Japan, that is somewhat outside the temperate region. This family forms on its own the order Holconoti, an example worth mentioning of the endemic occurrence of a taxonomic group of this high rank in the North Pacific. Among other families we may mention the *Hexagrammidæ* and *Jordaniide*, the last-mentioned consisting of three primitive genera which link the families Hexagrammidæ and Cottidæ.

Of the temperate shelf fauna of the northern hemisphere the Pacific

region thus contains a several times greater number of species and genera than the Atlantic region and only in the Pacific region are endemic families to be found. The above statement which is made primarily with regard to fishes, crustaceans and echinoderms may well also apply more or less in the same form to others of the major animal groups. This fact has also been noted previously by zoogeographers; first by P. Schmidt (1904–5) and Jordan (1905) who expressed, on good grounds, the opinion that *a considerable part of the North Atlantic boreal fauna and the Polar Sea arctic fauna is derived from the North Pacific.* Recently Djakonov (1945) has expressed himself strongly on similar lines as regards the echinoderms.

This view is also supported by the following facts: the fish families Cottidæ (including the Icelidæ), Agonidæ, Liparididæ and Zoarcidæ are in the Pacific represented also by several species in the deep water of the equatorial region and further to the south in the cold-water region of the southern hemisphere, while these families have only one single species in the Atlantic south of the northern temperate region. This seems to indicate a greater age for these families in the Pacific. The crab genus *Cancer* (fig. 56) shows the same peculiarity.

Among the fish families which are well represented in the northern sea, the Gadidæ have been regarded as an exception to this rule in that they have the main mass of their species in the Atlantic and not in the Pacific. In the extent which was earlier conceded to this family, it is however by no means particularly characteristic of the northern shelf region. The picture becomes different if, in accordance with more recent opinion, certain groups of species are removed from the Gadidæ and grouped in special families: the Bregmacerotidæ with their main distribution in tropical seas, the Moridæ in the Pacific and the southern hemisphere, the Merluciidæ even in the tropical Pacific, in the southern hemisphere and in the deep sea, as well as the Gaidropsaridæ (mainly in deep sea, also in the Mediterranean) and if the "gadids" are regarded as consisting only of that group which Jordan & Evermann proposed as a sub-family Gadinæ, that is to say the species which older taxonomists included in the old collective genus *Gadus* with the addition of *Gadiculus.* Within this group *Gadiculus* belongs to the deep sea region, while a subgenus of the old Gadus, i.e. *Micromesistius,* to which among others belongs the eastern Atlantic species *poutassou,* is to be found both in deep water and in the southern hemisphere. The rest of the species of the group *Gadus* are distributed in the following manner: eight live only in the temperate region of the Atlantic (three of them also in the Mediterranean) and two only in the temperate region of the

Pacific, while one is common to both; six are exclusively or mainly found in arctic seas. Atlantic, therefore, predominates and the hypothesis of an Atlantic origin for the northern Pacific species finds some support in this fact. The conclusion is, however, not altogether undisputable when the considerable arctic distribution is taken into account.

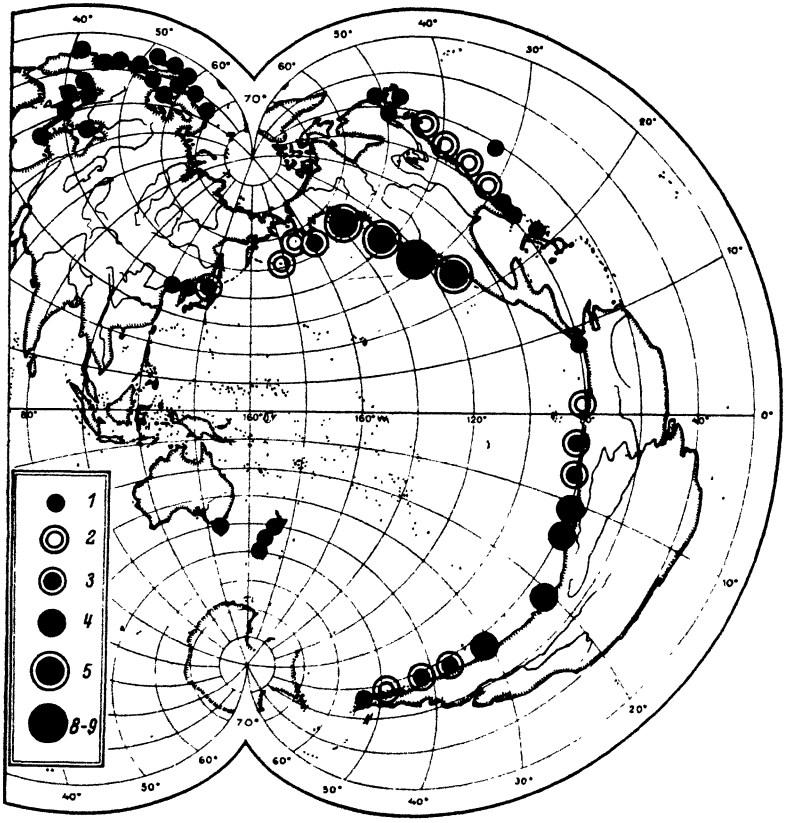


FIG. 56.—The crab genus *Cancer*: map of the distribution and number of species in the particular regions. In Tasmania and southern Australia the species in question was possibly introduced by man. (After S. Ekman, 1935.)

Discontinuous Atlanto-Pacific distribution

The common cod, *Gadus morrhua*, inhabits both the boreal Atlantic and the northern Pacific, the latter with the subspecies *macrocephalus*. The same is true of the rock flounder, *Hippoglossus hippoglossus*, and its North Pacific subspecies *stenolepis*, and the herring, *Clupea harengus*, and its North Pacific subspecies *pallasi*.

Certain experts regard these Pacific forms as different species, others only as races or subspecies. Their very close relationship is, however, beyond doubt. But in the Polar Sea which lies in between these regions, these species are not to be found. Invertebrates with a similar distribution are the well-known prawn *Pandalus borealis* (fig. 57), the bryozoan *Membranipora membranacea* and the sea-urchin *Echinarachnius parma*. In the Atlantic the latter is only to be found on the American side.

Such *discontinuous circumboreal*† animals are not particularly

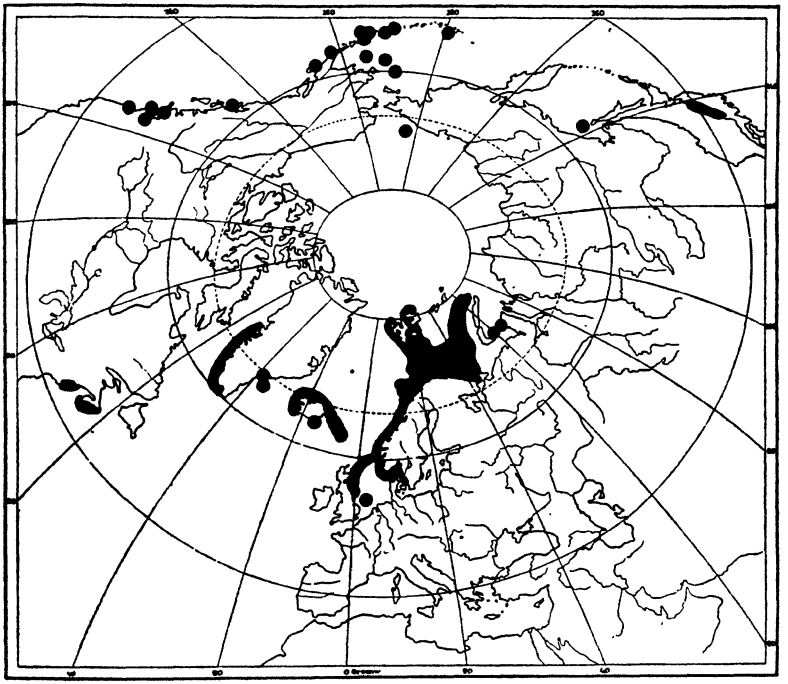


FIG. 57.—Distribution of the prawn *Pandalus borealis*. (After Heegaard, 1941.)

rare (see for instance the list compiled by L. S. Berg[43]). In several cases, as in the examples just quoted, it is a question of the occurrence of one and the same species within two separate regions, in other cases an Atlantic species may be represented in the Pacific by a species which is more closely related to the Atlantic one than to any other. An example of this are the flatfishes *Glyptocephalus*

† This term is to be preferred to the ambiguous "amphi-boreal" which may equally well apply to the occurrence in both the eastern and western North Pacific or eastern and western North Atlantic and does not express the fact of discontinuity.

cynoglossus in the North Atlantic and *G. stelleri* in the Sea of Japan and southern Okhotsk Sea. The present discontinuity is undoubtedly based on a former continuity which became interrupted by climatic changes. We must suppose that the present arctic seas had formerly a milder climate which made it possible for boreal and subarctic species to migrate between the northern regions of the Atlantic and Pacific along a route north of the Asian or American continents.

After the last Ice Age, that is in the post-glacial period and probably contemporary with the post-glacial temperature optimum in Scandinavia (cf. p. 127) there was a possibility of such a migration even for non-arctic species. During this time the climate of the arctic region, too, was warmer than it is now. Certain molluscs lived then off Spitsbergen which have now shifted their most northern habitat further to the south, so for instance *Cyprina islandica*, *Mytilus edulis* and *Littorina litorea* (Jensen & Harder[257]), and in the waters of western Greenland (at 66° 45′ N.) lived *Anomia ephippium*. Merely from present-day distribution it is, however, quite clear that there must have existed also inter- or pre-glacial possibilities for communication between these two marine regions, namely where the circumboreal distribution of a genus has reference to different species in the two regions. The post-glacial period was, without any doubt, too short to allow the development of new species. That a northern inter-oceanic communication existed during the Tertiary Period has already been mentioned in the survey of the history of the Atlantic boreal fauna (p. 121). Very little, however, is known of possible inter-glacial communications. As far as the particular communication through the Bering Strait is concerned, this did not only occur during the post-glacial period but also during the Pliocene.

Palæo-climatic conditions for the development of cold-water faunas

The question of the importance of the North Pacific as the centre of origin of a great part of the North Atlantic fauna, which we have touched upon above, must be regarded in historical perspective. In that respect not only geographical but also climatic considerations must be given prominence. We begin with the North Pacific.

During the Ice Age North-east Asia was in part glaciated; the glaciers of the mountains of Kamchatka flowed into each other to form a network, while in eastern Siberia the higher mountain ranges were glaciated as far as the Bering Strait;[11] the low-lying regions seem to have been free from ice, which was probably due to the dry climate.[17] Only the highest mountains of Japan had small glaciers. Alaska, too, is supposed to have had a colder climate than now but

only certain parts of the country were covered by inland ice and the great North American glacier region intruded into Alaska only to a comparatively small extent.[17, 584] The marine fauna of Oregon points, according to Dall,[99] to a somewhat colder climate than at present. This is in accordance with J. P. Smith's[485] hypothesis of a moderate climatic deterioration during the lower Pleistocene, that is at the beginning of the Ice Age, whereby the present-day climate of Puget Sound shifted as far as San Diego. According to Dall the upper Pliocene was warmer on the coast of West America than the Miocene which preceded it; apart from this the accepted view seems to be that the climate of the Pliocene on the west coast of North America was fairly cold, perhaps even colder than in the Quaternary Period. This may, however, not be valid for the whole of the Pliocene Period; because Harmer's investigations in England show that a Pliocene connection existed between the North Atlantic and North Pacific faunas and this must have taken place across the present arctic regions. This may have happened in the upper Pliocene because a warmer climate than usual was to be found in the North Atlantic at that time (cf. above, p. 121). This is in accordance with the description of a Pliocene mollusc fauna from Nome in Alaska[103] which possibly (but cf. table 24 on p. 168) indicates a warmer climate since several of the species in question have the northern limit of their distribution at present off the Aleutian Islands. Dall also favours a Pliocene connection with the North Atlantic. The faunas of the middle and upper Pliocene in eastern Sakhalin clearly show a cold-water character (Kryshtofowich, 1932, after Berg[43]).

The climate of the Miocene was at first fairly cool north of Oregon but it began to get warmer in the upper Miocene. The Miocene fish fauna of California was not fundamentally different from the present one[269] and as regards the climate of Kamchatka Berg[43] summarizes the Russian results as indicating that the fauna was probably boreal. The climate of Japan is taken to have been a little cooler than now.

Very little seems to be known about the Oligocene maritime climate. During the Eocene the north-west American marine fauna points to a warmer climate than the present[485] and a tropical fauna then lived as far as Alaska (the southern boundary of Alaska lies at 55° N.). But during the Eocene, too, the climate of its most northern regions seems to have been non-tropical.

In conclusion we may say that in the Tertiary the climate was always a temperate one, at least in certain parts of the northern Pacific. This agrees well with the view that during the whole of the Tertiary Period favourable conditions obtained in north-eastern Siberia and Alaska for the development of a temperate forest

fauna (Stegmann, 1932). It is of particular importance for our further arguments that in the early Tertiary Period, too, Alaska and northern Siberia seem to have had not a tropical but a temperate climate.

In considerable contrast to this are the findings with regard to the North Atlantic and Atlanto-Arctic regions. Forests containing a considerably greater amount of species than in the present Central Europe were to be found on Spitsbergen during the early Tertiary Period[579] and the same is roughly true for Greenland. It is said, however, that there is no completely convincing proof for a tropical or subtropical climate at any period in the arctic. But this cannot be valid for the regions which are at present boreal. During the upper Eocene the flora of England and Ireland had a character which is now to be found in the Malay archipelago and in tropical America.[17] The whole of Central Europe was tropical. As far as the marine fauna is concerned, nearly all the molluscs of the Tertiary Period found near Cape Dalton on East Greenland (69° 24′ N.) are identical with Eocene species from England, or closely related to them.[426a] It seems probable, therefore, that the North Atlantic had during the early Tertiary Period a tropical or subtropical climate in higher (present-day) latitudes than the North Pacific. To this we must add a purely geographical fact of equal importance. It is almost certain that a land bridge existed at the beginning of the Quaternary and the end of the Tertiary Period between northern Europe and Greenland-America. If its existence could be postulated for the early Tertiary Period—some scientists assume this state of affairs for the whole of the Cretaceous and Tertiary Periods—the following might have been the course of development of the fauna of the present temperate North Atlantic: during the early Tertiary Period there existed a tropical or subtropical climate, followed by a temperate climate with at the most temporary and difficult communication with other northern cold-water regions. This supposition would provide a sufficient explanation of the present poverty in species of the North Atlantic fauna. Even if we concede that this supposition is not yet proved, it is still possible to assert that, *during the whole of the Tertiary Period the North Pacific offered much more favourable conditions for the development of a fauna adapted to a cold-temperate climate than the North Atlantic.*

CHAPTER VIII

THE ARCTIC FAUNA

OTTO FABRICIUS' famous "Fauna grœnlandica" of 1780 initiated many zoological investigations into the arctic fauna. As neighbouring lands of North Europe the arctic regions with their curious nature have long excited great interest. Glacial geology, oceanography, botany and zoology here mastered new territory and new seas. Thus for instance the marine fauna of Spitsbergen was investigated among others by Swedish expeditions, the sea round Greenland has been studied by Danish zoologists more intensively than any other arctic marine region; since the Swedish expedition of the "Vega" under A. E. Nordenskiöld, which was of importance also to zoology, opened the way along northern Siberia, these regions, too, have become better known through Russian and Norwegian expeditions; the Americans have investigated the Bering Sea and the north coast of Alaska and the North-east Asian marine fauna has been described by Russian scientists in a number of treatises, which are apparently important but unfortunately mainly written in Russian and so almost inaccessible.

Hydrography and climate

The temperature conditions in the arctic regions may be seen from table 23 (the Atlantic-arctic region) and table 24 (the Pacific-arctic region). In the *Atlantic-arctic* region the relationship of the arctic shelf fauna to temperature is better known than for the Pacific-arctic. So it may be stated with some degree of confidence for this region where the most clear-cut change of faunas between arctic and boreal takes place and thus it may be possible to determine the approximate isotherms for the regional limits between the two faunas. From this point of view we may direct our attention to the figures for the temperatures in the Barent Sea between the North Cape and Bear Island (column A), since this part of the sea may be regarded as lying on the boundary of the zoogeographical arctic region, which thus has within the zone of 25–75 m. depth a summer temperature of at the most 5–7° C. It is worth mentioning that a relatively high temperature on the surface during the afternoon in July has been registered also in the extreme arctic fjords (columns F and H). But it is of very short duration and does not exert a

TABLE 23

SUMMER TEMPERATURES (° C.) IN ARCTIC SEAS NORTH OF THE ATLANTIC. A: BETWEEN NORTH CAPE AND BEAR ISLAND 72° 40′ N., AUGUST 30; B: BARENTS SEA OFF THE KARA STRAIT 70° 33′ N., AUGUST 4; C: NORTH KARA SEA (ONLY BOTTOM TEMPERATURES REPORTED); D: SPITSBERGEN, MOUTH OF THE ICE FJORD 78° 10′ N., JULY 18; E: NORTH OF SPITSBERGEN 80° 23′ N., AUGUST 13; F: EAST GREENLAND, SCORESBY SOUND, THE INNER PART 71° 30′ N., JULY 23; G: WEST GREENLAND, SOUTHERNMOST PART 60° 22′ N., OCTOBER 10; H: WEST GREENLAND, DISKO BAY 69° 07′ N., JULY 6; I: NORTH-WEST GREENLAND, MELVILLE BAY 75° 17′ N., AUGUST 1; K: NORTH-WEST GREENLAND, SMITH SOUND 78° 14′ N., AUGUST 8. (*h*)=High Arctic. After available sources.

Depth	A	B	C(*h*)	D	E(*h*)	F(*h*)	G	H	I(*h*)	K(*h*)
0m.	6·9°	3·6°		3·76°	0·3°	8·36°	2·31°	8·60°	2·90°	−0·41°
10						0·57	2·40	7·02	0·66	−1·46
25			20–40 m.							
			−1·52 to −1·60	20 m. 1·37		−1·00		0·86	−1·40	−1·45
50	6·2	−0·8		0·18	−0·45		3·03	0·02	−1·29	−1·40
75			−1·48					−0·16	−1·22	−1·34
			to −1·82							
100	4·7	−1·5		−0·35	0·96	−1·16	5·75	0·07	−1·06	−1·29
200	3·9		−1·97	−0·93	1·25		120 m. bott.	0·40	163 m. bott.	
300			to 0·60	0·78	240 m. bott.	−1·23		225 m. bott.		
1000				400 m. bott.		1·00				672 m. bott.
						1450 m.bott.				

zoogeographical influence for the reason that the main part of the fauna of these regions is first to be met with some distance below the shoreline, since the ice prevents most animals from colonizing the shallowest part of the water.

We have already seen when discussing the boreal fauna, that the southern boundary of the arctic region is by no means parallel with the latitudes. This is a consequence of the paths of ocean currents. At the most northern region of Norway the Gulf Stream separates into an eastern branch which flows into the Barent Sea and a northern branch which is still noticeable near Spitsbergen as a layer of water with positive degrees of temperature underlying the colder polar water. In the same way the warm current in the Barent Sea, the North Cape Current, makes its influence felt faintly even in the northern deeper parts of the Kara Sea. On the other hand it does not flow into the White Sea, although it lies considerably further to the west, since the White Sea is inaccessible to the fairly deep-flowing North Cape Current because of its narrow and shallow connection with the Barent Sea. It has a permanently negative temperature in its deeper interior region. This deep region is therefore high-arctic and is separated from the high-arctic central part of the Polar Sea by a great distance; it constitutes an high-arctic relict region.

Along the east coast of Greenland the East Greenland Current flows in a southern direction; it turns towards the north-west at the southern tip of Greenland until it flows west and south in the Davis Strait, under the impact of the cold polar current, which from Baffin Bay follows the coast of North America and is there known as Labrador Current (cf. p. 136). Under the influence of this current the southern limit of the arctic region on the American side lies considerably further to the south than on the European side.

Our view of the extent of the zoogeographical arctic region in the *North Pacific* can unfortunately not be based directly on the distribution of the animals since this is not yet sufficiently known internationally, but we must for the present place the border region in those waters which have the same maximal temperatures (approximately 5–7° C. below the surface layer) as are found in the Atlantic-arctic region's boundary with the boreal zone. We may be guided in this by some tabulated extracts from the available hydrographic data concerning water temperature during the hottest period of the summer, which in the case of the sea means the latter part of July and August. We begin with the American side of the Bering Sea and the Polar Sea (table 24).

We found earlier that the American side of the Bering Sea is not distinctly arctic as regards temperature until we reach the Bering Strait, if by arctic temperature we mean a temperature which is not

TABLE 24

THE HIGHEST SUMMER TEMPERATURES OFF THE ALASKAN COAST OF THE BERING SEA AND THE POLAR SEA.[36, 185 etc.] A: AT UNALASKA IN THE ALEUTIAN CHAIN; B: BETWEEN UNALASKA AND THE PRIBILOF ISLANDS; C: OFF PRIBILOF ISLAND; D: OFF NUNIVAK ISLAND; E: NORTON SOUND; F: BERING STRAIT; G: NORTH-EAST OF BERING STRAIT; H: SOUTH-WEST OF POINT BARROW

Depth	Bering Sea					Bering Strait	Polar Sea	
	A 53° 57′ N.	B 55° 30′ N.	C about 57° N.	D about 60° N.	E 63° 30′– 64° 30′ N.	F 65° 20′–66° N.	G 66°–68° N.	H 70°–71° N.
0 m.	7·55° C.	7·4–10·2° C.	6·52–7·91° C.	6·29–9·43° C.	10–13·42° C.	7·27–12·29° C.	7·7–10·78° C.	0·09–6·83° C.
10	7·20	6·9–9·3	7·10–7·26	6·16–7·89	10·72–11·50	3·91–11·39	8·3–10·29	−0·11–5·31
20–25	6·67	6·5–8·6	2·96–7·47	6·11–7·71	6·90–6·92	2·44–4·92	6·13–8·12	−0·51–5·11
50	6·33	4·6–7	2·84–6·21				4·65–5·28	
100	5·25	3·24–5·2	3·8					
200		3–4·1						

higher than that prevailing at the southern limit of the zoogeographical arctic region in the Atlantic part of the Polar Sea. It should be noted that this opinion is not primarily founded on the temperature of the surface water, for locally this may reach relatively high figures even in the arctic regions, but first and foremost upon the temperature of the stratum of 20–25 m. depth. South of the Bering Strait the temperature of this stratum in July–August is not arctic but as a rule more than 6° C. (table 24). This is due to the considerable influx of warm water which flows north from the continuation of the Kuroshio Current, the North Pacific Current, through the great gateway into the Bering Sea between Kamchatka and the Aleutian Islands and the lesser gateways between the various islands of this archipelago. On the American side of the Bering Sea an uninterrupted stream of temperate water flows northwards while along the Asian coast a southerly current of cold polar water cools down the sea. This contrast is very noticeable especially in the narrow Bering Strait.

The contrast appears clearly from a comparison between table 24 and table 25 where we see how the temperature of the 25–100 m. layer is much lower on the coast of North-east Asia than on the Alaskan side. Off the mainland coast of the Sea of Japan the water has in fact a lower temperature at a depth of 50 m. than close to the north-east of the Bering Strait, despite the fact that the Japanese observation station lies at least 25 degrees further to the south. The coastal water in the whole of the Asian parts of the Bering Sea may be considered as arctic as well as the sea round Kamchatka, the Okhotsk Sea and, as we have seen earlier on (p. 155), the coastal waters of the northern Kurile Islands. The Okhotsk Sea in particular has the reputation of being the cold store of the North Pacific. Even in July at a depth of 10–20 m. the temperature is negative in a large sector and off the Shantar Islands, in its western part, drift ice may still appear in July and August.

The endemic fauna

The lack of accessible detailed data on the fauna of the Okhotsk Sea, the Sea of Japan and the Bering Sea, makes it at present impossible to distinguish between the purely arctic and the arctic-boreal elements in these seas. We shall therefore have to confine ourselves in the following account to the Polar Sea.

It seems that many species of sponges are endemic to the Polar Sea.[224] Since however a great part of the species determinations which concern the more southern regions are according to experts doubtful and thus make a zoogeographical comparison difficult, we must here omit this group. Among the Cnidaria the hydroids

TABLE 25

THE HIGHEST SUMMER TEMPERATURES AT STATIONS OF THE NORTH-EASTERN COAST OF ASIA[9,185,472]

Depth	Okhotsk Sea 47° N.	E. Kamchatka 54° N., July	E. Kamchatka 57° N.	Cape Navarin 62° 20′ N.	Gulf of Anadyr 64° 10′ N.	Gulf of Anadyr 65° N.	Bering Strait about 66° N.
0 m.	13·4° C.	9·9° C.	9·5° C.	6·80° C.	7·10° C.	9·20° C.	1·72–7·65° C.
10				6·60	7·10	0·24	−0·19–5·91
15			3·9				
20							1·65–2·66
25	2·0	2·0	0·9	5·52	−1·18	−0·58	1·63–1·74
50	0·6	0·9	0·6	1·34	−1·20	36 m. bott.	1·72–2·57
100	−1·1	0·4	0·4	75 m. 1·24	75 m. −1·70		
200	−0·4		0·6				
1000	400 m. 1·1		500 m. 3·5				

show several examples of purely arctic species, which however belong to genera also represented in the boreal zone. Among Pennatularia, *Virgularia glacialis* is an arctic-subarctic shelf species. Approximately 60% of West Greenland's Zoantharia and Actiniaria are arctic.[73] Among the Bryozoa not less than 80 species are endemic within the arctic-subarctic region.[52] But no purely arctic genera have been established.

The Crustaceans possess a considerable number of purely arctic

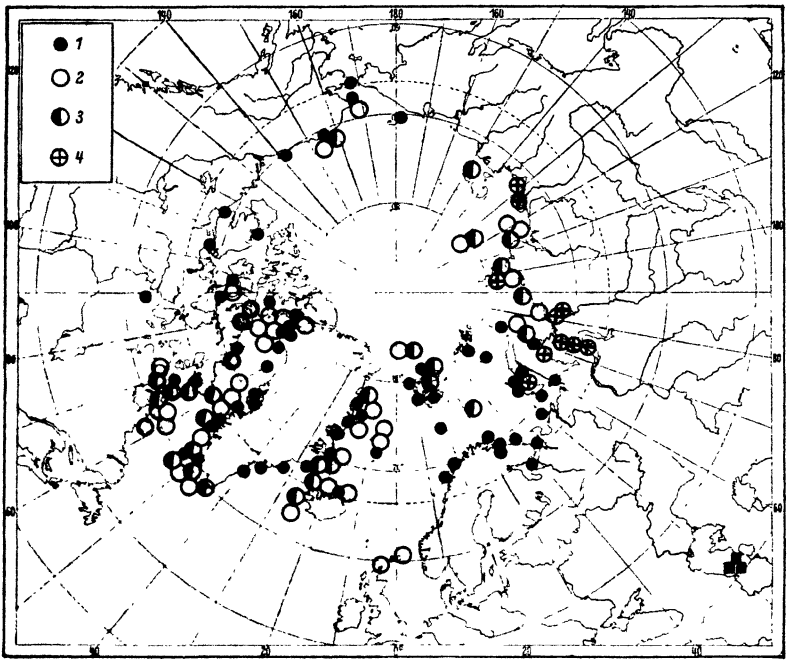


FIG. 58.—Distribution of the amphipod genus *Pseudalibrotus:* 1. *P. littoralis*, 2. *P. glacialis* (pelagic), 3. *P. nanseni* (pelagic), 4. *P. birulai* (brackish-water). Two species, *P. caspius* and *P. platyceras*, live in the Caspian Sea. (After Gurjanova, 1932, with additions.)

species among the amphipods and even several genera which are either wholly or predominantly arctic, for instance *Onisimus* with eight purely arctic and three arctic-high-boreal species, *Pseudalibrotus* (fig. 58) with four arctic species of which one pelagic form is also found somewhat outside the arctic region, as well as two species which are relicts in the Caspian Sea, and *Acanthostepheia* with three arctic species. The *Mesidothea* (fig. 59) among the isopods are purely arctic although *M. entomen* lives as a relict in the Caspian, the Baltic

and various northern inland lakes; *M. megalura* is abyssal-arctic. *Mysis oculata* has been mentioned earlier (p. 133).

Among gasteropod molluscs the family Buccinidæ, and especially the genera *Buccinum* and *Sipho*, contain several arctic species. Particular mention must be made of the mussel *Portlandia arctica* whose earlier name *Yoldia arctica* gave its name to the well-known

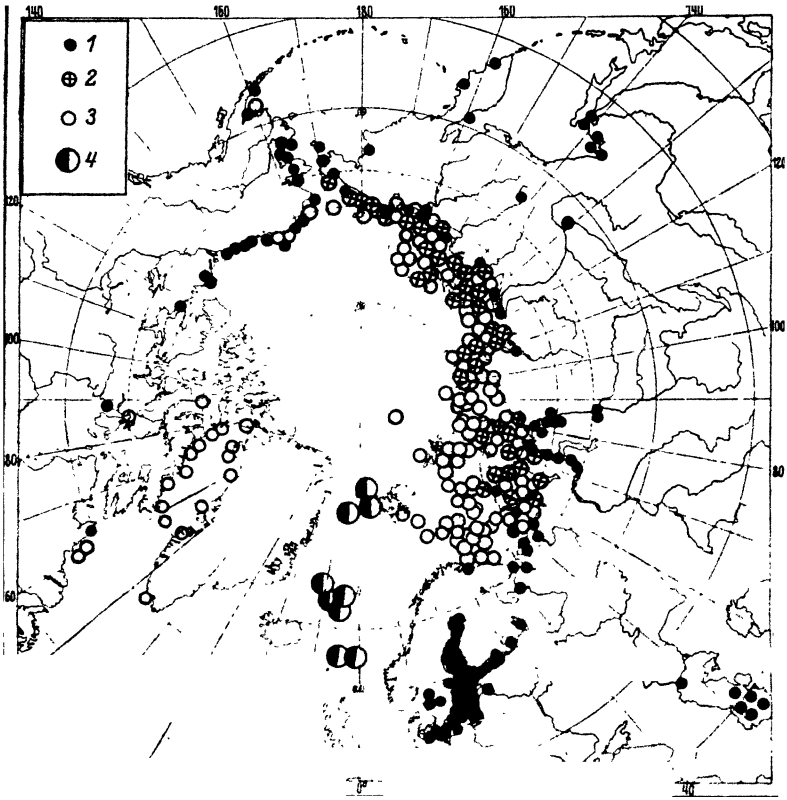


FIG. 59.—Distribution of the Isopod genus *Mesidothea*. 1. *M. entomon*, 2. *M. sibirica*, 3. *M. sabini*, 4. *M. megalura* (abyssal). (After S. Ekman, 1935.)

Yoldia Sea (cf. p. 128). Another common mussel of the Polar Sea is *Yoldia hyperborea*.

Among the numerous echinoderms which belong to this region we must mention the two starfish genera *Urasterias* and *Icasterias*, each containing only one species (*U. linckii*; *Ipanopla*, figs. 64, 65), further the ophiuroids *Ophiura nodosa* and *Ophiopleura borealis*, the latter also living in the deep regions of the Norwegian Sea. Examples of purely arctic holothurians are *Myriotrochus rinkii* and *Ludwigia*

glacialis (=*Cucumaria glacialis*). The ascidians possess a purely arctic genus, *Rhizomolgula*, with the single species *R. globularis*.

Arctic fishes are met with in particular among the families which are most prominent in the boreal marine regions: the Cottidæ (including Icelidæ), Agonidæ, Liparididæ, Blennidæ, Zoarcidæ, Anarhichadidæ and Gadidæ, as well as others. Among the most important species we mention here: *Cottus* (*Myoxocephalus*) *quadricornis*

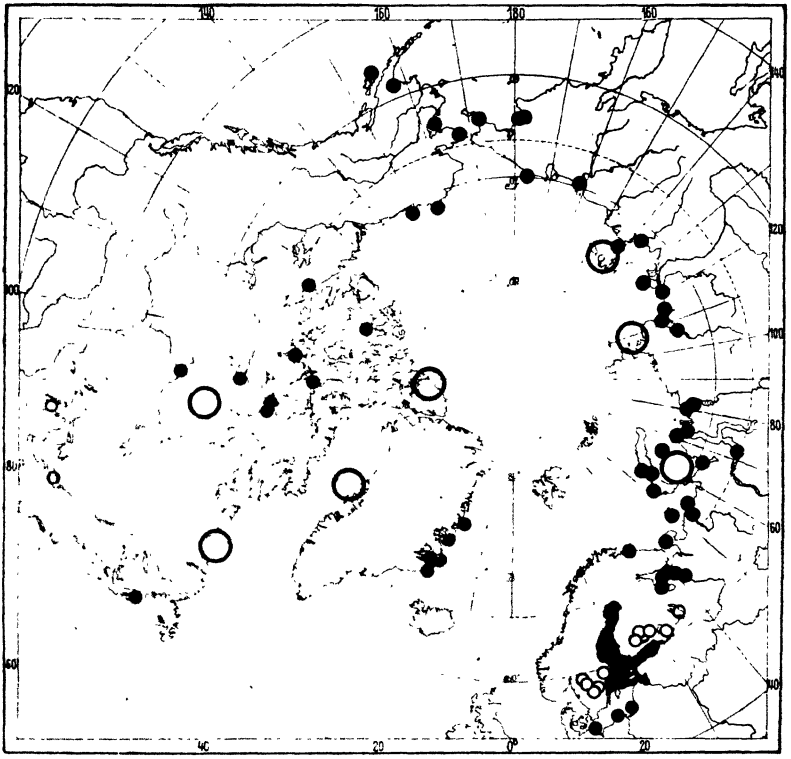


FIG. 60.—Distribution of *Cottus* (*Myoxocephalus*) *quadricornis*. The large circles mark not precisely indicated finds, the small open circles finds in inland lakes. (After S. Ekman, 1935, with additions.)

(fig. 60) whose occurrence as relict has been mentioned earlier; *Gadus* (*Boreogadus*) *saida* (polar cod fig. 61), which is found further to the north than any other fish; *G.* (*Eleginus*) *navaga*; and *Mallotus villosus* (capelin). If we confine our survey to the Polar Sea and leave aside the arctic regions of the Pacific, we can see from table 26 the degree of independence of the fish fauna of the Polar Sea in comparison with the boreal fish fauna.

The percentage figures of 60 and 40 for genuinely arctic species and genera respectively are remarkably high and show that the arctic shelf region occupies an independent position as far as the fish fauna—and also other animal groups—is concerned, much more independent than for example the boreal Atlantic fauna compared with the warm-temperate. With regard to the genera it must however

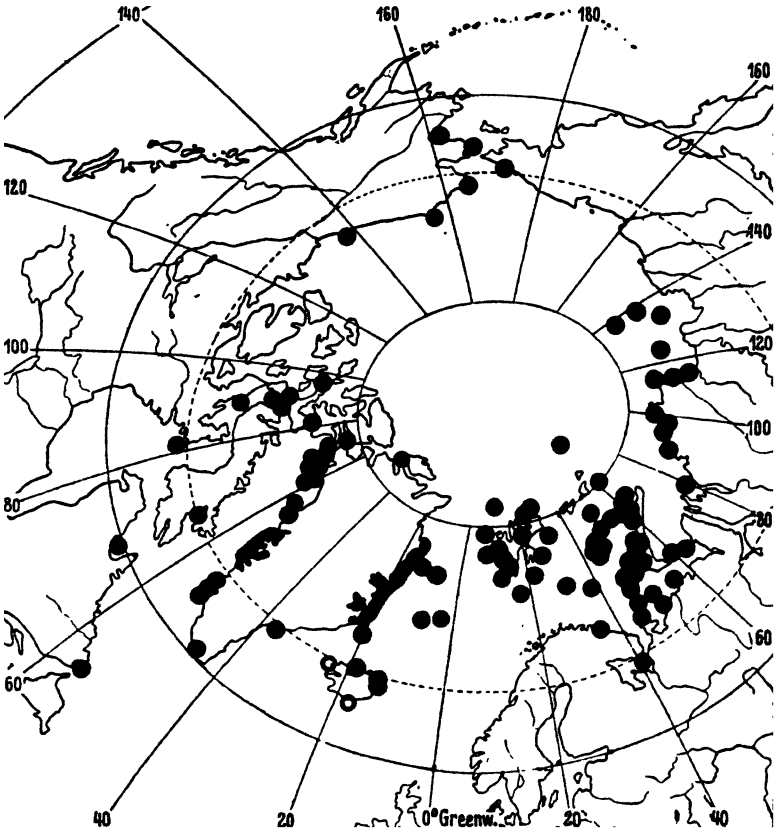


FIG. 61.—Distribution of the polar cod, *Gadus saida*. The open circles at Iceland mark only occasional occurrence. (After v. Hofsten, 1920, with additions.)

be said that the systematics of Jordan *et al.* 1930 and a few later authors, which I have followed here for the sake of uniformity, has in my opinion carried too far the division of the genera of the earlier taxonomists into small genera, which deserve rather the term subgenera. If the taxonomic value of the term genus is made to conform to the one in general use at present in European memoirs, the number

of aretic genera given in table 26 ought to be reduced. No endemic arctic families are found among the fishes.

TABLE 26

THE SHELF FISHES OF THE NORTH POLAR SEA: THE NUMERICAL PROPORTIONS OF SOME ZOOGEOGRAPHICAL CATEGORIES. THE SPECIES ENDEMIC FOR THE ARCTIC PACIFIC ARE HERE EXCLUDED. ALL SPECIES WHICH OCCUR IN THE SHELF REGION ARE INCLUDED IN THE TABLE, BUT THE PARTIALLY ABYSSAL ONES (BELOW 1000 M.) ARE EXCLUDED FROM THE GENUINE ARCTIC-SUBARCTIC (SHELF AND ARCHIBENTHOS) GROUP

	Reported from the Polar Sea, total number	Genuine arctic-subarctic group		
		Total number	Occurring also in arctic Pacific south-west of Bering Strait	Not in the Pacific
Species	80	48=60%	14=29% of 48	34=71% of 48
Genera	45	18=40%	9=50% of 18	9=50% of 18

For the non-endemic fauna we have already given examples of arctic-boreal species (p. 111). Many of the southern elements of the arctic region also occur, however, south of the boreal region. Very many of these southern species are to be found among the polychætes, for example *Nereis pelagica* and *Telepus cincinnatus*, which are both cosmopolitan. The polychæte fauna of the arctic differs from the normal in that the arctic-subarctic element is much weaker than the rest of the constituents. An evaluation by the criteria used in table 26 for the fish fauna shows (according to a list by Ditlevsen,[125]) that the polychætes which also occur in the boreal (perhaps even more southern) regions constitute 72% of the polychæte fauna in the arctic waters of western Greenland, while purely arctic or arctic-subarctic species constitute only 28%.

It is a fairly common phenomenon among arctic-boreal species that in the arctic they occur mainly in the upper shelf region, whereas their boreal representatives are found in deep water, that is, expressed in technical terms, the species in question show *boreal submergence*. Examples of this are, among many others, the crustaceans *Eupagurus pubescens* and *Spirontocaris lilljeborgi* and the fish *Artediellus uncinatus*. The starfish *Pontaster tenuispinus*, which in the arctic is found as far up as 60–70 m. depth and in the boreal region usually does not ascend beyond the 200 m. zone, lives also in the Bay of Biscay but at a still greater depth. This species represents, therefore, a transition to examples like the brittle-star *Ophiacantha bidentata*, which in high-arctic regions ascends up to 5 m. depth, in low-arctic regions to 23–30 m., in the boreal region to 200 m. and in the central

Atlantic, for example off West Africa, is met only in the abyssal region.

Several of the arctic-boreal species in the arctic show an interesting and zoogeographically important anomaly of distribution. *Pandalus borealis*, which represents a fairly large number of species in this respect, lives off north-eastern Spitsbergen, northern Novaya Zemlya and in the Kara Sea under high-arctic conditions, but in spite of this it avoids the rest of the high-arctic regions north of Siberia and North America (fig. 57, p. 161). This anomaly is probably to be explained by assuming that the individuals which now live in high-arctic waters owe their occurrence there to transport from warmer regions, without which they could not exist in these uncongenial places, at least not for any length of time. It is possible that these species do not propagate in these high-arctic regions; or perhaps they do not propagate sufficiently to ensure the colony an existence for decades or centuries. The extreme limit of distribution for the species in such cases is what we shall define as limit of the (sterile) expatriation area when discussing the pelagic fauna (p.317).

Subregions

The animals of the arctic fauna, too, exhibit differences in tolerance of temperatures ("thermopathy"). It is possible to distinguish between *high-arctic* species which only live in the coldest water, and *low-arctic* species which prefer regions nearer the subarctic mixed zone and *pan-arctic* species which are at home in both the high- and low-arctic waters. The boundary between the high-arctic and low-arctic region may be placed, according to v. Hofsten,[237] and Lemche,[298] at the isotherm for 0° C. or at a slightly higher temperature. The high-arctic animals are therefore mainly bound to negative degrees of temperature but can in certain cases endure temperatures up to 4° C., probably when the food conditions are so favourable that the general metabolism can be maintained. This seems extraordinarily active in high-arctic animals to judge from their high oxygen consumption[556].

The following tracts are high-arctic within the upper shelf region: the sea off East and North Spitsbergen, the most northern and eastern parts of the Barents Sea, the Kara Sea and the rest of the Siberian Polar Sea, the North American Polar Sea with the exception of a small part immediately north-east of the Bering Strait, further north-western Greenland north of 72–73° N. and eastern Greenland north of 68° N. To this we should add that the White Sea below about 15 m. depth houses a high-arctic relict fauna which is tied to the negative temperature obtaining there nearly the whole year round, since it varies between +0·5° and −1·4° C.

Within the arctic shelf fauna the pan-arctic forms constitute by far the majority. We mention a few of the endemic high-arctic forms: the prawn *Sclerocrangon ferox* (fig. 62), the amphipod *Pseudalibrotus birulai* (fig. 58), the isopod *Mesidothea sibirica* (figs. 59, 67), the sea-cucumber *Ludwigia* (=*Cucumaria*) *glacialis* and several mussels. The most remarkable of these is *Portlandia arctica* (fig. 63). This mussel is circumpolar and common in the better investigated localities, but it does not occur in eastern Greenland south of 68° N. or in the well-investigated western Greenland south of Thule at 76° 30′ N.[256] Dead shells have been found, however, in more southern parts of West Greenland but these are, so far as can be judged, relics from a colder period. *P. arctica* is tied to water of negative degrees or very little warmer; exceptionally it has been found in water-temperatures as high as 4° C. but it must be borne in mind regarding this and other burrowing arctic animals that the tempera-

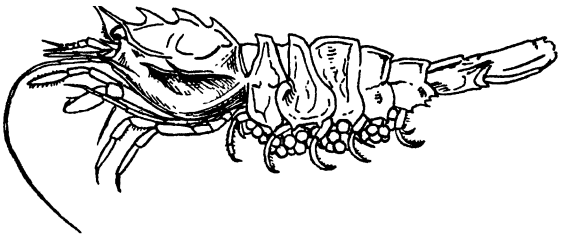


FIG. 62.—The prawn *Sclerocrangon ferox*, half natural size. (After G. O. Sars, redrawn.)

ture in the mud does not rise as high as in the surface water during the warm summer days. This species is therefore a stenothermal cold-water mussel, but it is not particularly intolerant with regard to salinity, being fairly euryhaline (27·6–35‰). Other high-arctic mussels are *Macoma torelli*, *M. loveni* and *Pecten groenlandicus*.

Like the arctic starfishes *Asterias* (*Urasterias*) *lincki* (fig. 64), *Poraniomorpha tumida* and others, *Portlandia arctica* belongs to the high-arctic relict fauna which lives in the White Sea.

Poorer in endemic species than the high-arctic group is the low-arctic which in the main can hardly be considered as independent of the subarctic region. To the low-arctic species belong, for instance, *Mallotus villosus* and a sea-cucumber *Chirodota lævis*.

The main division of the fauna of the arctic shelf must, however, be made on a different basis from that of climate. Two main subregions can be distinguished. One includes the *North-west Pacific* arctic seas which have been discussed before: the western Bering

Sea, the coastal waters of Kamchatka, the northern Kurile Islands, the greater part of the Okhotsk Sea and certain layers of the Sea of Japan on the continental side. The other subregion is made up of the Polar Sea north of America and Asia as well as the arctic parts of the North Atlantic. This region may conveniently be called *polar-arctic*. The Bering Strait constitutes a very sharp dividing line between these two subregions of the great arctic region. Russian scientists have stressed that there are only very few species in common to both subregions. Examples among the fishes are *Gymnelis*

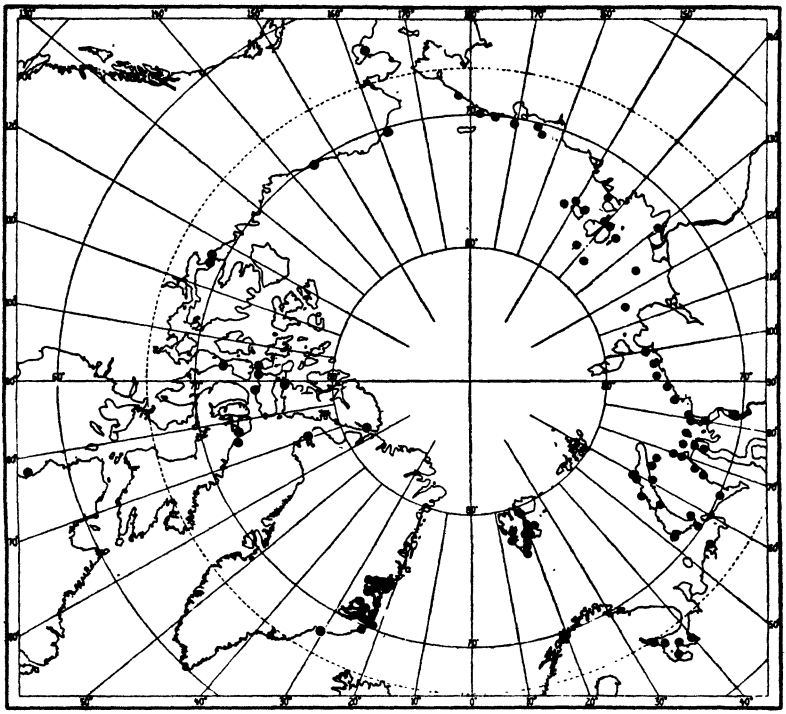


FIG. 63.—The present distribution of *Portlandia arctica*. (After Ad. S. Jensen, 1942.)

viridis, *Eumesogrammus præcisus*, *Icelus spatula*, *Lumpenus fabricii*, *Stichæus punctatus*, *Pholis fasciatus*, *Liopsetta glacialis*, all of which occur also in the Okhotsk Sea. Among the invertebrates we may mention the isopod *Mesidothea entomon* (fig. 59), the arctic-temperate amphipods *Pontoporeia femorata* and *Haploops tubicola*, which descend into the cold-water region of the Sea of Japan and among the starfishes *Ctenodiscus crispatus*. It must be emphasized that even

if only a few species live in both the Pacific arctic and the polar-arctic region, it is, however, relatively common for a polar-arctic species to possess so closely related a species in the former subregion that both may be regarded as having originated through differentiation from the same parent species, that is they are twin-species. This is connected with the history of their distribution and this in its turn with the geological history of the Bering Strait, which was in several tertiary periods elevated and formed a land-bridge.

For reasons which we mentioned previously we shall have to

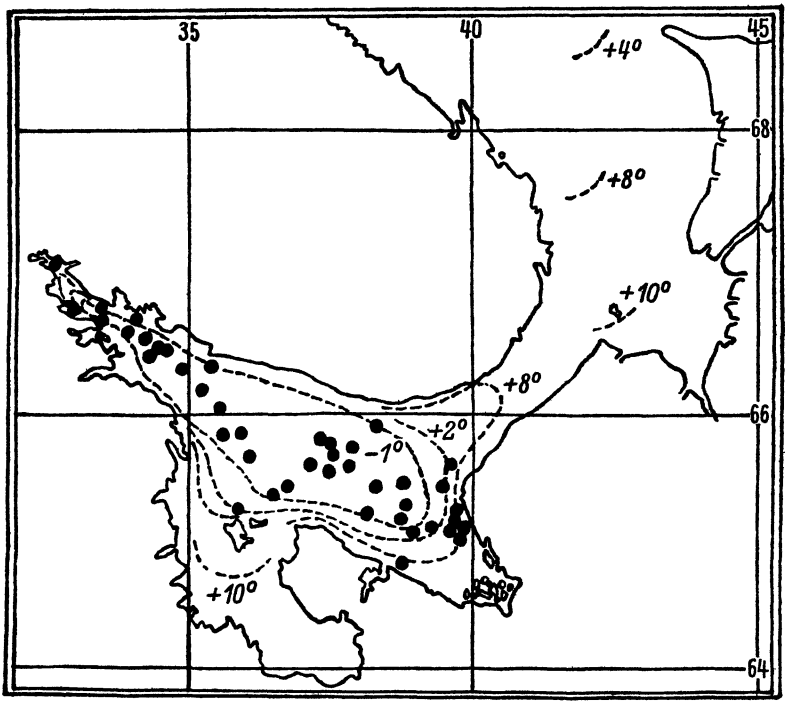


FIG. 64.—Finds of the starfish *Urasterias lincki* in the White Sea and isotherms for the maximum bottom temperature. (Compiled from maps by Schorygin, 1926.)

confine ourselves to the polar-arctic subregion. Many of its species are circumpolar. This type of distribution is shown on the maps which we have given for *Portlandia arctica* (p. 178), *Mysis oculata* (p. 133), *Mesidothea entomon* and *M. sabini* (p.172), *Gadus saida* (p. 174) and *Cottus* (*Myoxocephalus*) *quadricornis* (p. 173). Others transgress the arctic boundary to a greater or lesser distance southwards, as for example the echinoderms *Strongylocentrotus drœbachiensis* and *Ophiura sarsi*, the amphipod *Haploops tubicola*, the

isopod *Munnopsis typica*, the prawns *Spirontocaris polaris* and *S. turgida*, the polychæts *Nereis zonata*, *Glycera capitata* and *Onuphis conchylega* and among the fishes the smelt, *Osmerus eperlanus*.

Several species are *discontinuous circumpolar* and are to be found partly north of the Atlantic, partly north of the Pacific but are missing in the high-arctic coastal waters north of Canada and Central Siberia. Most of these species are mainly boreal; there are only a few genuinely arctic or subarctic species, for instance the fish *Mallotus villosus*.

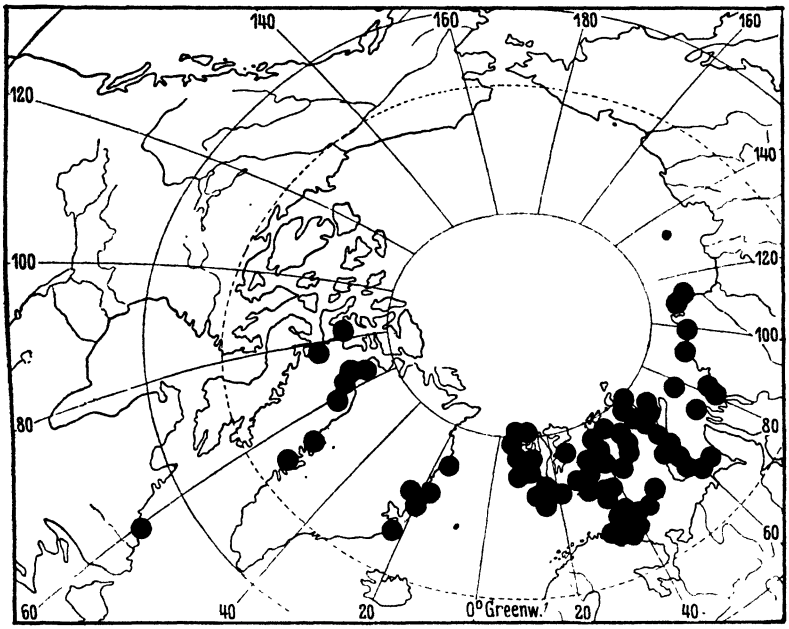


FIG. 65.—Distribution of the starfish *Icasterias panopla*. (After v. Hofsten, 1915, with additions.)

There are among the arctic species also other types of distribution. An *Atlantic-arctic* group lives in the polar region north of the Atlantic: near Labrador, Greenland and Spitsbergen, the Barent Sea and even in the Kara Sea. Species of this kind are the alcyonarian *Eunephthya glomerata*, the starfish *Icasterias panopla* (fig. 65); among the fishes the cyclopterids *Eumicrotremus spinosus* (fig. 66) and *Cyclopterus lumpus* (arctic-boreal), as well as *Lumpenus lampetriformis* (arctic-boreal). We may also include here the two seals *Phoca grœnlandica* and *Cystophora cristata*, which, however, because of their dependence on the drift ice, may be regarded as pelagic.

A group of high-arctic species belong to a special North Siberian

fauna with its focus in the Kara Sea and the Nordenskiöld Sea (east of the Taimyr peninsula and around the New Siberian Islands; also called the Laptev Sea), as for instance amphipods of the genera *Onisimus* and *Pseudalibrotus* (*P. birulai*, fig. 58), the isopod

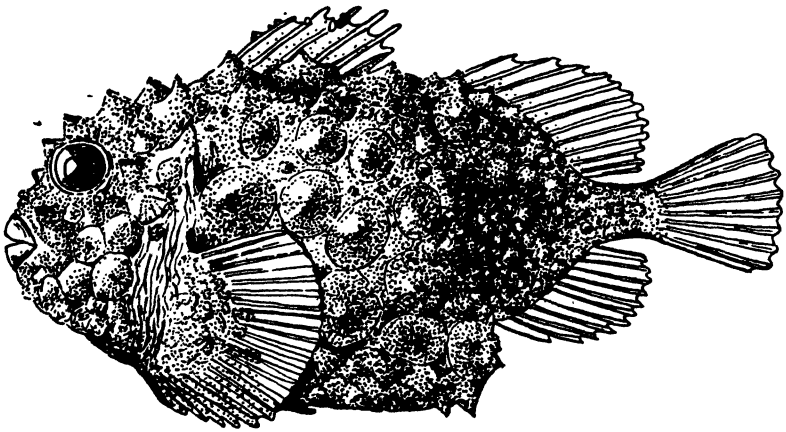
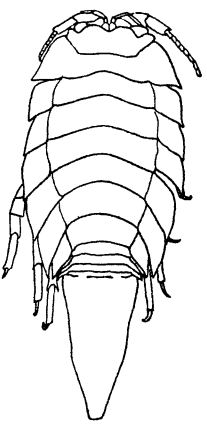


FIG. 66.—The cyclopteriid *Eumicrotremus spinosus*, natural size. (After Ad. S. Jensen, 1944, redrawn.)

Mesidothea sibirica (fig. 67), the holothurian *Psolus sadko* and the fish *Gadus* (*Arctogadus*) *borissovi*. Several species have spread from their centre within the region in question towards its boundaries, for example *Lycodes jugoricus*, which has also been caught in the Barent Sea and the White Sea and *Ludwigia* (=*Cucumaria*) *glacialis* which is also found off Spitsbergen, but being a shallow-water animal could not penetrate further to the west across the deep water near Greenland. Wide, long, stretches of coastal waters in the Siberian Polar Sea are very shallow and their salinity is reduced by the water of the great Siberian rivers until it is only 15–23‰ at the sea floor (polyhaline brackish water or oligohaline seawater; cf. p. 117). From the fauna in this estuarine water the Baltic and Caspian formerly received their glacial marine relicts. The whole of the Siberian Polar Sea between Novaya Zemlya and the Wrangel Island has on the surface and as far as 200 m. depth negative temperatures throughout the year.



size.

The species common to the North-west Pacific arctic subregion and the Polar Sea are within the latter distributed mostly north of America but are less frequent north of Siberia to the west of the Wrangel Island, and it has been concluded that migration from the Bering Strait has taken place first and foremost along America. This may possibly be correct. The explanation might be the lately mentioned decrease in salinity in the coastal waters of Siberia. It is, however, possible that absence of several species north of Siberia is only apparent and due to the fact that precisely these oligohaline coastal waters have been most investigated and it is not impossible that several other species may live in the somewhat deeper and more saline water at a greater distance from the coast. Investigations in the northern part of the Kara Sea have shown differences between the southern and northern parts of this sea.[198] But the route along

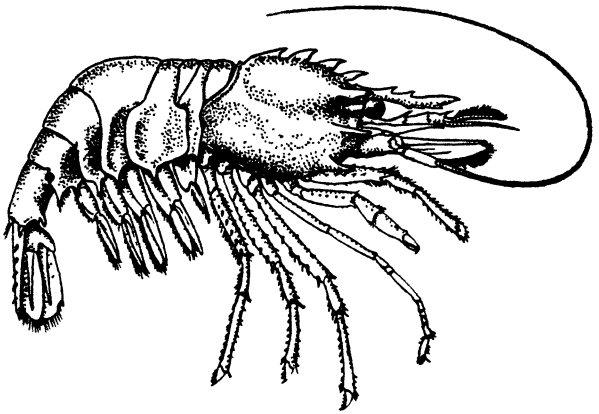


FIG. 68.--The prawn *Spirontocaris grænlandica*, natural size. (After Boone, redrawn.)

Canada's north coast was certainly the only one for several species, namely for those which, starting eastwards from the Bering Strait, have not reached further than Greenland and the north-east of North America. In the examples given below a number of arctic-boreal species are also included. Several have rounded Greenland and reached its eastern coast, as for instance the decapod crustaceans *Nectocrangon lar* and *Spirontocaris grænlandica* (figs. 68, 69) and the amphipod *Pontogeneia inermis*. Others, however, have reached West Greenland but not East Greenland, as for instance the crustaceans *Chionoecetes opilio* (figs. 53, 54, pp. 151, 152), *Spirontocaris fabricii* and *S. macilenta*, the echinoderms *Asterias polaris* and *Stegophiura stuwitzi*, and the fishes *Stichæus punctatus*, *Eumesogrammus præcisus* and *Pholis fasciatus*. To this another fish, *Hemitripterus americanus*

may be added, which has a discontinuous circumboreal distribution and in the Atlantic is only found on the American coast. Its Pacific subspecies is at times regarded as an independent species. A similar distribution is shown by the sea-urchin *Echinarachnius parma.*

Some ecological-zoogeographical peculiarities

Although in this work we generally had to leave out the natural grouping of benthic species into various kinds of associations, (biocœnoses) a few related questions will be treated briefly since they contribute to the characterization of the arctic region.

In none of the larger zoogeographical regions of the oceans are

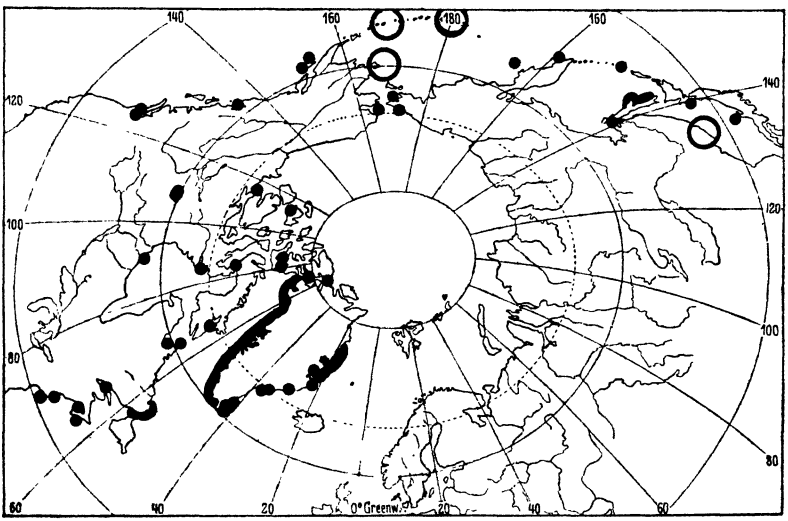


FIG. 69.—Distribution of the prawn *Spirontocaris grœnlandica.* The large circles mark not precisely indicated finds. In addition, several localities in the Pacific which are not to be found in the relevant maps. (After S. Ekman, 1935.)

the ecological conditions so narrowly restricted as in the arctic (and antarctic) region. By this we mean of course first the low temperature. It is a common rule, a "fundamental principle of biocœnotics" that the more specialized or extreme the habitat (biotope) is, the poorer in species but the richer in individuals will be the biocœnosis (Thienemann[548]). This is particularly true of the arctic and especially the high-arctic region. Stuxberg in 1882 pointed out this fact in an unfortunately little-known paper and he mentions as species which are particularly frequent in the Siberian Polar Sea *Mesidothea sibirica* (or *entomon*; he did not distinguish between these two species, cf. fig. 67), *M. sabinei, Diastylis rathkei, Portlandia arctica, Chirodota lævis* (a holothurian), etc. Of the large isopod mentioned,

M. sibirica, he caught at three stations during the "Vega" expedition 101, 350 and 800 individuals. *Diastylis* was caught in thousands and of the large crab *Chionoecetes opilio* (fig. 53) he caught 407 in one dredging haul. Other species which occur in swarms are (530) *Arca glacialis*, *Pecten grœnlandicus*, *Alcyonidium gelatinosum*, *Spiochætopterus typicus*, *Ctenodiscus crispatus*, etc. Of *Ophiura nodosa* 2000 individuals were caught in one haul in the Kara Sea.[469]

Another peculiarity which is common in the high-arctic and to a lesser degree in the low-arctic regions is the almost complete lack, or at least the great dearth, of sessile animals within the tidal zone. This is mainly due to the destructive influence of the drift ice.

The boundary between arctic, subarctic and boreal regions which we have drawn earlier has during the last decades shifted to the north, at least within the Atlantic-arctic region. An increase of the temperature of the air (which for instance has resulted in a reduction of the glaciers) and of the seawater has occurred, with the consequence that a considerable number of boreal species have invaded the region which formerly was beyond their northern boundary. This climatic improvement is not a unique phenomenon in the present geological period. Apart from the post-glacial warm period similar increases in temperature took place during the nineteenth century, but they were shorter than the present one and did not happen simultaneously in the various parts of the Atlanto-Arctic. Thus such a period occurred in western Greenland during the years 1845–9, in Spitsbergen, however, from 1873–82, both being characterized by the fact that the cod appeared in great numbers considerably to the north of where it had been before. The present climatic change began approximately simultaneously in the various Atlantic–arctic tracts, roughly in the decade of 1920 or perhaps a little earlier. It affected the whole region between western Greenland and Novaya Zemlya, partly also the Kara Sea as well as the northern boreal tracts. The warmer climate still continues. The changes in the marine fauna are shown by the fact that several economically important fishes, such as the cod and herring, occur considerably further north than formerly. For instance near western Greenland where the cod was formerly not the object of regular fishing industry was caught to an extent of 6000–8000 tons annually during 1929–37. The Greenland Administration were able to set up year by year an increasing number of cod fishing stations; in 1939 there were 53 such stations, the most northern at 70° 40′ N. (north of Disko). The herring fishery showed to a certain extent a similar development. Single individuals of herring have been caught right up at 72° 30′ N. and they have spawned in south-westernmost Greenland. Other fishes with a similar shift of distribution into the arctic region of the

Bering Sea are the mackerel (*Scomber scombrus*), the haddock (*Gadus æglefinus*), the coalfish (*Gadus virens*) and others. These climatic changes, the biological significance of which is summarized by L. S. Berg[44] and Ad. S. Jensen,[255] are in the main due to the northern continuation of the Gulf Stream, in that at the entrance to the Norwegian Sea the temperature of the Atlantic Current was invariably higher in May–June 1935 and 1936 than it was at the beginning of the century. The mean temperature north of Spitsbergen in the Atlantic water was for August at 200–400 m. depth in 1912 only 1·7° C., but it rose in the years 1922 and 1931 to 3·7° and 3·18° C. respectively; and in the Polar basin, where at the beginning of the century water colder than 0° C. occupied a layer from the surface down to a depth of about 200 m., the cold layer has, according to several observations, during 1927–35 shrunk to a depth of less than 100 m. and the layer of warmer Atlantic water has increased correspondingly.

The poverty of the polar-arctic fauna will be discussed later on in connection with the treatment of the Antarctic fauna (p. 227).

The relationship of the arctic, temperate and tropical faunas to one another

We should first look at table 27.†

In table 27 we should first note the lines printed in italics and the corresponding figures in bold type. We observe that a good half or three-quarters of all genera represented in the polar arctic or the total arctic region respectively are to be found also in the temperate region, while only 8% of the latter region's genera are to be found also in the tropical-subtropical region. This closer affinity between the two northern regions emerges if possible even more clearly if we consider the representation of the families. While the 20 and 33 families of the polar arctic and the total arctic region respectively are all represented also in the temperate region, and the affinity is thus 100%, it is only 38% for the temperate and the tropical-subtropical region. We might add that several of the temperate region's families represent four orders and one suborder which, at least on the American side of the Pacific, do not go south of this region, and this further heightens the contrast.

† The table is partly based on a table given by Andriashev (1939, pp. 38–52). Any uncertainty regarding my excerpts is due to the fact that Andriashev only gives those species of the fish fauna of the Okhotsk Sea which are also to be found in the Bering Sea. The figures for the Pacific are therefore only approximate. For the sake of uniformity and comparison the table follows throughout the same taxonomic system. The circumstance that many genera and families in my and probably several other zoologists' view should be regarded as subgenera and sub-families respectively (cf. p. 150, the footnote) does not invalidate the results of the comparison.

TABLE 27

THE AFFINITY BETWEEN THE NORTHERN AND THE TROPICAL FISH FAUNAS OF THE SHELF, ACCORDING TO REPRESENTATION OF THE GENERA AND FAMILIES IN THE DIFFERENT CLIMATIC REGIONS

	Genera	Families
Of the 45 genera and 20 families in the polar arctic region occur:		
in the polar arctic but not in the temperate region	21=47%	0
both in the polar arctic and the temperate region.	24=53%	20=100%
Of the 93 genera and 33 families in the total arctic (polar and Pacific arctic) region occur:		
in the total arctic but not in the temperate region	23=25%	0
both in the arctic and the temperate region .	70=75%	33=100%
Of the 260 genera and 80 families in the temperate occur:		
in the temperate but not in the tropical (-sub-tropical) American Pacific	240=92%	50=62%
both in the temperate and the tropical (-sub-tropical) American Pacific	20=8%	30=38%

The boundary between the warm-water fauna and the temperate fauna is therefore a much sharper zoogeographical division than the boundary between the temperate and the arctic fauna. This rule is obviously true not only as regards the fishes but also for most of the other animal groups of the shelf, for instance crustaceans and echinoderms. In other words: *in the northern hemisphere the fauna of the shelf may be divided into two main groups, a tropical-subtropical and a northern.* On the east coast of the Atlantic these two groups have, however, been mixed with each other to such an extent that the boundary between them is much less sharp than in the Pacific.

CHAPTER IX

THE WARM-TEMPERATE FAUNAS OF THE SOUTHERN HEMISPHERE

In the northern hemisphere, which contains the great continental masses, there is a connection between the various temperate and arctic shelf regions which is geographically almost continuous, although it runs through climatically different regions. In the southern hemisphere, however, the great shelf regions are separated from each other by wide expanses of ocean and almost as large tracts of abyssal deep sea. These circumstances have, of course, brought about different conditions of distribution for the shelf fauna in the two hemispheres.

We now turn first to the faunas of South Africa and South Australia which link up closely with the tropical regions, so that their treatment can follow closely on the preceding account.

THE FAUNA OF THE SOUTH COAST OF AFRICA

We found earlier that the tropical fauna off South-east Africa has its southern boundary in a certain tract south-west of Durban. The coast in the vicinity of this town and in Natal has on the whole a distinctly tropical fauna. Algoa Bay to the west, between Cape Padrone and Port Elizabeth, is regarded by a number of zoologists as a transitional region between the north-eastern and south-western faunas, for example as regards the decapod crustaceans,[27, 299] amphipods,[458] echinoderms,[355] ascidians[211-214] and molluscs,[327] whereas others place the transitional zone in Natal, others again off the Cape of Good Hope. That the south coast approximately from Algoa Bay to Cape Agulhas or Cape Point in the west constitutes an independent zoogeographical province, at least as regards the tidal fauna, has been clearly shown by the thorough investigations undertaken by T. A. Stephenson and his collaborators during the nineteen thirties and forties. This region is sometimes called the Cape Province, which however is not altogether a satisfactory name, since Cape Town and the Cape peninsula are situated just on the boundary of another province.

The different views held by different investigators are due partly to the complicated course of the faunistic boundaries, and these

depend in their turn on the very complicated hydrographic peculiarities (fig. 70). The Mozambique Current, which off the coast of Natal is called the Natal Current, flows off the south-east coast of Africa. It continues westwards along the south coast, where, after the southernmost cape of Africa, Cape Agulhas, it receives the name of Agulhas Current. This warm current which is so strong (at times almost 7 km. an hour) that vessels proceeding westwards make use of it to enable them to counter the strong westerly gales, meets the cold West Wind Drift off the western border of the Agulhas

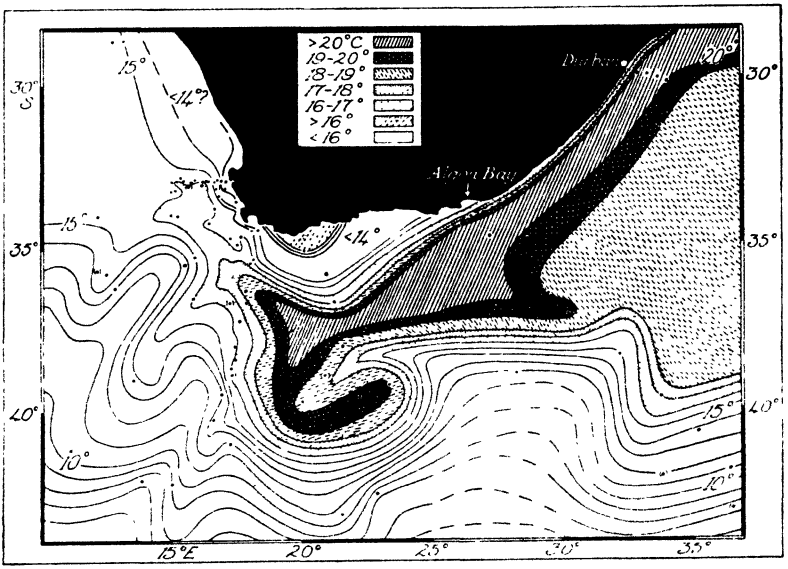


FIG. 70.—Distribution of water of different temperatures at a depth of 50 m. in the month of October, off the South African coast. (After T. A. Stephenson *et al.*, 1937, modified from Dietrich, 1935.)

bank and is split up by it. The result is a more violent mixture of cold and warm water than exists anywhere in other oceanic regions. A part of the West Wind Drift wedges itself between that branch of the Agulhas current which flows close to the southern coast and the outer branch which flows over the Agulhas bank. Thus it comes about that the coastal water off the south coast of Africa is actually warmer than the water at some distance from the coast and that this water still further out to sea, namely off the Agulhas bank, gives way once again to warmer water. It has also been established that the tropical-subtropical molluscs[326] and hydroids[493] of the Indian Ocean penetrate further westward on the Agulhas bank than they do nearer the coast. Here we see again how a rational solution of

zoogeographical problems of the coastal waters is possible only if we regard as faunistic regions certain kinds of water and not certain areas of sea, delimitated by geographical landmarks.

The temperature of the water at a depth of 50 m. may be seen in fig. 70. The surface temperature of the southern and south-eastern coast during the warmest and coldest periods of the year is seen from the following table.

TABLE 28

SURFACE TEMPERATURE DURING THE WARMEST AND COLDEST MONTHS

	February	August
Durban	(24–) 25° C.	21° C.
Port Elizabeth (Algoa Bay)	23	20
Cape Agulhas	20–21	15–16
Cape Town	20	14
Soldanha Bay 1° N. of Cape Town	15	13–14

We see from this that immediately to the north of Cape Town a distinct drop in temperature occurs, so that the Cape of Good Hope constitutes the boundary between two temperature regions. We also see that the temperature within the area from East London or Port Elizabeth down to Cape Town or Cape Agulhas agrees fairly well with the water temperature which elsewhere in this book has been termed subtropical. More important, however, are the affinities of the fauna. According to Stephenson's[509] graphic representation reproduced here in fig. 71 the tidal zone of this region has about 34% of species which are endemic or at least have here their centre of distribution (the groups of species B and C in fig. 71). In the literature the percentage of endemic species is sometimes put still higher. But these statements are obviously exaggerated in that these high percentages are based on a combination of material from the south coast and material from tropical Natal. In some cases where it was possible to consult the primary data the percentage was found to vary between 25 and more than 50%. Here, too, the higher figures may be too high and may have to be considerably reduced when the neighbouring faunas outside the tidal zone, especially the south-west African and south-east African north of Durban, which are at present still very imperfectly known, have been further investigated.

Among the most characteristic species of the region we may mention the gastropods *Cominella cincta*, *Haliotis midæ*, *Patella cochlear* (fig. 72) and *Turbo sarmaticus*, all of which belong to the tidal zone. Among the decapod crustaceans are found three monotypical genera which so far have not been encountered in other

regions; and among the fishes more than 10 species of the genus *Clinus*. Particularly noteworthy is the brachiopod genus *Agulhasia* whose only living species is a South African one while a fossil species is known from the Cretaceous deposits of Europe. The fish genus *Chilodactylus* with its single species *fasciatus* is confined to the south coast of Africa.

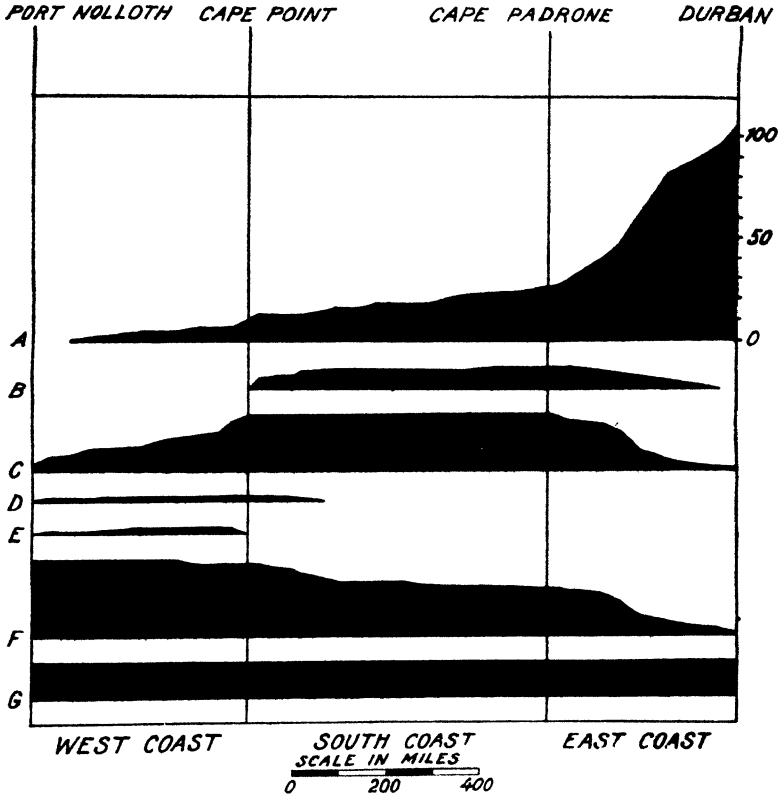


FIG. 71.—A diagram illustrating the distribution of the geographical components of the intertidal fauna along the South African coasts, based on the distribution of 202 species (in A 105 sp.). A= the warm-water component, C= the south coast component, F=the cold-water component, G=the ubiquitous component. Subsidiary components of more limited range are B, D and E. (After T. A. Stephenson, 1944.)

Most zoologists who have written on the geographical position of the fauna of the south coast of Africa have stressed the poverty of the species as compared with the fauna of Natal, but they emphasize its close taxonomic affinity to the latter and thus to the Indo-West-Pacific fauna. Barnard[34] in his great monograph on

South African fishes assigns the whole fauna of the south coast as far as False Bay at Cape peninsula to the Indo-Pacific fauna. Fig. 71 shows a steep fall in the number of species at the transition from Natal to Algoa Bay. A fairly rapid decrease in the number of species is presumably also true for the less superficial zones of the shelf.

Stephenson, who has unique personal experience of the fauna of the south coast of Africa, designates it warm-temperate and for this reason I, too, although with some hesitation because of the more subtropical character of the temperature of the water, have included it among the temperate faunas. Stephenson states that his sublittoral zone, too, which runs immediately below the tidal zone, seems to agree faunistically with the latter. How far down within the shelf region this agreement extends is not precisely known. Several species among the octactinians seem to be endemic.[63a] The use of the terms subtropical or warm-temperate is of real and not merely of formal interest, for its close affinity to the tropical fauna of the Indian Ocean indicates that from the evolutionary point of view the fauna in question is most closely related to the latter, so that the term subtropical would be the correct one. Its considerable degree of independence manifested in the rather high percentage of endemic species is, however, noteworthy. And that its closest connection is with the tropical fauna seems also questionable so far as the tidal fauna is concerned. The graphic representation in fig. 71 and Stephenson's list (1944, pp. 342–8) shows (species group F as against A) that the connection with the south-west African fauna is at least as close as with the fauna of Natal, so far as we can judge from our present-day knowledge.

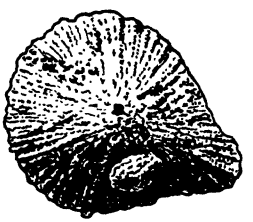


FIG. 72. — The limpet *Patella cochlear*, with a small limpet on the back. (After T. A. Stephenson, 1939, redrawn.)

This brings us to the relationship of the south-coast fauna to that of the south-west coast, the so-called Namaqua fauna. The following species are characteristic for both coasts within the tidal zone; they have at the most only an insignificant distribution elsewhere: the anemone *Bunodactis reynaudi*, often attaining amazing abundance, the polychæte *Gunnarea capensis*, which forms enormous aggregations, almost reefs (fig. 73), the snail *Littorina knysnænsis*, the limpet *Patella argenvillei* and a number of species of the fish-genus *Clinus* already mentioned.

We must omit here species with a more or less cosmopolitan

distribution. But several elements which are common to both the south and south-west coasts of Africa on the one hand, and the North Atlantic or the temperate and cold parts of the southern hemisphere on the other, will be dealt with in connection with the fauna of the south-west coast of Africa.

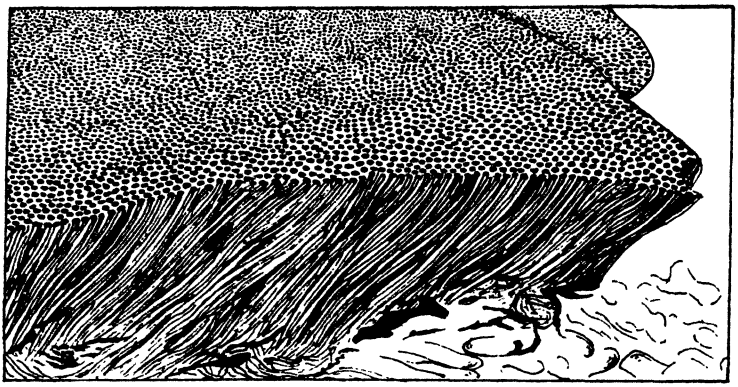


FIG. 73.—A mass of tubes of the polychæt *Gunnarea capensis*, at Cape Peninsula. Such masses cover large areas of the rocks at certain localities, and attain a thickness of 38 cm. or more. (After T. A. Stephenson, 1938, redrawn.)

THE FAUNA OF SOUTH-WEST AFRICA (THE NAMAQUA FAUNA)

North of the Cape Peninsula we encounter a fauna which has certainly much in common with the fauna of the south coast and yet possesses a fairly pronounced degree of independence. W. Michaelsen who more than anyone else contributed to our knowledge of the fauna in question by his zoological expedition to the western and south-western coasts of Africa, has called the faunistic region of the south-west coast the *Namaqua region*, placing its approximate northern boundary at about 18° S. That this boundary may be conveniently placed between 17° and 20° S., that is to say somewhat north or south of Cape Frio, has been confirmed also by other investigators of the West African fauna. The tropical-subtropical warm-water fauna may also be regarded as extending southwards approximately as far as this region, as we found earlier.

The hydrographical conditions are peculiar. Not only is the coast dominated by the cold Benguella Current, but in addition to this the upwelling water lowers the temperature still further. This water is as cold as that off the coast at a depth of 300–400 m. and is therefore regarded as coming from this deep layer. Thus the south-west

coast has the coldest water of all Africa. Immediately north of Cape Town a big drop occurs and the water temperature is rather low almost as far as the Great Fish Bay, where a tropical-subtropical fauna distinctly predominates over the temperate fauna. The temperature close to the coast is somewhat lower than as given in table 29, the figures of which apply to water somewhat further out to sea. Still, we see that the marine climate is not so cold as in the boreal region of the northern hemisphere but bears a greater resemblance to the warm-temperate region. For instance, the bottom temperature in Saldanha Bay north of Cape Town is 9–10° C. at a depth of 100 m. during the whole year.

TABLE 29

SURFACE TEMPERATURES IN FEBRUARY AND AUGUST IN THE SOUTH-WEST AFRICAN OR NAMAQUA REGION

	February	August
Off Great Fish Bay, 17° S.	20° C.	15° C.
Off Swakopmund-Walvis Bay, 22–23° S.	17	12–13
Off mouth of Orange River, 28° S.	<14	13
Off Saldanha Bay, 33° S.	15	13–14
Off Cape Town, 34° S.	20	14

The upwelling water influences the fauna in other ways than by lowering the temperature. This water brings dissolved nutriment from the bottom which the planktonic algæ can utilize. In the ordinary way the production of phytoplankton is limited by the fact that the water contains only traces of phosphates and nitrates; but since the upwelling water carries considerable amounts of these salts and at the same time the illumination is optimal, the production of certain algæ, especially the dinoflagellates, rises enormously and the water becomes a deep red because of their brown or orange-yellow chromatophores. Such a "water-bloom" or "red water" may occur more occasionally on other coasts. It happens regularly on the coast of South-west Africa between Walfish Bay and Lüderitz Bay in the spring and causes a high mortality among the fishes, crustaceans, molluscs and other invertebrates through the amount of hydrogen sulphide which is formed in the bottom sediment by the rotting masses of dinoflagellates and diatoms. The latter algæ also occur in great quantities. It is possible that contributory causes of the mortality among the animals are some toxic substances contained in dinoflagellates. Within a broad belt off the coast—according to M. Brongersma-Sanders[64] who paid special attention to this phenomenon it is 30 km. wide—the sea floor down

to 140–150 m. depth consists of an almost azoic field covered with soft dark-green mud smelling of hydrogen sulphide which contains the corpses and skeletons of animals. In the interim periods between the times of water-bloom the sea is rich in such fishes as swim freely in the upper strata, but the fauna of the sea floor is decimated almost to extinction. The poverty in species which, according to Michaelsen and other investigators, characterizes the Namaqua fauna, seems chiefly due to these hydrographical-planktological features. Stephenson, on the other hand, found within the tidal zone a fauna rich in individuals of great size. The reason for this contrast between the tidal zone and the deeper-lying sediment is not difficult to discover. In the tidal zone, with its great change of water due both to storms and tidal currents, no sapropelic mud can be deposited; here the organisms have the advantage of a supply of water rich in nutriment. In the calm water above the sea floor, at considerable depth, masses of dead algæ are, however, able to stagnate and rot undisturbed. This accords also well with the fact that Brongersma-Sanders (fig. 1, p. 7) found close to the shore and inside the azoic zone " a narrow belt where the bottom consists of fine grey sand in absence of green sulphurous mud; here living fauna and flora abound".

This same coast has been stated by investigators with personal experience of it to be unfavourable for the benthic fauna because of its predominantly sandy floor and lack of protection from the surf.

On the whole the region must be designated as imperfectly known so that we cannot judge accurately how large a proportion of its species should be considered endemic. Stephenson has investigated the tidal fauna in the southern part of this region. From his list (pp. 342–8) it appears that of the species of this fauna at most 17% are endemic. Some of these may possibly be also contained in the northern warm-water fauna or the temperate fauna of the North Atlantic. The south-west African fauna seems to have greater affinity with the Atlantic fauna than with that of the Indian Ocean. As particularly characteristic for the tidal fauna we may single out the molluscs *Mytilus meridionalis*, *Cominella delalandei* and *Patella granatina*.

A few groups of species are of special interest. One of them consists of species with a main distribution in the North Atlantic and which are at present not known from the tropical coast of Africa and therefore seem to have a discontinuous north-south distribution in the East Atlantic, that is they have a kind of bipolarity, provided that this expression does not imply distribution in the polar regions as such. Such species are, for instance, the polychætes

Nephthys hombergi and *Sabella pavonina*, the molluscs *Venus verrucosa* and *Cerithium vulgatum*, the brittle-star *Ophiothrix fragilis* and the ascidian *Leptoclinides capensis*. These species occur south of the equatorial region in the same form as in the North Atlantic and thus show in neither region divergencies of a degree which could justify the setting up of new races or varieties. That these species are in fact bipolar in the sense just specified must, however, be regarded as not proven or rather as improbable. Our knowledge of the West African coastal fauna is so incomplete that the absence of the species in question from tropical West Africa cannot be regarded as established. There are grounds for suspecting a submergence in the equatorial region. As we have seen earlier (p. 56) there is a fairly low temperature already at a depth of 100 m. within the whole of this region and a further consideration is that a considerable portion of the catches to which we owe our knowledge of this fauna has been confined to the sea floor above the 30 m. level.

Other species with a similar discontinuity of distribution as those just mentioned are represented in South and South-west Africa by special varieties, while the type lives in the North Atlantic. Here belong several echinoderms such as *Astropecten irregularis*, with the southern variety *pontoporœus*, *Hippasteria phrygiana* with the southern variety *capensis*, *Marthasterias glacialis* with the two southern varieties *rarispina* and *africana*, *Brissopsis lyrifera* with variety *capensis* and *Echinocardium flavescens* with variety *capense*. For these species a true discontinuity in distribution may be assumed with better reason, provided the differences are of a genotypical nature. These find a probable explanation in a theory which Darwin had already put forward for other cases of bipolarity, namely that the decrease of temperature during the glacial period could have made possible a continuity of distribution. To a certain extent there is a parallel between the species in question and several paired species which consist of a northern and a very closely related southern species. Examples are the two northern fishes *Merlucius merlucius* and *Zeus faber* with their extremely closely allied southern forms *M. capensis* and *Z. capensis*; and the European lobster, *Homarus vulgaris* and the South African *H. capensis*. That the divergence of the species in the latter cases took place so late as during or after the glacial period must, however, be regarded as unlikely.

Another interesting group of species shows a distribution which, apart from the south and south-west coast of Africa, includes distant regions within the temperate or even antarctic parts of the southern hemisphere. Several of these species are enumerated in table 30.

TABLE 30

SOME SPECIES OF THE AFRICAN SOUTHERN AND SOUTH-WESTERN COAST WHICH OTHERWISE LIVE EXCLUSIVELY IN THE TEMPERATE OR COLD REGIONS OF THE SOUTHERN HEMISPHERE

South and South-west African species	Distribution in other regions
Sea-anemone: *Phellia aucklandica*	Auckland Isl.
Polychæts: *Arenicola loveni* .	Southern South America, South Australia
„ *assimilis* .	South Georgia, Magellan region, Falkland Isl., Kerguelen, Tasmania, New Zealand, the "Antipodes" and Macquarie Isl.
Crustaceans: *Squilla armata*	Patagonia, Cape Horn, Chile, New Zealand, South-west Australia
Jasus lalandii .	Tristan da Cunha, Juan Fernandez, Southern New Zealand, South Australia, Tasmania, New Amsterdam, St. Paul, Auckland and Campbell Isl.
6 species of Amphipoda	
Molluscs: *Argobuccinum argus* .	Temperate South America and islands of the South Sea
Mytilus magellanicus .	Temperate South America and islands of the South Sea
Echinoderms: *Amphiura angularis*.	Kerguelen, Marion Isl., Magellan region
Ophiomyxa vivipara	Magellan region, Tristan da Cunha, Kerguelen.
Dermechinus horridus	Magellan region, South Australia
Ascidians: *Corella eumyola* . .	Southern South America, New Zealand, Chatham Isl., Auckland Isl., Tasmania, St. Paul
Fishes: *Callorhynchus capensis*	It is probable that *C. capensis* and *C. milii* from South Australia, Tasmania, and New Zealand are nothing more than varieties of *C. callorhynchus* (syn. *C. antarcticus*) from the southern South America

There are possibly a few more genera than species with such a distribution. Only a few examples can be mentioned here. The sea-anemone *Halianthella* has a species *annularis* off the Cape peninsula which is closely related to *H. kerguelensis* from the Kerguelen and Macquarie Island. The gastropod genus *Bullia* with various species is represented only in the temperate and cold parts of the South Sea. The monotypic starfish genus *Spoladaster* has the species *brachyactis* in South Africa and belongs to a family (Ganeriidæ), the rest of whose genera are antarctic or antiboreal. Much the same is true of the amphipod genus *Paramoera* and to a certain extent of most of the family Pontogeneiidæ to which it belongs. In this connection we remember the South African penguin *Spheniscus demersus* whose genus has three other species in the Falklands, in

western South America from its southern tip to Peru and in the Galapagos Islands; and the south-west African eared seal *Arctocephalus pusillus*. Considering possibilities of distribution both these species are, however, rather to be regarded as pelagic.

SOUTHERN AUSTRALIA AND TASMANIA

About 1880 Haswell and Bell, and later Döderlein[127] and several other investigators, drew attention to the difference between the coastal faunas of northern and southern Australia. When we discussed the tropical-subtropical fauna of Australia we found that the region of transition between this and the more southerly fauna may, on the west coast, be placed at the region north of Perth, and on the east coast at 32–34° S. (region north of Sydney). As in many other cases these limits, too, are due to hydrographical conditions. The south coast is influenced by the fairly cold West Wind Drift which branches off to the north both along the west and the east coasts where its two branches encounter warm currents in the transitional regions just mentioned. The water temperatures in the region in question may be seen from the following table:

TABLE 31

TEMPERATURES IN THE COASTAL WATERS OF SOUTH-WESTERN, SOUTH-EASTERN AND SOUTHERN AUSTRALIA

	February surface	August surface	200 m.	400 m.
South-western coast:				
Abrolhos Islands, 29° S.	22–23° C.	19° C.	15° C.	9° C.
Fremantle at Perth, 32° S.	21–22	18	14–15	9
South-western corner, 35° S.	19–20	16	13–14	9
South-eastern coast:				
32° S.	25	17–18	16	12–13
Sydney (Port Jackson), 34° S.	22	16–17	15	12
Southern coast:				
Bass Strait, 40° S.	15–16	12	13	10–11
Great Australian Bight	20	13	13	9–10
Tasmania, southern point, 43° 20′ S.	13·5	10·5	10·5	9

It emerges from this table that the southern marine region starting at about 32° S. on the west coast and 34° S. on the east coast has a marine climate which in comparison with other regions may be called warm-temperate.

THE COMPOSITION AND ORIGIN OF THE FAUNA

Important contributions to marine zoological knowledge were made by the expedition undertaken by Michaelsen and Hartmeyer to South-west Australia in 1905.

The Australian distribution of the echinoderms is better known than that of any other animal group, thanks especially to the investigations of the American echinoderm specialist H. L. Clark. He has collected his own and other results in a lengthy monograph in 1946. As has already been mentioned (p. 26) he has also subdivided the Australian fauna into zoogeographical provinces, distinguishing among others a "Flindersian Province", which is to a large extent identical with the South Australian one which we are now discussing. He separates from this, however, the most south-easterly coast of New South Wales and the east coast of Tasmania; but both of these should, as far as the fauna is concerned, clearly be united with the rest of the southern region. Clark's monograph contains data on all the Australian echinoderms, their taxonomical position and distribution. On the basis of these facts it is possible to analyse the fauna also from other zoogeographical points of view, as he himself has indicated. The table below is based on a fresh compilation. It excludes the stalked crinoids which belong for the most part to the deep sea, the holothurians, whose taxonomy is in some respects still uncertain, and a number of species which Clark designates as insufficiently known. For purposes of comparison corresponding figures have also been supplied for the tropical-subtropical echinoderm fauna.

TABLE 32

ZOOGEOGRAPHICAL ANALYSIS OF THE ECHINODERM FAUNA OF AUSTRALIA (COMATULID CRINOIDS, ASTEROIDS, OPHIUROIDS AND ECHINOIDS)

	South Australia		Australian warm-water region	
	Species	Genera	Species	Genera
Total number	180	105	424	182
Endemic	140=78%	20=19%	198=46%	14=7%
Outside South Australia resp. the Australian warm-water region occurring:				
Only in the tropics or further north	33=18%	43=41%	204=49%	113=63%
Only south of the tropics	6=3%	8=8%	10=2%	8=4%
Both in the tropics and further south	1=1%	34=32%	12=3%	47=26%

The 78% of endemic species and 19% of endemic genera confirm Clark's analysis that the South Australian coastal region is sharply divided from the more northern tropical-subtropical region and is very much more sharply defined. Its general independence emerges from the figures just quoted in comparison with the corresponding

figures for the warm-water region (46 and 7 respectively), and as far as the particular position of South Australia compared with the warm-water region of Australia is concerned, only 50% of its genera have been established for both regions.

Among the species which are most characteristic for this region by reason of their common and endemic occurrence we may mention the crinoid *Ptilometra macronema*, the starfishes *Paranepanthia grandis* and *Patiriella gunnii*, the ophiuroids *Placophiothrix spongicola*, *Ophionereis schayeri* and the often brownish-black *Ophiocoma canaliculata*, as well as the sea-urchins *Amblypneustes pallidus* and *Heliocidaris erythrogramma*. Among endemic genera are the crinoid genus *Ptilometra*, the only member of the family *Ptilometridæ*; further, among the starfishes *Tosia* with four species and *Uniophora* with not less than nine species, as well as *Nectria* with four species, although a fifth one also lives in New Zealand; the ophiuroids *Conocladus* and *Astroconus* which are very closely related and together form an endemic group of six species within the family Gorgonocephalidæ. Finally, among the sea-urchins there are the genera *Amblypneustes* with six species and *Holopneustes*, *Ammotrophus* and *Eupatagus*, each with two species. The remaining 13 echinoderm genera endemic in South Australia are monotypical.

If we want to find out from which other parts of the world's ocean the South Australian shelf has received its echinoderm fauna, our analysis must proceed beyond the figures in the table. First, as far as the species are concerned, light can be shed on the origin of a considerable number of the 140 endemic species. A closer investigation, the details of which we have no space to reproduce, has shown that 52 of them belong to genera with a preponderantly tropical (possibly also more northerly) distribution and a considerably weaker representation in South Australia. A smaller number are also to be found in New Zealand, but not in any other temperate zone of the southern seas. Examples of this are *Ophiothrix* and *Echinocardium* and others. Because of the preponderantly tropical distribution of these genera it is probable that their South Australian species derive from tropical ancestors and that the same is true for their species in New Zealand, whose marine fauna on the whole clearly shows an affinity with the Australian (cf. pp. 204–5). Together with the 33 species which live exclusively in South Australia and the tropical belt, there are thus 85 species of tropical origin which occur in South Australia. A corresponding investigation of the possible affinities of the endemic species of South Australia to genera with a purely temperate distribution results in an addition of only six species to the six species mentioned in the table, which have their distribution exclusively south of the tropical belt. The sum is

therefore 12. An examination of the genera with reference to the families to which they belong shows that the group of genera of tropical origin has the total sum 72. The group of exclusively temperate genera, on the other hand, loses two of its eight genera and thus has only six genera. The final result is, therefore, that of the South Australian echinoderm fauna:

immediate† tropical origin is present in 47% of the species and 68% of the genera;
immediate temperate origin is present in 7% of the species and 6% of the genera.

The echinoderm fauna of temperate South Australia is therefore characterized partly by its pronounced independence, particularly in species, and partly also, as far as the origin of the fauna is concerned, by a strong affinity with the tropical fauna but only a weak affinity with the other temperate faunas of the South Sea (except for New Zealand).

THE TERTIARY FAUNAL AFFINITIES OF SOUTH AUSTRALIA

The above-mentioned percentages for the derivation of species and genera from tropical or temperate regions are naturally for various reasons only approximate, but they prompt the following reflections on the prehistoric zoogeographical position of South Australia.

The length of time for which the present species have had their present-day morphological shape can be determined with a certain degree of probability. We have seen earlier on that the species in so-called twin pairs on both sides of Central America (see pp. 30, 36) may be presumed to have started their divergent development at a time when the open connection between the Atlantic and Pacific in these regions was finally interrupted through the raising of the land during the early part of the Pliocene, or approximately 5–10 million years ago (cf. p. 66). Twin-species are many times more numerous among echinoderms,[148] fishes and crabs than the very few species which live in an identical or almost identical form on both sides of Central America. The time mentioned, 5–10 million years, was thus more than sufficient for the differentiation of species among these

† In the calculations made here of tropical and temperate origin we have taken into consideration for the species only the distribution of the species itself or its genus, and for the genus only their own or their family's distribution, that is to say in each case the distribution of the next higher taxonomic entity. For the sake of brevity I call this the "immediate origin". It is clear, however, that if, for example, a species belongs to a genus endemic in the temperate region and this genus in its turn is of tropical origin, the species in question is also of tropical origin, although not in respect of its nearest taxonomic member.

animal groups. The conditions with regard to the crinoids and decapod crustaceans in the Red Sea seem to indicate a time of only one to two million years as sufficient for the development of species, but appears not so conclusive as the Central American cases. On the other hand, the data for some sea-urchin species suggest a greater age[189]; for in fossil remains of 20 present-day species one is reported from the Oligocene, three from the Miocene, 11 from the Pliocene and five from the Pleistocene Period. But here we must bear in mind that the often minute morphological traits (the structure of the pedicellariæ, etc.) which constitute the characteristic features of modern species, can by no means always be observed in fossil material, so that a number of present-day names of species when applied for fossils indicates a close relationship with the modern representatives rather than a complete identity of species. In view of this, Mortensen in his great critical *Monograph of the Echinoidea* (pts. 1–4: 1), thinks that no recent species of sea-urchin can be traced to an earlier period than the Pliocene, as far as is known. The various recent species are naturally of various ages but taking into account the facts just set out, the average age of the species belonging to the animal groups in question may be put at a few million years (at the most four to six, late Pliocene to Recent time).

With regard to genera, a compilation of the palæontological data in the above-mentioned echinoid monograph shows the following facts. The number of genera described, considered by Mortensen as valid, which are to be found in Mesozoic and Tertiary deposits reaches the imposing number of 250, of which 33 survive into modern times. The oldest of the 33 is *Salenia* which reaches back as far as the Lower Cretaceous where the genus appears with 60–70 species. According to the time-scale given on p. 66 this comprises a period of roughly 100 million years. Almost as old are *Cassidulus*, *Procassidulus* and *Stereocidaris* which are found at least as early as the Upper Cretaceous, thus indicating an age of at least 70 million years. *Stereocidaris*, which with its 15 recent species belongs to the most flourishing modern echinoid genera, had many species in the Cretaceous and Eocene but is not known from later fossil deposits, an example of the incompleteness of palæontological evidence. Among genera of a somewhat later occurrence we may mention especially *Echinolampas*, which is found with a great number of species in the Eocene—an earlier and less critical account includes approximately 250 fossil species concentrated in the Eocene—and continued with a diminishing number of species into modern times, when it contains seven species. For most of the present-day genera the Miocene is, however, the earliest period ascertained. The average age expressed in million years, according to the time-scale just

mentioned, is between 35 and 40 million years for the 33 genera; in other words, the time reaching from the present to the later or middle Oligocene. Thus this may be the average age of the present-day genera. These, however, have not yet completed their existence but have a future of unknown duration.

In view of the sources of error present in calculations of this kind it is desirable to use all possibilities of control which can be devised. I have, therefore, examined the period of genera which no longer possess a future, that is to say of extinct genera, again on the basis of Mortensen's monograph. Among 200 such genera I have chosen those which possess at least 10 species which, as far as one could see, were established with certainty. 48 of these Tertiary and Mesozoic genera were shown to have a well-documented average existence of 50 million years; because of the considerable gaps in the palæontological evidence it would not be too audacious to increase the average to 60 million years, that is almost as long a period as the Cretaceous alone, or as long a time as the whole Tertiary Period. This accords well also with what we assumed above as the approximal mean age for the present-day genera, apart from their future. As we have seen above, some of them are considerably older without, however, showing any signs of senility. The age of the family is naturally higher than that of the genera. Of the 17 recent families of which fossil species are known one, the *Cidaridae*, reaches back to the Lower Carboniferous, five to the Jurassic and six to the Cretaceous.

We have shown above the close affinity of the South Australian echinoderm fauna with the tropical fauna and its considerably weaker affinity with the specific fauna of the temperate South Sea and we thus formed an opinion about its climato-geographical origin on the basis not only of the position of the species and genera, but also of the families. If we combine these results with what has been just indicated as the palæontological age of the echinoid families, we may say that with reference to the sea-urchins, and in all probability also the greater part of the South Australian shelf fauna, *a weak affinity with the rest of the temperate southern fauna and a considerably closer affinity with the tropical fauna was a characteristic feature at all geological periods from the Cretaceous inclusive.*

Here we leave the echinoderms. Our knowledge of the representation of the rest of the animal groups confirms on the whole the result of the analysis of the echinoderm fauna. Thus the independence of the region is marked by the characteristic crabs *Naxia aurita, N. spinosa, Nectocarcinus integrifrons, Leptograpsus variegatus* and so on,[32]† and Myers[368] maintains in a comprehensive survey that the

† I have not had access to Hale's more detailed work of 1927.

Australian-New Zealand fish fauna, in which the tropical element are possibly included, is characterized by a number of endemic genera and by a few distinctive families, the *Leptoscopidae*, *Odacidae*, *Patæcidae*, *Brachyonichthyidae* and *Limnichthyidae*.

The faunistic affinity of South Australia with distant shelf regions within the non-tropical South Sea is, as we have already shown, not close but may be illustrated also with examples from other groups than the echinoderms. Thus the genus *Serolis*, which is very characteristic for the antarctic and temperate regions but lives partly in deep water and forms a family on its own, has seven species on the South Australian shelf. Another example worth mentioning may be found among the fishes. The superfamily Nototheniiformes which is completely confined to the marine region south of the tropical belt, contains one family, the Bovichthyidæ, which are widely distributed in the temperate zone but is missing in the Antarctic. It possesses two purely marine species in South Australia belonging to the genus *Bovichthys*, *B. angustifrons* and *variegatus*, the latter also in New Zealand and Auckland Island, and also the anadromous river fish *Pseudaphritis urvillei*.

The penguins, too, may be regarded as true marine animals because they are dependent on a distribution by water owing to their inability to fly. Three genera are represented in South Australia, the *Eudyptes* (=*Catarrhactes*), *Pygoscelis* and *Eudyptula*. The first two are circumpolar, antiboreal and antarctic; *Eudyptula* occurs, however, only in Australia and New Zealand. The Australian *Pygoscelis* is a subspecies *tæniata* of the species *P. papua* which occurs again only at the Kerguelen Islands. *Eudyptes pachyrhynchus* and *Eudyptula minor* are said to extend along the east coast of Australia as far north as 32° to 34° S.

Finally we must mention the seals. The eared seals (family Otariidae) are represented in South Australia by the genus *Arctocephalus* (=*Callorhinus*); it has obviously immigrated from the south, since the only possible connection between the North and South Pacific distribution of this family was along the west coast of South America. The elephant seal, *Macrorhinus* (=*Mirounga*) *leoninus*, which has a circumpolar distribution, formerly inhabited Tasmania and the islands of the Bass Strait, where it is now however extinct; the southern circumpolar *Lobodon carcinophaga* (crab eater) and *Hydrurga leptonyx* (sea leopard) on the other hand, visit the South Australian coast only in the course of their migrations.

NEW ZEALAND

A glance at a map shows that the North Cape of the North Island of New Zealand lies on the same degree of latitude as the

mixed zone between the warm-water fauna of South-east Australia and the temperate fauna. The temperature figures in table 33 show that the most northern part of New Zealand, too, has about the same distinctly temperate water climate as the northern boundary zone of the South Australian fauna. It must, however, be mentioned that New Zealand extends over 13 degrees of latitude and shows fairly considerable climatic differences between north and south which should be reflected also in the fauna. This has been noted for instance with reference to the molluscs whose distribution was described by Finlay (1925), who also gave a summary of the history of the fauna. Regan[428] did the same as far as the fishes are concerned. Finlay's regional division of the mollusc fauna has since been supplemented by A. W. B. Powell.[419] According to these two investigators the distribution of the mollusc fauna justifies the following division of the New Zealand area.

1. Northern point of North Island (Aupourian Province);
2. The remaining main part of North Island and the northern part of South Island (Cookian Province);
3. Southern part of South Island together with Stuart Island (Forsterian Province);
4. Chatham Islands (Moriorian Province);
5. "Subantarctic Islands" (Auckland and Campbell Islands) and Macquarie Island (Rossian Province).

TABLE 33

TEMPERATURES OF THE COASTAL WATER OF NEW ZEALAND AND THE ISLANDS SOUTH OF NEW ZEALAND

	February surface	August surface	200 m.
New Zealand, North Cape, 34° 20′ S.	20° C.	14·5° C.	14° C.
Cook Strait, 41° 15′ S.	15·5	11	12
Chatham Island, 44° S.	16	12	9
Stuart Island, 47° S.	13	8·5	7·5
Auckland and Campbell Islands, 52–52° S.	10–11	5–6	6–6·5
Macquarie Island, 54° 49′ S.	7–8	4	5

New Zealand's coastal fauna shows clearly a high degree of independence: in animal groups which are not particularly well adapted to passive transport the endemic species seem to represent round about 60% of the total number. The fauna which seems most closely related (except that of the Chatham, Auckland and Campbell Islands) is that of South Australia. This implies also that a more secondary influence of the tropical Indo-Australian fauna is evident

but less apparent in the common stock of species as in the derivation and distribution of the genera. To this we must add a clearly established affinity with other regions of the South Sea south of the warm-water zone. A few examples from the best-known animal groups follow.

Among 88 sponges Dendy[120] was able to describe 68% as new to science; whether these are really endemic for the region is, however, very doubtful because of our incomplete knowledge of the sponges in the surrounding marine regions.

The polychæte fauna has been investigated by Augener[20] who confirmed a view already put forward by Ehlers[138] that this fauna may be classed with a temperate South Sea fauna of wide distribution and has special connections with Australia. About 24% may be regarded as endemic according to our present knowledge; in the north a not very strong tropical element must be added and, as is also the case in other marine regions, the polychætes show a greater percentage of completely or almost completely cosmopolitan species than most of the other animal groups. Thus a number of species occur off New Zealand which are well known from the North Atlantic, for instance *Hyalinoecia tubicola*, *Flabelligera affinis*, *Sternaspis scutata*, *Terebellides stroemi*.

Marcus[323, 324] draws attention to the very pronounced affinities of the Bryozoa with those of Australia and stresses the fact that New Zealand shows a closer faunistic relationship with southern South America than it is possible to find among any other group of shelf animals in two so widely separated coastal regions. In the same region of distribution which for the Bryozoa shows an unexpectedly high degree of uniformity, he includes also South Africa, Kerguelen, South Australia, the antiboreal islands south of New Zealand and even South Georgia. This accords also well with the means of transportation open to the Bryozoa since there is no animal group apart from the Hydrozoa with so large a proportion of species which normally live on the stalks of algæ or on other drifting material. The influence of the West Wind Drift has here been independent of the duration of the larval stage.

As to the decapod crustaceans, Chilton & Bennet[76] point out the independence of the crab fauna of New Zealand. About half, possibly an even greater proportion of them, are endemic. In the rest the Australian element is preponderant.

Mortensen[350] has made a compilation of all echinoderms found in New Zealand and the Auckland, Campbell and Chatham Islands, on the basis of collections made by himself and others. From New Zealand apart from the islands 114 shelf species are known. Of these 64% are endemic, 17% are known only from New Zealand

and the above-mentioned islands, 14% are also found in Australia but only 2·5% also in the Magellan region and 4·5% in the extra-Australian tropical zone or in more northerly tracts. The connection with Australia is, therefore, as far as this animal group is concerned, fairly weak and still weaker is the connection with South America, but the endemic element, on the other hand, is strong. Among species of this kind we may particularly mention *Apatopygus recens* from Cook Strait and Stewart Island which together with *A. occidentalis* from South Australia is the only survivor of the family Nucleolitidæ which occurred with many species in tropical and other seas during the Jura, Cretaceous and Tertiary Periods up to the Miocene. It may thus be in certain respects compared to the well-known reptile *Sphenodon*. Noteworthy are also *Astropecten primigenius*, the most primitive of all Astropectens, and the genus *Pseudechinus* which has developed four endemic species.

The fish fauna of New Zealand contains, according to modern taxonomy, over 100 genera.[266] In the absence of an analysis of this fauna it may be sufficient to point out here that New Zealand also has members of the above-mentioned purely antarctic-temperate superfamily Nototheniiformes, namely two species of the genus *Notothenia* and three species of *Bovichthys*. Of these five species two are endemic while the others are distributed among the temperate islands of the South Sea, southern South America, South Australia (one species) and even Kerguelen (one species). An approximately similar distribution, i.e. apart from New Zealand also in the islands south of it, off Tasmania and southern South America, is shown by *Galaxias attenuatus*, whose family also belongs exclusively to the temperate South Sea.

No less than nine penguins belong to New Zealand proper, but of these only one species, namely *Eudyptula minor*, extends north as far as North Island where it occurs as far as the North Cape. The rest are found only on the South Island including Stewart Island and Snares Island and belongs to genera with a very wide distribution in antarctic and antiboreal regions, apart from *Eudyptula* which is confined to New Zealand and South Australia.

The seals are represented in New Zealand by one *Eumetopias* species, two *Arctocephalus* species and the elephant seal, *Macrorhinus leoninus* (=*Mirounga*), which here reaches as far as the South Island and Chatham Islands. All these species live otherwise or have their nearest relatives in temperate or cold seas.

CHATHAM, AUCKLAND AND CAMPBELL ISLANDS; MACQUARIE ISLAND

These islands, including the geographically comparable Bounty or Antipodes Islands, which faunistically are almost unexplored, are often called "the Subantarctic Islands of New Zealand". This term sometimes includes the Macquarie Island which, however, from a zoogeographical point of view, occupies a different position. This island and the Auckland and Campbell Islands are climatically cold-temperate and not warm-temperate, but they are discussed here because of their more or less pronounced faunistic affinity to New Zealand.

The Chatham Islands are joined with the South Island of New Zealand by an under-water ridge less than 1000 m. deep and have the same marine climate as South Island, while New Zealand is separated from the temperate and the greatest part of tropical Australia by an abyssal region more than 4000 m. deep.

The little that is known of the coastal fauna of the Chatham Islands shows consequently a striking similarity with the coastal fauna of New Zealand.[159, 339, 350]

The fauna of the Auckland and Campbell Islands is somewhat better, but still imperfectly, known. Geologists are of the opinion that a direct connection with New Zealand must have existed in the earlier Tertiary. The islands contain a number of species which are not found off New Zealand and several of these may be truly endemic, but the fauna shows, nevertheless, a close connection with New Zealand, for instance the sponges,[65] crustaceans[76, 501] and echinoderms.[282, 350] The aptitude of the polychætes for widespread distribution is also shown here, for all species found in the Auckland and Campbell Islands live also in New Zealand. On the other hand the molluscs[217] and the higher crustaceans show a somewhat closer connection than other animal groups with the Antarctic. The important group of fishes, the Nototheniiformes, shows the following distribution of the eight species in the region of the Aucklands and Campbells, including a few catches from the fairly near-by Antipodes Islands: two endemic, three also off New Zealand, three off southern South America, two off the Macquarie Island, one near other temperate islands, one off Kerguelen and one off South Australia.

It is remarkable that the penguin genus *Megadyptes* with its single species *antipodum* is confined to the Auckland, the Campbell and Macquarie Islands and the Snares and Stewart Islands situated close to New Zealand's South Island. This comparatively small region is, accordingly, distinguished by the possession of an endemic penguin genus. As regards the fish fauna, which according to T.

Regan is mainly like that of New Zealand, this ichthyologist combined the islands mentioned above (with the possible exception of the Macquarie Island) as well as the southernmost part of South Island as an "Antipodes district". *Megadyptes* provides a further illustration of this classification.

The Macquarie Island lies a little to the north of the Antarctic Convergence and has a surface temperature of about 7° C. in the summer and 4° C. during winter. Its marine fauna is known among other sources from collections by the Australasian Antarctic Expedition. Only six echinoderm species are found there, and five of these are not known from other regions, the sixth only from New Zealand and the Auckland and Campbell Islands. The five possibly endemic species belong to genera with a wide distribution in both the antarctic and temperate regions of the South Sea. Five fish species are known from the island. Four of them are found off Kerguelen, two off the Auckland and Campbell Islands, both of them also in the Antarctic and one off Marion and Crozet Islands. These two animal groups indicate therefore a closer connection with the region of New Zealand and Kerguelen than with the antarctic mainland and, apart from that, a well-marked independence. Roughly the same may be said of the island's 15 known polychæte species,[41] which all belong to the tidal zone, as well as of the amphipod fauna,[375] of whose 16 species not less than 11 seem to be unknown from other regions, two of them representing two new genera. Among these endemic species *Pontogeneia chosroides* and *Paramœra hamiltoni*, both belonging to the family Pontogeneiidæ, occur abundantly. 30% of the 35 marine molluscs known from the island seem to be endemic and the same percentage it has in common with the Kerguelen, about 20% is in common with the Antarctis, but, as far as is known, a lesser number with New Zealand. Of the 10 isopods only one is known from another region (Antarctis). For the penguin genus *Megadyptes* see p. 207.

THE FAUNA OF PERU AND NORTHERN CHILE ("PERU FAUNA")

The temperate zone of the west coast of South America is under the influence of two factors which reduce the water temperature of the shelf zone, namely the so-called Peru or Humboldt Current and the cold upwelling water. The Peru Current is a northern branch of the West Wind Drift. This current divides into two branches at the point where it touches the southernmost part of South America. One of these branches rounds the southern tip of the continent and continues on its east coast as the Falklands Current to the north, the other, the Peru Current, immediately turns north on the west

coast, which it follows up to Point Aguja at 6° N. Here it meets a warm-water current which drives it away from the coast and thus the Peru Current merges westwards into the South Equatorial Current. Before it finally loses its cold temperature in these equatorial regions it cools down the water near the Galapagos Islands so that these islands, although they are situated on the Equator, possess a shelf fauna not wholly tropical. The temperature of the coastal water in this and the antiboreal part of South America may be seen from the following table:

TABLE 34

TEMPERATURES OF THE TEMPERATE COASTAL WATERS ALONG PACIFIC SOUTH AMERICA, ETC.[472]

	February surface	August surface	200 m.	400 m.
Callao (Lima), 12° S.	19° C.	16° C.	12° C.	—
Iquique, 20° 20′ S.	19	15·5	11	—
Juan Fernandez, 34° S.	19	14	10	—
Chiloe 43° S.	16	9·5	7·5	3° C.
Cape Horn, 55° 30′ S.	8	5	6	3–4
Falkland Islands, 51–52° S.	8·5	4·5	—	3–(4)
Patagonia, 45° S.	15	7	—	3
Off La Plata mouth, 33° S.	20	10	—	5

When discussing the tropical-subtropical fauna we found that in no other part of the world's oceans does the southern limit lie so far to the north as on the west coast of South America, where it may be placed approximately at Point Aguja or possibly even further north in the Gulf of Guayaquil on the border between Peru and Ecuador. The temperature here sinks very quickly from north to south as is apparent from the following figures;[194] they apply to June–August and are therefore not altogether comparable to the temperature for August given in the last table.

Gulf of Guayaquil, 3° S.	surface 24° C.
Cape Blanco, 4° 15′ S.	22
4° 30′ S.	17
Payta, 5° 10′ S.	17
Point Aguja, 6° S.	17
Callao, 12° S.	17
Iquique, 20° 20′ S.	16

It is very difficult to decide where the warm-temperate fauna which presumably lives on the shelf of Peru and northern Chile has its southern limit, since no part of the Pacific is so little investigated as regards to its fauna as these regions. It may even be questioned whether the temperate fauna along the west coast of South

America is divided into two fairly independent components, a warm-temperate and a cold-temperate fauna. It seems, however, probable that this is the case and that the transitional region between the two, poorly defined as it is, lies approximately north of the large island of Chiloe. From the point of view of temperature, it is perhaps possible to place here the beginning of the cold-temperate region, reckoning from the north, a fact which emerges from table 34. The distribution of the molluscs[100] and the decapod crustaceans[422] is best known. Almost half the latter seem to be endemic for the "Peru fauna". Unfortunately there is no survey of the distribution of the genera.

As has already been mentioned, upwelling is a very conspicuous feature within the Peru Coastal Current. This phenomenon does not occur everywhere within this current but mainly in four regions between 3° S. and 33° S., changing its position at different times, the most considerable upwellings, however, being fairly stable round about 5° S. and 15° S. The cold upwelling water has been found to come from a depth varying between 40 and 360 m. Just as on the south-west African coast it also occasions on the coast of South America, too, the development of abundant phytoplankton because of its wealth of mineral salts and consequently also a rich zooplankton. In winter the warm Equatorial Countercurrent turns south along the coast of Ecuador, where it is known as "El Nino", and converges with the Peru Current. During this mixing process the exceptionally rich plankton and also other animals are destroyed wholesale, the dead organic masses sinking to the bottom and undergoing decomposition. Such a condition in which a great amount of hydrogen sulphide develops which poisons the water is called aguaje or "the Callao painter" because the paint of ships is blackened. In extreme cases dead fish cover the beaches, and the guano birds flee from the region and sometimes even die because of the poisonous food they have eaten (Gunther[194]).

The *Juan Fernandez Islands* must apparently be included in the warm-temperate region although as a fairly independent appendix. The collections made by C. Skottsberg seem to indicate a strong endemic element in the fauna, for instance among the fishes approximately 50%[436]. The South American element is also considerable, the specific South American element being however not richer in species than the more general circumtemperate.

CHAPTER X

THE ANTIBOREAL FAUNAL REGIONS AND THE ANTARCTIC†

BEFORE we progress further in the zoogeographical account it is necessary to survey several aspects of the hydrography of the Southern Ocean which are important for an understanding of the zoogeographical relationships.

The hydrography of the Southern Ocean

The whole of the temperate oceanic region in the southern hemisphere and the greatest part of the antarctic oceanic region is influenced by the *West Wind Drift*. No other ocean current can compare, either in its length or its width, with this circumpolar current. It washes all temperate oceanic islands in the Southern Ocean, the southern part of South America, the south coasts of Africa and Australia and branches off into currents flowing into a northerly direction near these continents. The strongest of these currents is the Humboldt or Peru Current along the west coast of South America which is felt as far as the Equator, as already mentioned; others are the Benguela Current off the south coast of Africa, the Falklands Current off the south-east coast of South America and the currents off the south-west and south-east coasts of Australia.

The West Wind Drift does not reach quite down to the Antarctic Continent. Its coastal region and ice fringe are washed by the *East Wind Drift* which flows in an opposite direction and is also circumpolar. The boundary between the West and East Wind Drifts runs on the whole at 65° S., but between 90° W. and 120° W. it reaches down to 70° S.

Within the region of the West Wind Drift we find a demarcation line of great biological and hydrographical importance, the *Antarctic Convergence* ("Subpolarer Zusammenschluss" in the German literature). It forms the northern boundary for the antarctic surface water in that this water which in the West Wind Drift does not move straight east but inclines to the north, here sinks below the warmer and lighter so-called subantarctic water. The Antarctic Convergence is characterized therefore by a fairly sudden change in temperature

† The antiboreal islands south of New Zealand have been discussed, pp. 207–8.

in a north–southerly direction. In general the temperature of the surface water lies during the summer between 3·5° and 4·5° C. (at the Kerguelen 5° C.) and in the winter between 1° and 2° C.; the higher figures apply to where the convergence is found at 50° S. and the lower where it is at 60° S. The position of the line of convergence changes a little from time to time but the line depicted along the coast in fig. 74 may serve as a mean.[319]

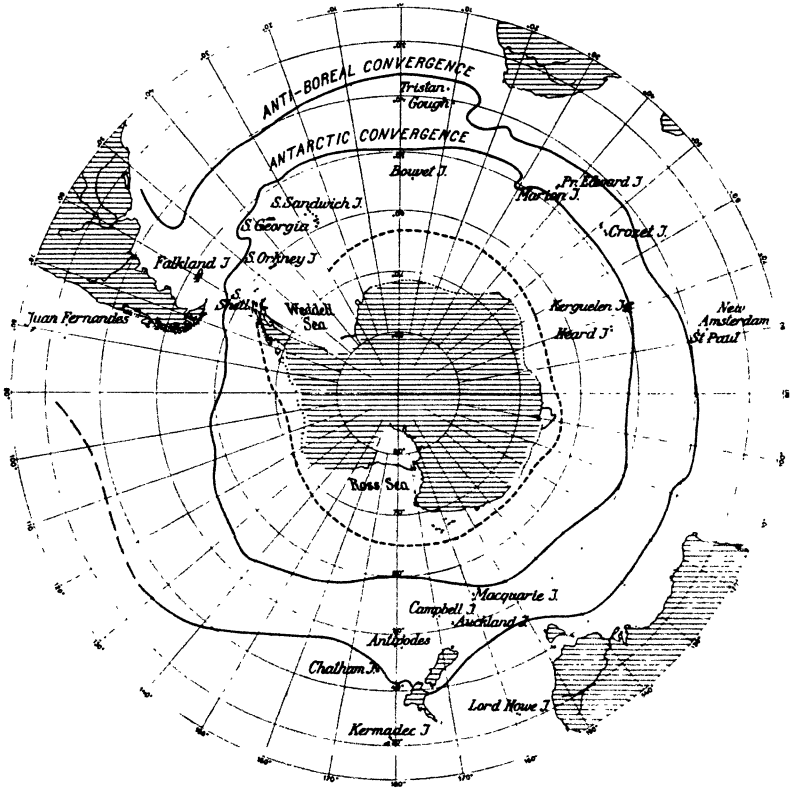


FIG. 74.—Map of the South Seas, compiled from relevant maps.

Further to the north another temperature limit is found within the temperate region which the hydrographers call the *Subtropical Convergence* (better: *Antiboreal Convergence*, see below). It runs for the most part between 38° S. and 40° S. but does not touch the continental coasts and thus does not influence their fauna. On the whole it follows the isotherms of the surface water of 14–15° C. during the summer, and 10–12° C. during winter.

The terminology used for the temperate region of the Southern Ocean is in a confused state since the terms do not correspond to those used for the equivalent regions in the northern hemisphere. Such a correspondence is much to be desired. The unsatisfactory hydrographical terminology has also influenced that of the biogeography. In the northern hemisphere a temperate zone, divided into a warm-temperate and cold-temperate belt, the latter usually called boreal, has long been distinguished between the tropical belt and the arctic region. South of the tropical belt, however, the warm-temperate region is called in hydrographical terminology subtropical ("subtropical water"), or only this region is called temperate while the cold-temperate region which lies between the warm-temperate and the antarctic is not considered to be temperate by certain hydrographers and by all of them is called subantarctic. The terms subtropical and subarctic have, however, been applied within the northern hemisphere to relatively narrow mixed or transitional zones between the tropical and warm-temperate regions and the arctic and cold-temperate regions respectively. If one starts from the correct presumption that corresponding marine regions in both hemispheres should have corresponding terms or that at least the same term should not be used for regions which do not correspond, the terminology ought to be altered. The terms used in the northern hemisphere are the older ones and must be considered as having priority. It would for instance cause well-founded opposition if the English coastal water and its fauna in conformity with the corresponding South Sea regions and faunas were called subarctic.

Consequently I shall use for the southern hemisphere instead of the hydrographer's term "subtropical water" the term *warm-temperate water*, instead of "subantarctic" the word *antiboreal* (cf. [21, 192, 146]) and thus instead of "Subtropical Convergence" the term *Antiboreal Convergence.*

Only the most southern part of South America contains a typical and wealthy antiboreal coastal fauna. From the point of view of climate, to the antiboreal zone belong also several isolated oceanic islands: Gough, Prince Edward and Marion Islands, the Crozet Islands, the Auckland and Campbell Islands and Macquarie Island, the latter however being very near the Antarctic Convergence. Kerguelen lies just in this convergence. Within the oscillatory region of the Antiboreal ("Subtropical") Convergence is situated Tristan da Cunha, St. Paul and New Amsterdam, while Chatham Island, east of New Zealand's South Island, lies within the warm-temperate belt. We shall discuss the zoogeographical conditions of some of these islands below.

ANTIBOREAL SOUTH AMERICA

It has been shown above that it is probable although not yet fully proven that the coastal fauna of antiboreal South America is fairly distinct from the warm-temperate fauna of the region to the north and that, if this proves to be the case, the boundary region between the two should be placed into the tract of Chiloe Island, or at about 40–42° S. At Tierra del Fuego the south Chilenian fauna continues immediately into the Patagonian Atlantic fauna which exhibits great similarity with the fauna of the Falklands and clearly extends some distance further to the north; how far is not known since the region between Patagonia and Rio de Janeiro is one of the world's least known regions as far as the coastal fauna is concerned. The greatest change in the fauna may possibly take place as far up at the mouth of the La Plata[72] where the temperature of the water rises extraordinarily quickly in a northerly direction. The climatic conditions of the antiboreal shelf region may be seen in table 34, p. 209.

It is also true for the Atlantic side of South America that no warm-temperate coastal fauna of an independent character has been demonstrated so far. Norman[386] places however the boundary for the "Patagonian Region" at 42° S. (i.e. six degrees south of the mouth of the La Plata).

The antiboreal South American coastal fauna has been investigated by several expeditions, especially the great South Polar expeditions at the beginning of this century, and it is now fairly well known as far as several of the animal groups are concerned. It is often called "Magellan fauna", a name which would be better reserved for a Magellan fauna which in the future may perhaps be established, for instance as a counterpart to a Falklands fauna or an Argentinian fauna.

I shall not confine myself in what follows only to the shelf (0–200 m.) but shall also include the archi-benthic region, since the greater part of the fauna of the shelf shows an inclination to descend also below this, an inclination which is more pronounced in the cold-water region of the Southern Ocean than is usually the case. As to the occurrence in abyssal regions (below 1000 m.) it may seem justified from certain points of view to exclude in surveys of regions of lesser depths those species which apart from the latter zones also occur abyssally, since such species may be supposed to possess the faculty of actively spreading across great abyssal depth and therefore are in a different position with regard to distribution than the other animals. On the other hand a species has just as much a right of being regarded as domiciled on the shelf if it has

actively immigrated there from the deep sea as if it has been passively transported to it by drifting seaweed. Partially abyssal animals, too, must therefore be reckoned in the total, but they can naturally not appear among the endemic elements of the shelf.

A compilation of echinoderm species and genera, which is as far as possible complete for the temperate and antarctic parts of the southern hemisphere, has been used for the following table, which also includes the fish fauna.

TABLE 35

GEOGRAPHICAL ANALYSIS OF THE ECHINODERM (ASTEROIDEA, OPHIUROIDEA, ECHINOIDEA) AND FISH FAUNA OF ANTIBOREAL SOUTH AMERICA

	Echinoderms		Fishes
	Species	Genera	Species
Total number	129	84	95
Endemic for temperate South America	68=52%	7=8%	73=77%
Also in the antarctic region	49†=38%	56=67%	3=3%
Also in the non-American temperate area as a whole; and others	20=16%	57=68%	19=20%
Specification for this group:			
Off Marion, St. Paul, Crozet, Tristan, or Gough Islands	16=13%	28=34%	2%
Off New Zealand or the Auckland–Campbell, Islands	4=3%	19=23%	8%
Off South Australia or Tasmania	3=2–3%	19=23%	1%
Off South Africa	6=5%	>10	1%
Also in the abyssal region	13‡=10%	47=56%	0%

First, as regards the echinoderms, we see from the table that half of the species of the region are endemic and that 38% are also found in the antarctic region. With the extra-American parts of the temperate region (the Oceanic Islands, New Zealand, South Australia and South Africa) antiboreal South America has 20 species or 16% of the total number in common, a relatively high figure considering the wide tracts of ocean which separate South America from these regions. We shall return later (p. 217) to the problem of the history of the distribution which is connected with this question.

Among species which, either because they are endemic or occur in great number, are especially characteristic of antiboreal South America we mention the asteroids *Anasterias antarctica* (end.), *A. pedicellaris* (end.) and *Cycethra verrucosa* (also in the Antarctic), the brittle-stars *Astrotoma agassizii* (also in the Antarctic and Kerguelen Island), *Gorgonocephalus chilensis* (ibidem), *Ophiomyxa*

† 12 of these also in the abyssal zone.
‡ All of these also outside South America.

vivipara (also in the Antarctic), *Ophiomitrella falklandica* (ibidem) and two species which occur in particularly great numbers, *Ophiactis asperula* (also in South Georgia) and *Ophiocten amitinum* (from South Georgia to South Africa and also in abyssal regions), and the sea-urchins *Austrocidaris canaliculata* (end.), *Arbacia dufresnii* (also in the Antarctic) and *Notechinus magellanicus* (endemic, but a variety at Gough and New Amsterdam). Among the seven endemic genera we notice *Austrocidaris* with three species, of which one however also occurs abyssally. The rest of the six endemic genera are monotypical. One of them (*Tetrapygus*) reaches, however, as far north as Peru.

The molluscs and amphipods agree fairly well with the echinoderms. Thus it was calculated in 1931 that approximately half of the amphipods of the region are endemic species[460] while roughly 15% are found also in the Antarctic and 12–13% in Kerguelen.

The fishes show however a different behaviour (see table 35). The largest number is, it is true, endemic. But it is not possible to give exact figures for this, as for other animal groups, because of the incomplete knowledge of the Pacific and Atlantic regions immediately to the north, but it seems from the list which J. R. Norman[385, 386] and Hart[209] have published on the basis of the English Discovery Expedition and material from various other expeditions, that approximately 77% of the total (95 species, after pelagic and other species not belonging to the shelf have been subtracted) are endemic, that is a somewhat higher percentage than of the echinoderms. A more important difference is that the connection with the Antarctic is weaker in that only three species (3%) are common to both regions as compared with 49 species (38%) of the echinoderms (37 species=29% if the most eurybath species are deducted). The fish fauna of antiboreal South America accordingly occupies a somewhat more independent position than the echinoderm fauna. In other words: the fishes are a little more bound to their locality than the echinoderms. Characteristic and endemic for this region are 17 species of the superfamily Nototheniiformes and two genera of the same group, of which one, *Cottoperca*, has three species, besides which eight species of the genus *Notothenia* form a natural group of the genus. This group is endemic for this part of South America, with the exception only that one of the eight also occurs at Campbell Island near New Zealand. Further, six genera of the family Zoarcidæ are endemic, among them *Austrolycus* with four, *Crossostomus* with three, *Iluocoetes* and *Maynea* with two species, and among the skates the genus *Psammobatis* (fam. Rajidæ) is characteristic of the temperate regions of Atlantic and Pacific South America. As far as the

connection with the rest of the temperate faunas is concerned, we should mention especially the family *Bovichthyidæ*, whose three marine genera (the family has, apart from this, a monotypical fresh-water genus in Australia) and 14 species belong exclusively to this marine region.

The fact that southern South America has an uninterrupted connection with the northern shelf region, and in particular the peculiar hydrographical conditions along the west coast have brought it about that its antiboreal fauna contains many elements which have relatives in the North Pacific and the Atlantic, but not in the tropical shelf region. Examples of such elements are among the fishes members of the families Zoarcidæ, Liparidæ and Scorpænidæ, among the crustaceans the genera *Lithodes* and *Paralomis* of the family Lithodidæ, and among the echinoderms *Florometra*, *Anteliaster*, *Ctenodiscus*, *Diplopteraster*, *Hippasteria*, *Echinus*. These seem to possess most of their species in the northern regions. Others, for instance the starfish genus *Solaster*, are so widely distributed in the Southern Ocean both in the Antarctic and the temperate region, that one may equally well assume a southern as a northern origin, while for *Porania*, *Bathybiaster* and *Ophiocten* a southern predominance is discernible. The genera *Henrica* and *Pteraster*, well known to European and American zoologists, are well represented in the cold southern seas but also in the deep-sea regions of the tropical zones. The connection between the faunas of the most northerly and southerly zones will occupy us when we discuss the so-called bipolarity.

THE ANTIBOREAL OCEANIC ISLANDS

Although the shelf region of these islands shows approximately the same hydrographical conditions, they do not, however, form a homogenous faunal region. The Auckland and Campbell Islands and Macquarie Island have already been discussed in connection with New Zealand, and Kerguelen, which lies just on the border of the climatically antarctic region, will be treated separately. The rest of the islands are still so insufficiently known that it is difficult to judge their zoogeographical position, with the possible exception of the Marion and Prince Edward Islands. These lie very near to each other and within the same shelf region. From them, in particular from Marion Island, we know 26 echinoderms and two fishes. Expressed as a percentage of these 28 species, the Marion group has 21% endemic species, 57% of the species are in common with Kerguelen, 39% with antiboreal South America, 32% with the Antarctic, 21% with other temperate islands, 3·6% (one species) with Macquarie Island, but no species is found to be in common with New Zealand,

the Aucklands and Campbells and none with Australia; four species are in common with South Africa, which is, of course, very much nearer.

KERGUELEN

To Kerguelen we may also add Heard Island which, though it lies 450 km. from Kerguelen, is nevertheless on the same under-water ridge of only a few hundred metres depth, and MacDonald Island which is situated between the two and serves as a connecting link for the fauna.

Kerguelen is situated right on the Antarctic Convergence, climatically speaking, therefore, on the border between the antarctic and antiboreal region. The surface temperature of the water in February and March, when it is warmest, is 5° C., in August 3° C. and in September 2° C.[319] Thus, from a climatic point of view there is no reason why the region should not be called antarctic. We shall now see what the fauna is like and in doing so we shall mainly consider the echinoderms and fishes.

Earlier investigations of the zoogeographical position of Kerguelen were confined to the fish fauna and it was lumped together not only with Heard Island, but also with Marion, Prince Edward's and Crozet Islands,[428] or even with Macquarie.[387] The result was that Kerguelen was included in the antarctic zone, although as a separate district, but this arrangement has been criticized also by ichthyologists. The distance to Kerguelen from Marion and Prince Edward Island is, however, greater, and the distance from Macquarie Island is more than three times as great as the distance from the shelf of the Antarctic Continent. It has therefore seemed to me the best course to investigate the position of Kerguelen (and Heard Island) by itself without combining it with the above-mentioned, distant islands. It seemed likewise desirable to supplement the fish fauna, which is relatively poor in species, with an animal group which is richer in species (table 36). The crinoids which inhabit the shelf suggest that the Kerguelen must be considered as an outpost of the Antarctis.[264]

As is to be expected from its isolated position, the fauna of Kerguelen consists to a large extent, approximately a half, of endemic species. Otherwise the temperate component appears relatively strong, but on this point we should take into consideration some facts which are not apparent from the table. Of the nine endemic fish species six show a closer relationship with antarctic species, while one is indifferent in this respect and only two are more closely related to more northerly types. And among the 31 echinoderm genera in both antarctic and temperate regions, five show a heavy

preponderance in the antarctic region. But it is clear that the echinoderms and fishes are not of a purely antarctic kind, nor have they, on the other hand, any clear bias towards the temperate side. It seems best, therefore, to regard Kerguelen as a transitional and mixed region. In other words: Kerguelen is *subantarctic* in the sense which brings this term into line with the term subarctic (cf. p. 101). In addition, its independence expressed by the high percentage of endemic species, must be stressed. It is considerably more marked than that of the subarctic transitional region.

TABLE 36

GEOGRAPHICAL ANALYSIS OF THE ECHINODERM FAUNA (ASTEROIDEA, OPHIUROIDEA, ECHINOIDEA) AND THE FISHES OF KERGUELEN

	Echinoderms		Fishes	
	Species	Genera	Species	Genera
Total number	69	42	15	7
Endemic	32=47%	1=2·5%	9=60%	1
Outside Kerguelen only in the antarctic region	9=13%	1=2·5%	1=7%	0
Outside Kerguelen only in the temperate region or even further north	14=20%	9†=21%	2=13%	1
Outside Kerguelen both in the antarctic and the temperate region	14=20%	31‡=74%	3=20%	5

Most of the temperate species of Kerguelen are found at one or more of the isolated islands in the antiboreal region of the Southern Ocean, particularly at Marion, Prince Edward and Crozet Islands, which are situated nearest to windward in the West Wind Drift, although at a distance of approximately 2400 and 1500 km. respectively, and have presumably contributed to the immigration of animals to Kerguelen.

Endemic in Kerguelen is the fish genus *Chænichthys* with two species. It belongs to the otherwise mainly antarctic family Chænichthyidæ, of the superfamily Nototheniiformes.

In the following surveys of the fauna of the shelf Kerguelen will therefore not be included in the antarctic region.

THE ANTARCTIC REGION

Introduction

We have seen that the border between the antarctic and the antiboreal *water* in a hydrographical sense lies in the Antarctic

† All 9 also in the tropics or even further north.
‡ Among these 18 also in the tropics or even further north.

Convergence at about 4·5° C. The zoogeographical boundary between the antarctic and antiboreal *fauna* is not necessarily this convergence, although theoretically this is probable. If we want to determine it rationally we should place it between what is the best known and most abundantly developed antiboreal fauna, that of southernmost South America, and the nearest clearly antarctic fauna, that of South Georgia. The summer temperature at Cape Horn is approximately 8° C. and that of South Georgia 3° C. It is, however, possible that South Georgia does not reach quite as far up and Cape Horn not quite as far down as the temperature limit for the antarctic fauna, and we should therefore for completeness sake compare the summer temperature of the surface water of Kerguelen, since this island, as we have found, has a nearly antarctic fauna. Its summer temperature is roughly 5° C. The temperature limit for the antarctic fauna consequently lies about 4–5° C. It is of interest to note how well the antarctic and arctic faunas agree as far as the temperatures are concerned.

With the exception of South Georgia, almost the whole of the antarctic shelf region has during the whole year a temperature of 0° C. or below in the surface layers.[471, 472] The only exceptions are the region near Bouvet Island which in the summer month of February has +1° C. at the surface, and the north-western coast of the Graham region (Bransfield Strait) which locally may have positive degrees of temperature as far down as 50 m.[89] But the South Sandwich Group and South Orkneys, too, have during February a mean temperature of 0° C., and with the exception of the Graham archipelago, the whole of the Antarctic Continent shelf has a summer temperature which falls below −1° C. The surface temperature in the Ross Sea at a latitude of 77° S. is −1·8° C. both in summer and winter. Negative temperatures are found as a rule to a depth of 200–400 m. Since the composition of species in the fauna both on the continental shelf and off the South Orkneys and the South Sandwich Group is more exclusively antarctic than near South Georgia, we are able to distinguish in the antarctic fauna a *low-antarctic* subdivision, which includes South Georgia, and a *high-antarctic* one which includes the rest of the region.[146] This high-antarctic region is substantially the Glacial District which Regan[428] postulated in view of the distribution of the fishes for the region which is situated within the extreme limit of the pack-ice. He proposed it to contrast with his Kerguelen District; but he included South Georgia in the Glacial District.

The temperature of the deeper layers of the Antarctic Sea shows a peculiarity which possibly exerts an influence on the vertical distribution of the shelf fauna. In the Weddell Sea, which we can

take as an example, the water is covered with pack-ice or drift-ice during the whole year and the surface water is colder than 0° C. and relatively of low salinity (<34·5‰). The uppermost 100 m. have a temperature of −1·7° C. But between 200–300 and 1500 m. lies an intermediate layer with positive degrees of temperature, in the Weddell Sea not warmer than 0·8° C., but in other antarctic regions up to 1·6° C. The salinity of this layer of water, which seems to come from more northern regions of the ocean, is a little higher, 34·67–34·69‰. Below this layer there is again cold water of from 0 to −0·5° C. with a salinity of 34·64–34·67‰. However, within the shelf region this stratification is absent and the water has negative degrees of temperature right to the bottom; locally the temperature may sink to −2·08° C.

It is not impossible to imagine that the warmer water of the intermediary layer may be connected with the eurybatic distribution which characterizes several species within the antarctic benthal fauna.

It is noteworthy that Antarctis is an exception among the continents in depth of the shelf, this being on an average about 400 m. close to the ice barrier[420] which in this case is often regarded as the shore.

The isolated *Bouvet Island*, 40° E. of South Georgia, lies a little further north than Cape Horn, but it lies south of the Antarctic Convergence, which hear reaches up to 50° S., and the water temperature in its neighbourhood is distinctly antarctic. Among the known species of its fauna are 12 echinoderms and three fishes. One species of each group seems to be endemic, and of the remaining 13, 12 occur also in the Antarctic and seven, apart from Bouvet Island, only there. The fauna which is known at present is thus distinctly antarctic.

The antarctic region can be delimited with more certainty from the neighbouring temperate regions than the arctic can since the antarctic shelf is not continuously connected with any temperate shelf. In those regions where the limits of the Antarctic would be expected to run there is no shelf but instead a more or less extensive abyssal region. The zoogeographer runs here no risk of drawing an artificial boundary where nature has none but only a broad mixed region. Nature itself has drawn the boundaries here with all desirable clarity. The old saying of Linné "Natura non facit saltus" finds here an exception which is not unwelcome to regional zoogeography. No other large faunal region in the world can match the Antarctic in the sharpness of its boundaries.

The composition of the fauna

This sharp delimitation is expressed also in the position of the fauna in relation to other faunas. Our knowledge of the antarctic

fauna is of course incomplete, but it is better than that which we possess of some of the other great faunal regions of the earth. Since the close of last century approximately 15 greater and lesser expeditions have worked in the antarctic regions and have brought home rich collections in spite of the exceptionally difficult natural conditions. In certain groups of animals the collection of species in the material brought home recently agrees fairly well with earlier known conditions although new species are continuously discovered. It is therefore possible to undertake an analysis of the fauna in respect to these groups without any great risks of misleading the reader.

TABLE 37

GEOGRAPHICAL ANALYSIS OF THE ANTARCTIC SHELF-FAUNA OF ECHINODERMS (ASTEROIDEA, OPHIUROIDEA, ECHINOIDEA) AND FISHES

	Echinoderms		Fishes	
	Species	Genera	Species	Genera
Total number	256	100	78	37
Endemic for the antarctic region	187=73%	27=27%	70=90%	24=65%
Also off Kerguelen but not in the tropics. . . .	23=9%	33=33%	4=5%	4=11%
Also in temperate South America but not in the tropics or further north . .	48=18%	19=19%	4=5%	6=17%
Also in the non-American temperate South Sea as a whole but not further north . .	12=5%	15=15%	4=5%	4=11%
Specification for this group:				
Off New Zealand, Auckland, Campbell or Maquarie Is.	1	5(+10)	2	1(+0)
Off other South Sea islands.	11	9(+13)	3	3(+0)
Off South Australia . .	1	1(+13)	0	?
Off South Africa . .	0	0(+6)	0	?
Also in the Tropics or even further north . . .	1	43=43%	1	6=17%
Also in the abyssal region .	31=12%	45=45%	0	8=23%

In the second and fourth column the figures in parenthesis are the figures for such genera which occur both in the southern temperate zone and the tropics or even further north.

The antarctic fish fauna contains, according to table 37, 90% endemic species and 65% endemic genera. In comparison with other zoogeographical regions these are very high figures. The same may be said of the corresponding figures of 73 and 27% for the echinoderms, although they are lower; we have already seen earlier on examples of the fact that these animals are not bound to so restricted areas as the fishes. We shall return to the rest of the figures in the table later on. Here we shall only point out the considerable number

of genera, especially among the echinoderms, which are more or less cosmopolitan with a distribution often in both tropical and more northerly regions and usually also in abyssal zones. In most cases the same genera enter into both groups, which in the table are represented by the percentages 43 and 45. Many of these genera are well known both from the North Pacific and North Atlantic, for instance *Henricia*, *Pteraster*, *Solaster*, *Amphiura*, *Ophiacantha*, *Ophiocten*, *Ophiura*, *Gorgonocephalus*. Several are distributed from the Arctic Ocean through the abyssal regions of the tropics to the Antarctic. This distribution is, however, also found in several other animal groups.

Most of the endemic genera of fishes and echinoderms are monotypical and others contain only two species, but others again are worth mentioning. Such are among fishes especially *Trematomus* with 14 and *Artedidraco* with five species, among which *T. loennbergi*, *T. scotti*, *T. bernachii* and *A. scottsbergi* have a wide distribution in

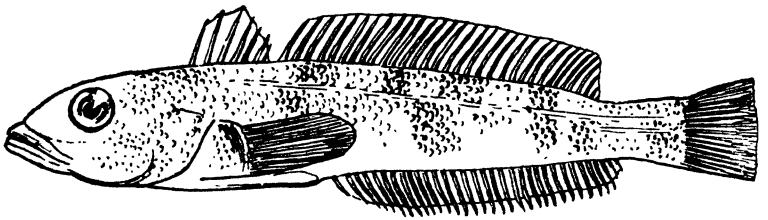


FIG. 75.—*Notothenia guntheri*, half natural size. After Y. R. Norman, in the Discovery Reports (*National Inst. of Oceanogr., London*); redrawn.

both the East and West Antarctic. *Bythydraco* has five species of which however two are abyssal, and two groups of the genus *Notothenia*, which is rich in species, are purely antarctic. The genera mentioned belong to the superfamily Nototheniiformes. We may also mention *Austrolycichthys* of the family Zoarcidæ.

More important endemic genera of echinoderms are among the starfishes, *Acodontaster*, which, however, goes a little outside this region with two of its 10 species, *Lysasterias* with six and *Notasterias* with five species; among the brittle-stars *Ophiomastus* with five to six, and among the sea-urchins *Amphipneustes* with six species. Among echinoderms not contained in table 37 we note among the shelf-dwelling unstalked crinoids the genera *Isometra* with four species and *Notocrinus*, which with its two species alone forms the family Notocrinidæ, and among the sea-cucumbers the genus *Staurocucumis* (also abyssal in northern regions).

The rest of the animal groups, for which lists have been compiled,

show in general similar examples of the great independence of the antarctic fauna. Our knowledge of certain groups is, however, still very defective; it has, for instance, been pointed out by taxonomists that for some of the groups the determination of the species in earlier faunistic lists is not sufficiently trustworthy. The examples must therefore be confined to a few groups.

Turbellaria. The antarctic turbellarian fauna is rich in peculiar and partly very primitive forms.[434] The polyclad family *Stylochoididae* is especially characteristic for the Antarctic Ocean and is unknown from more northerly regions than the Falklands.[50]

Polychæta. The facts known about polychætes in other seas show that these animals have better possibilities for distribution than most others; many species have a more extensive area of distribution than most other species of the shelf. The antarctic polychæte fauna seems, however, to consist of approximately 50% endemic species.[41]

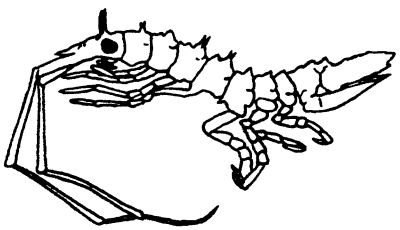


FIG. 76.—The isopod *Antarcturus franklini*, ♂, 2·4 × natural size. Distribution: Antarctis, Falkland Islands. (After Nordenstam, redrawn.)

Crustacea. Among the 63 species of amphipods which K. Stephensen[506] has lately investigated, there were only two new species and among the 41 isopods examined at the same time, only one new species. The antarctic fauna of these two groups seems now relatively well known. There are approximately 310 species of amphipods, of which 70–75% seem to be endemic; and 130 species of isopods, of which 75% are endemic. For the amphipods, Schellenberg[459] has pointed out a very noticeable difference between the northern and southern hemispheres regarding the position of the arctic and antarctic faunas compared with the boreal and antiboreal fauna. Whereas in the northern hemisphere the endemic amphipod fauna of the arctic is less rich in species than the arctic-boreal, in the southern hemisphere the conditions are reversed. This has been confirmed by later investigations.[375, 506] These conditions are fairly generally true for the antarctic and antiboreal regions; they apply, of course, to all animal groups of whose antarctic species more than 50% are endemic.

The isopod genus *Antarcturus*, although not endemic, is yet characteristic of the Antarctic in so far as it possesses there most of its shelf-dwelling species. The Antarctic contains 14 species, among which 10 are endemic; Kerguelen has three, the temperate Southern

Ocean region eight and the tropical parts of the Atlantic and Pacific eight species. All the last-mentioned belong however to the deep-sea region and the genus is not found north of the tropics. *Antarcturus* gives the impression of having originated in the antarctic and having spread from there into the temperate and tropical regions, where its newly developed species kept their original character of cold-water stenothermy.

Pycnogonida. I am indebted to Dr. J. W. Hedgpeth for the following survey of the pycnogonids. The sea spiders are extraordinarily well represented in the Antarctic. About 100 species are known from these waters, some of them, however, representing widely distributed abyssal genera. Many of the cold South Sea endemic genera are found both near the shore of the Antarctic Continent and in the Magellanic district, such as *Austrodecus*, *Austropallene* and *Austroraptus*. One of the characteristic genera of antarctic waters is *Ammothea*, represented by 13 antarctic species. The genus *Achelia* is a world-wide littoral genus, represented by several antarctic species, but rarer in the arctic regions. The most abundantly represented genus in the Antarctic, both in species and number of individuals is *Nymphon* (including *Chætonymphon*), to which 44 antarctic and antiboreal species have been referred. The most singular and characteristic aspect of the antarctic fauna is the presence of several ten-legged forms (two spp. of *Decalopoda*, two spp. of *Pentanymphon* and one *Pentapycnon*), and the enormous 12-legged *Dodecalopoda*. In only one other part of the world are such polymerous forms found, the American tropics (*Pentapycnon* from French Guiana and Porto Rico, *Pentacolossendeis* from Florida Strait).

Molluscs. Of this class, which is very rich in species and zoogeographically important, we knew in 1913 (Thiele[547]) 257 shelf species of gastropods and 79 species of lamellibranchs. Of these 93% and 79% respectively were endemic (the others in Kerguelen and the antiboreal sea). Several genera of gastropods are endemic in the Antarctic, for instance *Prosipho* with at least 20 species (five however also in Kerguelen), *Submargarita* with 10 (one in Kerguelen) and *Lævilitorina* with nine species. Among the nudibranchiats *Notæolidia* with its six species is an exclusively high-antarctic genus.[392]

Other results contained in the literature confirm the conclusion which can be reached from the results given here: that the antarctic shelf fauna in complete accordance with its sharply defined geographical limits is remarkably independent, *more independent than any other fauna of approximately the same regional dimensions*. This is true both for species and genera.

Subregions

It has already been mentioned that the antarctic region can be subdivided in a high-antarctic and a low-antarctic subregion, the latter consisting of *South Georgia* and the nearby Shag Rock Bank. Both are situated south of the Antarctic Convergence. The surface temperature of the water during the warmest time of the year (February–March) is 2 to 3° C. and during the coldest (September) −1° C.[319] In Cumberland Bay in South Georgia, where most of the zoological collections have been made, it varies in the beginning of March between 1 and 2·5° C. The 100 m. depth has between 0·5 and 1° C. and the 200 m. depth approximately 1° C. Negative temperatures can be found off the northern coast at a depth of as little as 50 m., but usually first at a depth of 100–150 m.[207, 358] The position of the fauna may be seen from table 38 which also contains comparable data from the high-antarctic province.

The table shows that the independence of the fauna of South Georgia as expressed in the percentage of endemic species is not very great, much less than in the high-antarctic province and also less than in antiboreal South American (52, respectively 77%, see table 35 on p. 215, and Kerguelen (47, or 60% respectively, see table 36 on p. 219). At the same time its affinity to the high-antarctic province is distinctly stronger. There can thus be no doubt of the antarctic nature of South Georgia also as far as the fauna is concerned. It has indeed been regarded as antarctic since Regan made it part of "the Glacial District" with respect to its fish fauna.

TABLE 38

THE ECHINODERM AND FISH FAUNAS OF SOUTH GEORGIA COMPARED WITH THE CORRESPONDING FAUNAS OF THE HIGH-ANTARCTIC PROVINCE

	South Georgia		High Antarctic	
	Echinoderms	Fishes	Echinoderms	Fishes
Total number of species	90	23	220	71
Endemic for S. Georgia, resp. the High Antarctic	19=21%	5=22%	131=60%	53=75%
Also in the High Antarctic	58=64%	16=69%		
Also in South Georgia			58=26%	16=23%
Also in antiboreal South America	29=32%	3=13%	32=15%	4=6%
Also in the abyssal zone	8=9%	0	29=13%	0

South Georgia contains a larger South American element than the high-antarctic province. The reason lies clearly in the fact that

from South Georgia and the southernmost part of South America under-water ridges extend, so that the distance between the two nearest parts of the sea floor of at the most a depth of 1000 m. is nowhere greater than approximately 400 km.[527] Nor does a greater distance divide the 1000 m. bottom within the so-called South Antilles Arc (South Sandwich Group, South Orkneys and South Shetlands) which connects South Georgia with the Antarctic Continent (Graham district). This has naturally had its influence on the antarctic invasion of South Georgia.

South Georgia has two endemic fish genera, *Psilodraco* and *Pseudochænichthys*, both monotypical and belonging to the superfamily Nototheniiformes.

In the high-antarctic region, too, it is possible to distinguish subregions namely *West Antarctic* with the Wedell Sea, Graham Land and the adjoining islands as its centre and *East Antarctic* with its centre in the Ross Sea and the regions lying to the south of Australia. According to what is known at present, both these subregions seem to have their characteristic species among the fishes[388] and other animal groups, but it remains to be seen to what degree this is due to our present incomplete knowledge of the details of distribution. Since the two subregions are in uninterrupted communication with each other and offer roughly the same climatic and hydrographical conditions, we should not expect *a priori* any great difference in the character of their fauna.

A comparison with the North Polar Sea

It was a surprise to zoologists who received the antarctic collections for examination to find the antarctic fauna so extraordinary rich in species. It is in fact by and large considerably richer in species than the one with which it is most natural to compare it, namely that of the North Polar Sea. In the comparison which we shall now undertake between the antarctic and arctic faunas we leave aside the North-west Pacific (the Sea of Okhotsk, etc.) and confine ourselves to that part which we have called above the Polar Arctic.

Table 39 contains some approximate figures for echinoderms and fishes. The latter are roughly equally numerous in both regions, but the echinoderm preponderance in the Antarctic is very significant with about five times as many species as in the Polar Arctic. The Arctic shelf, for instance, does not possess a single sea-urchin. In both these animal groups the endemic element is considerably stronger in the Antarctic, which is clearly due to the fact that its geographical isolation did not occur in the Pleistocene but took place during a remote geological period.

TABLE 39

COMPARISON BETWEEN THE ECHINODERM AND FISH FAUNA OF THE ANTARCTIC AND THE POLAR ARCTIC

	Asteroidea, Ophiuroidea, Echinoidea				Fishes			
	Species		Genera		Species		Genera	
	Antarctic	Polar Arctic	Antarctic	Polar Arctic	Antarctic	Polar Arctic	Antarctic	Polar Arctic
Total number	256	52	100	32	78	80	37	45
Endemic . .	73%	29%	27%	9%	90%	60%	65%	47%
Both in Antarctic and further north	27%		73%		10%		35%	
Both in Polar Arctic and in temperate regions .		71%		91%		40%		53%

I am not able to present figures for other animal groups, but from summary statements by specialists it is clear that gorgonarians, amphipods, isopods, pycnogonids, bryozoa, zooplankton, etc. all show a higher, partly considerably higher number of species within the Antarctic than within the Polar Arctic, although the latter is very much more fully explored than the Antarctic. An exception are the decapod crustaceans, but this group is poor in species in both regions (only 21 species in the Polar Arctic). On the other hand the Antarctic has six species of the Pterobranchia genus *Cephalodiscus* which is missing altogether north of the tropics.

If we analyse the *present* conditions for the fauna of the two regions under comparison, the quantitative preponderance of the Antarctic seems very surprising.[146, 459] The north polar region contains a greater profusion of archipelagos and therefore a very more extensive shelf surface, while the antarctic coast slopes relatively steeply down into abyssal regions. Further, the north polar region is in continuous connection with the boreal faunas along two Atlantic and two Pacific continental coasts, while the Antarctic Continent is everywhere separated from the northern shelf region by the abyssal sea.

It is noteworthy in this connection that the Antarctic possesses a greater number of species also in comparison with the antiboreal region of South America with regard to certain groups of animals, such as, for instance, the amphipods and echinoderms. According to data quoted above, the number of echinoderm species is twice as great in the Antarctic as in antiboreal South America.

It is clear that the antarctic shelf has been a centre of development for marine animals during long geological periods. A cold climate has continued without disturbance from the transition between the Cretaceous and the Tertiary Periods into recent times (Priestley & Wright). Just as the Indo-Malayan fauna is the richest tropical marine fauna in the world and lives in a region which has been exempt from any great climatic changes for longer than for instance the tropical Atlantic, so the rich antarctic marine fauna lives in a polar region which for a very long time seems to have had a constant antarctic climate. This is possibly a sufficient explanation of its wealth in species. But why the North Polar basin does not show a similarly rich fauna must be explained otherwise. One can hardly dismiss the suspicion that the North Polar Sea shelf does not present a satisfactory sample of what nature is capable of accomplishing in extremely cold conditions, when the rest of the circumstances are favourable. It is not improbable that faunistic development was arrested here. At the height of the glaciation during the Quaternary Period, when the fall in temperature was maximal, the Polar Sea must have been covered with ice further out in its peripheral parts than at present. The American and Siberian coasts which in the milder climate of our present time are for the most part covered with ice also during the summer, must have been so to an even greater extent at that time. In the opinion of most geologists we must further imagine that the under-water ridges between Scotland, the Faroes and Greenland were at the same time situated above the surface of the sea; according to a summary by G. Schott[471] presented in his great work on the Atlantic Ocean, the existence of these land bridges dates from the Miocene into the Ice Age. And since even the narrow and shallow Bering Strait was at times situated above the sea level, namely for several Tertiary and Quaternary Periods,[17] the North Polar Sea was thus almost completely shut off from the other oceans of the world for many thousands of years; at the same time the shelf region which the fauna was able to inhabit was considerably restricted. The increased glaciation was unfavourable to the development of phytoplankton and thus also to the supply of nutriment for the bottom fauna. A partial change of salt water into brackish water as a consequence of the isolation from the oceans may perhaps have caused an impoverishment of the primary fauna.[594] The possibility for development of such an isolation as the one just described consists, as we saw, mainly in the fact that the centre of the North Polar Sea coincides with the centre of polar cold and that it is delimited by land masses on the periphery. In the Antarctic, on the other hand, it is not the sea but a continent which lies in the cold centre. The shelf and archibenthal slope, it is

true, are situated on the periphery, as in the North Polar Sea, but in the Antarctic there is no mainland coast which might become an enclosing barrier. The winter ice has never lain like a lethal roof over the bottom fauna because the ice is broken in most parts of the coast annually by the storms of the Southern Ocean, and even where it remains uninterrupted it leaves beneath it free passage for the ocean currents. It is in this purely geophysical contrast and in the different histories of the two polar seas which they have for that reason experienced that we should presumably find the main explanation for their dissimilarity as regards the wealth of their faunas.

RETROSPECT OF THE SOUTHERN OCEAN SOUTH OF THE TROPICAL BELT

In the above analysis of the faunas of the Antarctic, Kerguelen and antiboreal South America it has been found that each of these three faunas shows a high degree of independence in relation to the other two. This independence is most striking in the antarctic fauna where it is demonstrated by 90% endemic species and 65% endemic genera among the fishes, and 73% endemic species and 27% endemic genera among the echinoderms. But Kerguelen, too, shows itself fairly independent with 47% endemic echinoderm species and 60% endemic species of fishes, and the same is true of antiboreal South America, where the comparable figures are 52 and 77%. The percentage of endemic genera is considerably lower for the last two regions than for the antarctic, but it is obvious from the figures in tables 35–37 that most of the echinoderm genera, which are common to all three regions or to two, are widely distributed also in the tropical belt or even north of it, usually in connection with occurrence in the abyssal region. These genera, because of their wide distribution, do not give any indication of a closer affinity of the faunas in one or the other direction. We can, therefore, affirm that the three regions in question represent three essentially independent zoogeographical regions even though this independence is more marked in the antarctic region than in the other two.

We shall now proceed to consider the temperate and antarctic regions of the Southern Ocean as an entity. In this we must in general disregard the South and South-west African shelf since the position of its sub-littoral fauna compared with the warm-water region is too little known and much the same is also true of the position of warm-temperate South America compared with the tropical region. South Australia is however included in the survey, and we shall now begin with the echinoderms.

We shall first try to determine where the greatest faunal change takes place, because its position is the most important indication for every regional zoogeography and besides it gives indications of the history of the faunas. We must first consider two main faunistic boundaries, one between the tropical and warm-temperate fauna, the other between the antiboreal and the antarctic fauna. A third boundary, too, is conceivable, namely between the warm-temperate and the cold-temperate or antiboreal fauna, but it may well be best represented off the two South American coasts, the faunas of which are at present unfortunately not sufficiently known. Nor is our knowledge of the faunas of the isolated oceanic islands anything like complete and in any case they are not sufficiently representative of their respective climatical regions. For this reason we have to place one of the two boundary regions relevant to our investigation between the tropical and the (warm) temperate region in Australia and the other between antiboreal South America and the Antarctic. Table 40† makes it clear how the four faunas stand to each other from the point of view of relationship. This is based on the distribution not only of the species but also of the genera and thus sheds light on zoogeographical conditions for the greatest part of the Tertiary Period (cf. p. 201-2).

If we imagine two faunas, a northerly and a southerly one, which adjoin each other and, owing to only inconsiderable climatic differences, possess almost similar faunas, the number of more warmth-loving species in the warmer region would be only slightly higher than in the colder region and the number of more cold-loving species in the first region only slightly lower than in the latter. But with more considerable faunistic differences in the above respect and thus with a stronger faunal change, the two regions would show greater independence of each other and the boundary between them would be of a more pronounced character. If we apply this consideration to the Australian faunal boundary in table 40, an index for the rate of the faunal chance is given for the species by the difference between 95 and 18 (=77) and between 2 and 81 (=79), and for the genera by the corresponding figures. We are therefore able to apply the following formulas: for the tropical-temperate contrast

† Every percentage figure in the table is the sum of the endemic elements and the non-endemic elements which show by their distribution that they belong more to one or the other category. But elements which do not permit such a conclusion are disregarded and do not appear in the percentage figures. The sum of the percentages is therefore less than 100. For the figures in the table represent percentages of the whole number of species and genera of the fauna in question including the indifferent elements which have been subtracted when making the estimate. It need hardly be pointed out that the figures, because of the sources of error which cannot be eliminated in such a calculation, must be only very approximate.

TABLE 40

THE CONTRAST BETWEEN THE FAUNAS ON BOTH SIDES OF THE TWO PRINCIPAL FAUNAL BOUNDARIES IN THE SOUTH SEA

	Echinoderms		Fishes	
	Species	Genera	Species	Genera
A. The boundary between the tropical northern and the warm-temperate southern fauna in Australia.†				
The index of the *northern fauna* for warm-water affinity	95%	86%		
The index of the *northern fauna* for cold-water affinity	2%	8%		
The index of the *southern fauna* for warm-water affinity	18%	60%		
The index of the *southern fauna* for cold-water affinity	81%	>30%		
B. The boundary between the antiboreal South America and Antarctic.				
The index of the *antiboreal fauna* for temperate affinity	73%	61%	97%	73%
The index of the *antiboreal fauna* for antarctic affinity	9%	19%	1%	8%
The index of the *antarctic fauna* for temperate affinity	8%	30%	1%	13%
The index of the *antarctic fauna* for antarctic affinity	82%	46%	93%	78%

† Compare table 32, p. 198 where a similar calculation is made in an almost similar way.

Echinoderm index: species 77%+79%, genera 26%+>22%; and for the antiboreal-antarctic contrast

Echinoderm index: species 65%+73%, genera 31%+27%;
Fish index: „ 96%+92%, „ 60%+70%.

The index numbers are very high for both faunal boundaries; since they are not the absolute numbers of species and genera but percentages, they are directly comparable with each other and with the highest conceivable maximum, which is 100. The strongly marked contrast in Australia is surprising, since the two faunas here stand in direct contact with each other, and have done so for long geological periods, both on the east and west coast. But this well-defined boundary is in line with the sharp contrast which we have found earlier on between the temperate and tropical North Pacific on the coast of America, with regard to both fishes and crabs. The sharp contrast between the antiboreal and antarctic faunas is also noteworthy. Table 37 (p. 222) has already shown that this contrast is considerably greater than in the corresponding boundary region in the northern hemisphere, which is also easily understandable in view of geographical circumstances. We are therefore able to state that while the northern hemisphere has only one climatical-zoogeographical main boundary within the shelf region, namely between the tropical belt and the great arctic and temperate cold-water region, the southern hemisphere has two such main boundaries, namely one between the tropical belt and the warm-temperate belt and one between the cold-temperate and the antarctic belt.

Above we have seen examples of many species and genera which are characteristic for each of the cold-water regions of the Southern Ocean. But there are, however, also a whole number of genera and even families which are characteristic for the whole of the great cold-water region as contrasted with the warm-water region to the north.

Among fishes we must point out in particular the superfamily *Nototheniiformes*, which contains many species, and is completely confined to this region; it contains five families, 32 genera and 105 species. Three families and five genera are common to the antarctic and the temperate region, among them the main genus *Notothenia* (fig. 75, p. 223). Among the approximately 215 echinoderm genera which are represented in the cold-water region roughly 44% are endemic there, while 6% are found in the northern hemisphere north of but not in the tropics, and thus 50% in the tropical regions. A number of them can, however, not be regarded as eurytherm forms since they have their main distribution further to the north and are mainly abyssal in the tropical belt (*Henricia*, etc.). Among the 44% endemic genera there are, it is true, many monotypical

genera and more than half possess at the most two species, but there are also some which are fairly prolific in species, for instance the starfishes *Anasterias* with 21, *Diplasterias* and *Perknaster* with nine species each; the brittle-stars *Ophiurolepsis* with 11 (and also one abyssal species in the tropical belt) and *Ophiosteira* with five species. Among sea-urchins we must first mention *Abatus* with 8 and *Pseudechinus* with seven species. To this must be added the echinoderm genera which have been described above as endemic for lesser regions. Special mention must be made of the fact that a whole family of starfishes, the *Ganeriidæ*, with their 21 species and five genera, among them the type genus *Ganeria* with five species, and the recently mentioned *Perknaster*, are restricted to the region (with two not certainly established exceptions) and live there throughout its whole extent apart from South Australia and New Zealand, namely in the Antarctic, southern South America, Kerguelen, Maquarie Island, Marion Island and Algoa Bay in South Africa. The generic group *Ctenocidarina* of the sea-urchin family Cidaridæ occupies an almost similar position. This group's seven genera and 19 species are confined to the region in question with the exception of two abyssal species which occur in the North Pacific.[352] Its main distribution is, in common with several of the above-mentioned examples, in the antarctic region (five genera, 13 species) and this is clearly its original home from which it spread secondarily through abyssal cold water to the north.

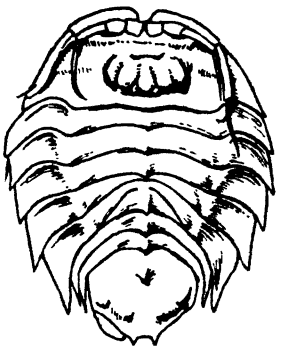


FIG. 77.—The isopod *Serolis pagenstecheri*, $1\frac{1}{5}$ × natural size. Distribution: South Georgia and the Shag Rock Bank. (After Nordenstam, redrawn.)

In other animal groups, too, we find genera and generic groups which are characteristic for the greater part of the non-tropical Southern Ocean. *Serolis* (fig. 77) is such an isopod genus. It forms the family Serolidæ on its own and contains roughly 35 species.[376a, 379, 480] It is distributed in the following regions (arranged according to the decreasing number of species of this genus found in them): Antarctic, antiboreal South America, South Australia, Kerguelen and other isolated islands in the Southern Ocean, North Pacific, North Atlantic, New Zealand and tropical Australia. Here, too, the centre of its development seems to lie far to the south and the migration to the most northerly regions took place through the abyssal regions. Much the same distribution is shown by the two genera *Antarcturus* and *Microarcturus*[204, 379, 506] which are closely

related. The former, which contains 31 species, has its centre in the Antarctic with 15 species, followed by the antiboreal South America with five species and Kerguelen with three, while Prince Edward's Island, New Zealand and South Africa possess one species each. This genus, too, shows tropical submergence, because eight species occur in the abyssal regions of the Atlantic and Pacific (500–4000 m. depth). *Microarcturus* has its 15 species distributed in the following way: six are found in South Australia, five in the Antarctic and a single species each in South America, Kerguelen, and South Africa. A similar position is occupied by the whole family Pontogeneiidæ among the amphipods; its 11 genera and 42–44 species are with the exception only of a few species, confined to the region south of the tropical belt, and all genera are exclusively or mainly found there.

The family Buccinidæ among the molluscs is well represented both in the northern and southern hemispheres in non-tropical seas, but with different genera. Characteristic for the Southern Ocean are for instance the genera *Probuxinum*, *Prosipho* and *Pareuthria* and among other mollusc groups *Modiolarca*, *Cyamium* and the cephalopod genera *Psychroteuthis* and *Crystalloteuthis*.

The penguins we have already discussed. They are very characteristic for this region. Of the 17 species the most northerly inhabit islands off South Africa, South Australia, Peru and the Galapagos, the latter group of islands being under the influence of the low temperatures produced by the Peru Current. The six genera form the family Spheniscidæ and even the order *Sphenisciformes* on their own. That a taxonomic group of this rank is confined to the colder parts of the Southern Ocean throws light in the role played by this region as a centre of development, although in this case we are not concerned with water-breathing animals.

It is well known that the physical geography and therefore also the zoogeographical relation of the Southern continents to one another has been the object of a great controversy, particularly since *A. Wegener* propounded his *continental drift theory*. According to this Australia, the Antarctic Continent and South America were still during the Eocene one continuous land mass or at least closely connected by shelf regions, and even at the beginning of the Quaternary Period (Pleistocene) Tasmania and the Antarctis were separated from each other only by a fairly narrow strait. We shall now see whether a study of the shelf fauna permits us to support one side or the other in this question.

First, as far as the position of the antiboreal fauna of South America compared with the antarctic fauna is concerned, we have seen that the abyssal region, which separates the two, is not especially

broad and their faunistic affinity can be understood without the assumption of a closer early connection between the two regions. On the other hand the faunistic dissimilarities can possibly be explained by climatic differences and need not contradict the hypothesis of a closer geographical connection during the late Tertiary Period. The zoogeographical results are thus neutral with regard to the hypothesis of a prehistoric land connection in this part of the Southern Ocean.

Among the land bridges in question, from a biogeographical point of view, the greatest interest can be claimed by the one between the Antarctic Continent and Australia; the assumption or rejection of this concerns, as is well known, also terrestrial animal and plant geography. We add the following supplement to what we have already said on p. 202. It is clear from table 37 that among the 14 echinoderm genera in the Antarctic which are also found in South Australia, only one is confined to regions south of the tropical belt, while the remaining 13 have their main distribution and most of their species north of South Australia, partly in the tropical Indo-Pacific and partly in the North Pacific (and also North Atlantic). Most of them also occur abyssally and the whole picture of the distribution of these genera seems more to indicate that they came both to the Antarctic and to South Australia from the north rather than that they reached South Australia via the Antarctic. Of all the 100 echinoderm genera in the Antarctic it is thus only one (*Cosmasterias*) which indicates a migration from there to Australia. We now turn to the South Australian 20 endemic echinoderm genera. These originated probably in such a way that species which immigrated to South Australia during the early part of the Tertiary Period later differentiated into genera (usually monotypical ones). If it was a connection with the Antarctic Continent which caused this migration one would expect that the newly formed endemic genera in South Australia would be taxonomically close to antarctic genera. But this is not the case. Of the 20 genera 16 indicate descent from tropical ancestors, while four are more indifferent in this respect; for none of them is an antarctic origin particularly probable.

At a time (Eocene or possibly later) when the Antarctic Continent according to Wegener stood in direct contact with South Australia, the regions on both sides of the contact zone must naturally have had much the same marine climate; but it is possible to object that the climate has now become so different in both that the formerly common fauna partly died out and that this might account for the present weak faunal affinity. Such an explanation appears, however, to be only a makeshift. The present-day affinities between the two faunas are too inconsiderable to be explained on those grounds.

No complete survey of the distribution of fishes has been made, but it can be said at least that the superfamily Nototheniiformes, which is more than any other group of fishes characteristic for the Southern Ocean south of the tropical belt, does not contain any genus with a distribution in Australia among its 26 genera represented in the Antarctic. The zoogeographical analysis of the shelf fauna pursued up to now seems to justify the conclusion that *the Antarctic Continent and South Australia were not connected by land or shelf with each other during the Tertiary Period.* For the term "Tertiary Period" I refer to p. 201–2.

As to the possibility of a former land or shelf connection between New Zealand and southern South America I confine myself to quoting Mortensen:[350] "Thus we need not have recourse to any former land or shallow water connection between New Zealand and South America (Patagonia) in order to explain the similarity in their Echinoderm faunas. It may rather be maintained, on the contrary, that the Echinoderm faunas of the two regions bear witness against such a former connection in post-mesozoic times."

Finally we shall survey the echinoderm fauna of the *isolated oceanic islands.*

The ecology of dispersal will serve here as main criterion and since it has been found that the species of the shelf very often also inhabit the archibenthal zone, I combine the islands which lie on the same under-water plateau of a depth of less than 1000 m. into a common region of distribution. Prince Edward, Marion and Crozet Islands thus form a common region, Kerguelen and Heard Island another, Auckland, Campbell, Chatham Islands and New Zealand a third. For the same reason under-water ridges which reach above the 1000 m. level are regarded as regions of the animal's occurrence which divide up the distance to other archibenthal regions into smaller subdistances, for instance the Meteor bank between Gough and Prince Edward Island, and Banzare bank between Kerguelen and the Antarctic. St. Paul and New Amsterdam I consider a common group because of the inconsiderable distance between them although they are separated by abyssal depth; and South Africa, too, has been discussed for those cases in which one of its species occurs exclusively within the cold region. From these assumptions I have calculated with the help of the bathymetric maps contained in G. Schott's work on the three oceans what distance across the abyssal depth (called in table 41 "Principal isolating abyssal distance") an animal species has to traverse in order to reach the island or island group from the nearest mainland, making use of the shortest possible abyssal distance, that is under the most favourable circumstances possible. A species which is found in

South America and Prince Edward group of Islands is thus considered to have taken the route across South Georgia, the mainland shelf of the Antarctic, the Banzare bank and Kerguelen, even if it is not recorded from these intermediate regions. The ability to migrate across long distances is thus certainly greater for several species than is shown in table 41, especially as the distribution shown in the table has sometimes been presumed to have taken place in other direction than the West Wind Drift. The results of these calculations are presented in table 41, in which only those islands and island groups have been included to which migration must have taken place along at least a 1300 km. long route across abyssal depth. All species mentioned occur naturally apart from the island or island group in question in at least one other region.

TABLE 41

THE DISTANCES OVER ABYSSAL DEPTHS WHICH A SPECIES MUST TRAVERSE WHEN SPREADING ALONG THE SHORTEST POSSIBLE DISTANCES FROM THE NEAREST CONTINENT TO THE ISLANDS OR GROUPS OF ISLANDS NAMED BELOW, AND THE NUMBER OF ECHINODERM SPECIES WHICH HAVE TRAVERSED THESE DISTANCES

Island or group of islands	Pr. Edward, Marion & Crozet Is.	N. Zealand region; S. Africa	Tristan & Gough Is.	Bouvet I.	St. Paul & N. Amsterdam
Principal isolating abyssal distance . . .	Crozet to Kerguelen	N. Zealand to S. Australia Pr. Edward I. to S. Africa	Meteor Bank to Agulhas B. or Pr. Edward I.	S. Sandwich Is. to Bouvet	Crozet I. to St. Paul
Length of that distance .	1350 km.	1500 km.	1700 km.	2000 km.	2400 km.
Number of echinoderm species which have traversed at least the distance just mentioned .	14	23	10	11	2

Many species of starfishes, brittle-stars and sea-urchins thus occur on isolated islands in the Southern Ocean to which migration must, under present geographical conditions, have taken place over abyssal marine regions of 1350–2400 km. in width. It does not seem probable that these islands were ever connected with each other or joined together essentially more than at present by under-water ridges at the time when the species existed in their present-day development. The continental shift which Wegener has assumed in his well-known theory, mainly concern the antarctic region and its nearest neighbours, for instance Kerguelen, Macquarie Island and Magellan region. These regions have not been included in the calculations for the table since migration to them could, even under present geographical conditions, take place over considerably smaller abyssal regions (Kerguelen 780 km., Macquarie Island 540 km., Magellan region from Graham region 520 km.). It may appear probable at the first glance that the 60 echinoderm species now under discussion could have spread to their present habitats over

abyssal stretches of the said 1300–2400 km. We shall, however, see immediately that this conclusion is not justified under all circumstances. We shall first, however, survey the possibilities of distribution.

There are in the main three ways of distribution which have to be considered. Spreading through abyssal bottom water must certainly have taken place in many cases. Some of the 60 species under discussion are found both in the abyssal region and higher up and we may safely assume, seeing that our present knowledge of the abyssal fauna of the Southern Ocean is very incomplete, that the number of such eurybate species is greater than the facts show at present. The occurrence of the genera in question also points to this. Of nearly 50 genera to which the 60 species belong, 32 are represented also by species in abyssal regions, and of these 32 10–12 are distributed also north of the tropics, usually right up to the Bering Sea, while they are missing in the tropical belt or are only represented by species which go down to abyssal depth. Among such genera are *Psilaster*, *Bathybiaster*, *Pontaster*, *Leptychaster*, *Porania*, *Solaster*, *Ophiolimna*, *Ophiocten*. The only explanation for the appearance of such genera both north and south of the tropical belt is that they have migrated through the latter in the cold deep water and the most likely assumption is that they have spread in the same manner from one island in the Southern Ocean to the other. The easiest way in which such a migration could have taken place is in the form of planktonic larvæ drifting with the deep ocean currents; active migrations of older stages is certainly imaginable, but would take many times longer and comprises a much smaller number of individuals.

Another manner of distribution which has played an important part for many species which live in shallow water is transport on drifting seaweed, etc. Its importance for the echinoderms with suckers on their feet and many other animals has been mentioned earlier and need not be further elucidated.

The third manner of distribution is drifting with surface ocean currents during the planktonic larval stage. As far as the echinoderms are concerned, Mortensen, as we have already seen (p. 73) has examined the duration of the planktonic larval stage in a great number of tropical species and has found that it varies between three and 58 days. The speed of the West Wind Drift is stated to be eight to nine sea miles (15 km.) in 24 hours. If we reckon with 10 sea miles (18·5 km.) in 24 hours and a planktonic life for an echinoderm larva of 60 days, that is a little more than the maximum as yet established, the distance traversed during the larval period is only 1110 km. and is thus less than 1350 km., which is the least distance in table 41

(p. 238). But it is possible that this may be of less significance. It is not inconceivable that the larval development of cold-water echinoderms may take a little longer than that of tropical echinoderms for which the experimentally established maximum was 58 days. It is also possible that in exceptional cases the West Wind Drift may flow with greater rapidity than 10 sea miles in 24 hours. And favourable circumstances may be of importance even though they only occur very seldom. An effective drifting of a number of larvæ every 1000th year means about 1000 such drifts during the time of existence of the species. The longer the time the greater the part played by the so-called chance factor, that is to say the interaction of unknown factors among the natural forces of so complicated a connection that human intelligence is unable to analyse it. It is therefore possible that larval drift with surface ocean currents (West Wind Drift) may have played a part for a few species of echinoderms in the colonization of oceanic islands of the Southern Ocean. For certain species of other animal groups, too, the same conclusion is valid. Among the species which, as has been said on p. 196, are common to Africa and other temperate or cold regions, there are for instance *Jasus lalandii* and *Squilla armata* whose larvæ (*Phyllosoma* and *Alima*) have an unusually prolonged pelagic life; both the *Arenicola* species, mentioned in the same connection, have a near relative (*A. cristata*) which has traversed the East Pacific between Polynesia and America; and so on.

What importance should be attributed to this means of distribution when we have to decide what the marine zoogeography of the Southern Ocean can tell us about former land connections and non-abyssal under-water ridges? The answer to this question depends not only on the ecological conditions of dispersal but also on the phylogenetic course of evolution, a fact which has not always been taken into consideration by zoogeographers who have dealt with these problems.

Two alternatives have to be taken into account.

(1) The development of closely related species from a common parent species may have taken place *by divergence*, by which the two resulting daughter species, which may in the present case be supposed to inhabit two shelf regions at a great distance from each other, differed from each other more and more so that they finally emerge as two clearly distinct species. It is for such a divergent development that the time necessary for the development of a new species may be calculated as having stretched from the later part of the Pliocene or the transition between it and the Pleistocene since the development of species on both sides of Central America, which we have given as an example (p. 200), is clearly due to divergence.

Divergent development of species in more or less isolated populations of a common parent species was in the long developmental history of the animal world clearly a very common way of origin of new species, no doubt the most common.

(2) But we must also take into account the possibility of another way in which species may originate, namely *parallel development.* It is conceivable that two populations of the same parent species which have become separated from each other earlier than we have assumed in the first alternative, for instance in the Miocene or Oligocene, have developed on parallel lines in spite of being isolated from each other, since they have lived in the same sea under the same external conditions, as may be supposed to have happened in some cases to populations in different shelf regions of the Southern Ocean. Parallel development has produced morphological identity and the two populations must therefore be regarded as belonging to the same species, but their history may be peculiar. In the earlier part of the Tertiary Period geographical conditions differed far more from present ones than at the end of the Tertiary Period, and it is thus conceivable that the recent regions of the two populations presented a common region for the populations of the mother species during the earlier Tertiary Period in spite of present-day isolation. And in spite of the identity between the two recent populations both are specifically different from the hypothetical parent species because of the long period of development. The fact that the same species lives at two isolated islands between which there exists no possible communication in the present time for the individuals of the species cannot prove in such a case that the two islands were less isolated from each other during the normal time of existence of the present-day species (end of Pliocene to present day).

It is impossible to know how often such an imaginary case of long continuing parallel phylogenetic development is realized in nature. The circumstance that identical species in the sea on both sides of Central America are so rare in comparison to twin-species shows that here divergent development was considerably more common than parallel development. But it is particularly relevant to discuss this question in connection with the zoogeography of the Southern Ocean. Of the eight species of the sea-urchin genus *Abatus* a few occur in two or more regions which are separated by abyssal depths, the rest occur only in one shelf region or in the various parts of the Antarctic Continent. *Abatus* species are brood-protecting and thus lack pelagic larval stages; and they have no suckers on their feet and thus cannot be transported by oceanic currents.[346, 347] It has therefore been assumed that their occurrence in separated regions is a proof of fairly late land

connections or under-water ridges between these regions. Here the possibility of parallel development should be taken into account. But another explanation is more probable. Several *Abatus* species are found at archibenthal depths. Their occurrence at these depths makes it not improbable that they also tolerate abyssal surroundings; the most southern abyssal regions are not so well investigated that this possibility can be rejected. Under these

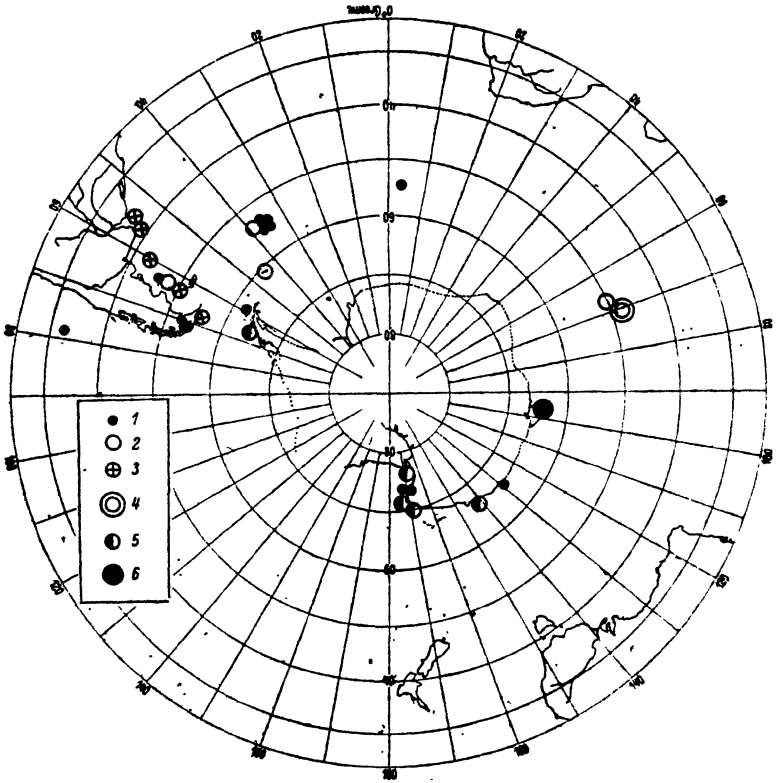


FIG. 78.—Distribution in the sea-urchin genus *Abatus:* 1. *A. cavernosus;* 2. *A. agassizi* (including *A. elongatus*); 3. *A. philippii;* 4. *A. cordatus;* 5. *A. shackletoni;* 6. *A. ingens.*

circumstances it would be precipitate to deny the possibility of a present-day communication between the different populations and to suppose that the distribution and ecology of these species proves the existence of a closer Quaternary or late Tertiary geographical connection between their present-day localities.

The final conclusion of this investigation is thus negative. Despite

the fact that a large number of echinoderms (and other animals) occur in two or more regions of the temperate or antarctic Southern ocean, regions which are separated from each other by very extensive stretches of ocean, it is not possible to draw from this the conclusion that their localities were in earlier geological periods considerably more closely connected than at present. On the other hand the same circumstances can naturally not disprove such a supposition. But as far as the theory of a Tertiary connection between the Antarctic Continent and Australia is concerned, the marine shelf and archibenthal fauna shows that such a Tertiary connection is unlikely. If it were right, Australia and Antarctic should have a greater number of *genera* in common than is the case; for this see p. 235-7. According to the theory of continental shift, as it appears on Wegener's well-known maps ([579], p. 18), Australia and the Antarctic Continent still formed a common continent during the Eocene, and contact between their shelfs was not lost until the end of the Tertiary Period. That this should have happened so late is very improbable in view of the fact that the two regions are now not only almost lacking in common species, which does not contradict the theory, but also have so very few common genera. The same is true for the fish fauna. Only one fish genus is common to Australia and the Antarctic, namely *Raja*, but this genus is of no significance for the present question because it is completely cosmopolitan and has for many species an abyssal distribution. Regan, too,[428] denies that the antarctic fishes show any indication of a connection with other continents and concludes that the Antarctic Continent has been washed for a very long time by an ocean of extremely low temperature. Wegener's most important theory, which has given such a valuable stimulus to zoogeographical investigations, ought therefore to be modified as regards the time for the connection between Australia and the Antarctic. The connection between South Africa and South America seems to be assigned to the lower Devonian, upper Carboniferous and lower Permian, Triassic, lower Cretaceous and Oligocene by supporters of the theory, whereas both continents are considered to have separated during the upper Cretaceous, in the Eocene and from the Miocene onwards.[583] We can only comment that, as far as echinoderms and marine fishes are concerned, the assumed Oligocene land connection cannot have been situated in a region of temperate marine climate. In that case it would have left behind a far greater number of common genera than do, in fact, occur.

CHAPTER XI

LONGITUDINAL DISTRIBUTION AND BIPOLARITY

LONGITUDINAL DISTRIBUTION

In the preceding chapters we have shown with the help of many examples that the species and faunas of the shelf are for the most part confined to definite climatical regions and thus their distribution in a north–southerly direction is fairly restricted. But on the west coast of Africa and America in particular several animals show a remarkably wide *longitudinal distribution.*

When discussing the West and South African faunas we noticed that some animal species are found along the east side of the Atlantic from the northern hemisphere through the tropics to the southern hemisphere. This phenomenon, respectively a longitudinal distribution of genera, also emerges from an investigation of the West American fauna, and to an even greater extent.

A good example is provided by the crab genus *Cancer* (fig. 56) which we mentioned on p. 159. The focus of its distribution lies in the North Pacific, particularly on the North American coast. On the North Asiatic coast the distribution does not extend south of Japan and on the Atlantic coast not south of Florida and the Mediterranean respectively, while in western America five species are found to extend to the northern and three other species to the southern part of the tropical belt. Five species live off the warm-temperate and antiboreal coasts of South America while only one is known from the east coast of this continent. Apart from this, one species lives off South Australia, Tasmania (possibly imported into both these parts from New Zealand), New Zealand and the Aucklands. It cannot be doubted that in this case the route of distribution between the northern and southern hemispheres lay along the east coast of the Pacific. Only an abyssal species occurs both north and south of the equator (*C. porteri*, Panama-Valparaiso).

The distribution of the crinoid genera *Promachocrinus*, *Solanometra*, *Anthometra* and *Florometra*, which formerly were combined in a common genus under the first-mentioned name, is also revealing. The three first are monotypical and occur only in the antarctic region and off Kerguelen, while *Florometra* has two species in the

Antarctic (Graham region) and apart from this inhabits the east, north and north-west coasts of the Pacific from Cape Horn to the Bering Sea and further down as far as Japan.[264] The similarity with the distribution of *Cancer* is striking (fig. 79). The great gap in the

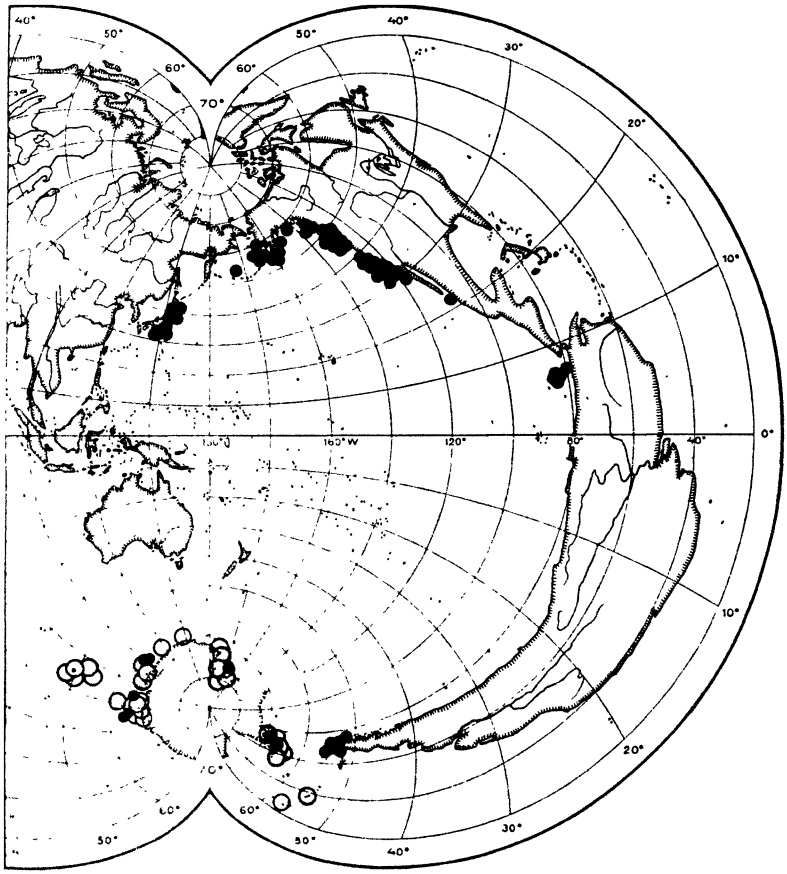


FIG. 79.—Distribution of the crinoid *Promachocrinus* group. Open circles mark finds of *Promachocrinus kerguelensis*, *Solanometra antarctica* and *Anthometra adriani*, the black circles mark the genus *Florometra*. North of the equator there are nearly 90 localities.

distribution off South America is clearly only apparent and is due to lack of investigations. This is shown by the fact that the same species, *F. magellanica*, is found both in the Magellan region, in the region of Panama and outside the entrance to the Gulf of California. These genera are not known from the Atlantic.

The starfish *Ctendiscus crispatus* is even more pronouncedly eurythermal. From the Northern Polar Sea, where it is circumpolar and is found even in high-arctic regions, it descends in Europe no further south than 60° N., in Atlantic America only to 40° N. and in North-eastern Asia to 41° N., while on the West American coast it is found in southern California, the Gulf of California, the Gulf of Panama and off the whole of the west coast of South America. In the Falklands and Argentine it is replaced by a closely related species. Very few animal species show such a degree of longitudinal distribution as *C. crispatus*. Almost the same distribution is shown by another starfish, *Ceramaster patagonicus* (Bering Sea, South Alaska, Gulf of California, Magellan region). A third example among starfishes is the genus *Pedicellaster*, whose two antarctic species, *formatus* and *antarcticus*, are closely related to the North Pacific *magister*, which inhabits the whole coastal arc Korea–Bering Sea–Washington–California with three races. The genus has another species in the Gulf of California, two species besides the one just mentioned in the Antarctic and one in South Australia, but none in the warm-water region of the Indo-West-Pacific.

Several examples of longitudinal distribution along the Pacific coast of America are to be found among fishes. Of these we must mention especially the family Zoarcidæ. This family has most of its genera and species in the northern hemisphere, but 12 genera (apart from one which is purely abyssal) occur right down in antiboreal South America or the Antarctic. Only four of these are common to both hemispheres, namely *Melanostigma* which has several of its species in northern regions up to Cape Cod and Alaska, two species in southern South America and one off South Georgia, the latter also in the North Atlantic deep water; *Lycodapus* with nine species from the Bering Sea to Lower California and one in the Magellan region; *Maynea* with one species in the Gulf of Panama, one in the Gulf of California, two in the Magellan region and one in South Georgia; and *Phucocoetes* with one species in the Gulf of California and one in the Falklands. Six genera are endemic antiboreal, viz. *Austrolycus* with four, *Crossostomus* with three, *Iluocoetes* with two, *Platea*, *Ophthalmolycus* and *Pogonolycus* each with one species. Finally, purely antarctic are the two genera *Austrolycichthys* and *Lycodichthys*, of which the first has one west-antarctic and two east-antarctic, and the latter one east-antarctic species. That the family Zoarcidæ thus only inhabits South America and the Antarctic in the southern hemisphere but not Australia, New Zealand or any of the oceanic islands is a good indication that the route followed by the distribution southwards was along the west coast of America; and that not only species but genera with one to four species have

evolved shows that the communication along this coast must have existed for a long time.

Four families of the order Cataphracti which possess numerous species in the North Pacific (Cyclopteridæ only one dozen) and a few in antiboreal South America and Antarctic may be ranged with the Zoarcidæ. The family Liparidæ has the genera *Liparis*, *Paraliparis* and *Careproctus* altogether with eight species in the Southern Ocean, three of which occur in southern South America, three in South Georgia and two in the eastern Antarctic. Each of these three genera possesses 17–18 species in the North Pacific, but all of them together have only seven species in the North Atlantic, that is hardly as many as in the antarctic and antiboreal regions. The family Agonidæ possesses one monotypical genus, *Agonopsis*, in southern Chile and the Argentine; the family Cottidæ also has one monotypical genus, *Neophrynichthys*, in the same regions while a closely related genus (*Psychrolutes*) occurs from the Puget Sound to the Aleutians. *Cyclopterichthys* of the family Cyclopteridæ has one species in southern Chile and another (syn. *Aptocyclus*) in the Sea of Okhotosk. These four families of the order Cataphracti, too, are like the family Zoarcidæ confined in the southern hemisphere to South America and the Antarctic Continent, where clearly South Georgia and the "southern Antilles arc" served as intermediary links in the passage.

Finally, the seals and eared seals, too, show a somewhat similar distribution. Among the former (family Phocidæ, sub-family Cystophorinae) this is true of the two closely related species of the genus *Macrorhinus* (the sea-elephants). The distribution of the eared seals, the genera *Arctocephalus*, *Eumetopias* and *Otaria* (fur seals and sea lions) shows, partly, a case of bipolar, rather than of longitudinal distribution. The distribution over the various continental parts of the Southern Ocean and the islands accords well with the pelagic life of these marine mammals in the interim periods between mating times.

The longitudinal distribution is clearly related to the peculiar hydrographical conditions on the coasts of Africa and South and Central America and it is, of course, on the whole confined to these two coastal regions. The influence of the Benguela Current on the temperature of the South-west African coastal waters has already been mentioned (p. 193), also the low temperatures at a depth of as little as 100 m. along the coast of tropical West Africa (fig. 20, p. 58). We may add that the temperature at 400 m. depth does not exceed 10° C. in any region of West Africa south of Cape Verde. The cooling influence of the Peru Current along the west coast of South America right up to the southern limit of the tropical region at about

6° S. has been mentioned on p. 209, as has the unusually low water temperatures even at inconsiderable depths in the shelf region of tropical West America. The annual mean temperature at a depth of 200 m. is, off the southern point of Lower California, only 10° C. and does not attain 14° C. in any part of the west coast of Central and South America.

Of the two main longitudinal routes for the benthal fauna, the West African and the West American, the latter is by far the more important. It has been used most by the fauna, since the fauna of the North Pacific is considerably richer than that of the North Atlantic. And since South America also reaches much further south than South Africa, the West American route reached right down to the Antarctic.

In those cases where the longitudinal distribution is interrupted in the tropical belt, distribution is bipolar according to the definition of this term which we shall give below. Among the above examples of fishes there is only one species which does not show such a tropical gap in distribution, namely *Melanostigma gelatinosum*. In this case neither the species nor the genus is bipolar. And to judge from what we know of the distribution of this species (p. 246) a route along the west coast of America seems not to be the only one; the communication between the northern and southern regions seems rather to occur across broader abyssal connections. In the rest of the examples bipolarity exists. The instances mentioned above show that eight bipolar fish genera have developed 16 endemic southern species and that among the five bipolar families 10 endemic southern genera have developed, which together contain 18 species. Bearing in mind the estimate given above (p. 200–2) of the mean age of the species and genera we may assume that the above-mentioned *Melanostigma* (whose position is in any case doubtful) which is common to both the northern and southern regions has spread to the region of the Southern Ocean only during the Quaternary Period, perhaps using possibilities of distribution which still exist. The 16 endemic southern species, however, must be supposed to have lived isolated from their northern relatives at least since the Pliocene and the 16 endemic southern genera since the earlier periods of the Tertiary. To what extent the fishes are typical for the fauna in general in this respect has not been investigated and we must here, as elsewhere, bear in mind that the premisses are uncertain in so far as our faunistic knowledge is incomplete. But with these reservations it seems probable that the cooling of the oceans during the glacial periods of the Quaternary Period has not greatly affected longitudinal distribution. The possibilities were clearly present even during the Tertiary Period.

EQUATORIAL SUBMERGENCE

When discussing the northern fauna we have seen already that animals which in higher latitudes live in shallow water seek in more southern regions archibenthal or purely abyssal waters (cf. chapter VI). This is a very common phenomenon and has been observed by several earlier investigators. We call it *submergence* after V. Haecker,[202] who in his studies on pelagic radiolaria drew attention to it. In most cases including those which interest us here, submergence increases towards the lower latitudes and may therefore be called *equatorial submergence.*

Submergence is simply a consequence of the animal's reaction to temperature. Cold-water animals must seek colder, deeper water layers in regions with warm surface water if they are to inhabit such regions at all. Equatorial submergence, therefore, presupposes a certain degree of stenothermy and eurybathy in the organisms in question. It is, however, possible that another factor than distribution of temperatures, namely illumination, may cause submergence. In the tropics the sun's rays fall vertically on the surface of the water at midday and therefore reach further down than in higher latitudes. Certain pelagic species have been found to be very sensitive to strong light, but for the benthic fauna the temperature is doubtless the most important factor of equatorial submergence.

Nearly all the examples of longitudinal distribution in the Pacific which are given above show such a submergence. It is a common occurrence and no further examples need be submitted. It has been discussed here because of its importance for the question of bipolarity. Together with abyssal regions the long continental communication along the Pacific coast of North and South America is the most important route of distribution between the northern and southern cold-water region for those organisms which by submerging are able to travel below the warm tropical surface water. Before true bipolarity is established we must first make sure that there are no present-day communication along these two routes.

THE CONCEPTION OF BIPOLARITY

This term should, strictly speaking, only designate the phenomenon that a species or genus etc. has as its region of distribution the two polar regions, that is the arctic and antarctic, but not the intermediate regions. This was the sense in which bipolarity was understood at first. It is, however, the discontinuity, the gap in distribution, not the arctic or antarctic distribution, which constitutes the main problem, and bipolarity has therefore, with few exceptions,

come to mean as regards distribution *a distribution spread over a region in the northern and one in the southern hemisphere with a gap in distribution between the two.* Most examples of bipolarity are actually found among the temperate and not among polar animals. The term "bipolar" is, in spite of this, scarcely misleading since the characteristic feature of this type of distribution is that it has, so to speak, been forced apart in the direction of the two poles (cf. "equatorial submergence" in the direction of the equator even if the species in question does not live in the equatorial belt itself).

In other respects, too, there is no unanimity as to the term bipolarity. Some scientists would regard as decisive not only positive but also negative characteristics and so take, for instance, the lack of common groups of species, families, etc., on the two cold-water regions as decisive for the phenomenon of bipolarity. But with such a wide conception the meaning of bipolarity might become too vague. It is more expedient to confine bipolarity to positively documented cases of similarity.

The term bipolarity need, however, not be inseparably linked with the problem of distribution. It is not even a purely biogeographical phenomenon. To avoid misunderstanding I shall give here a summary of the various kinds of bipolarity which in my view must be taken into consideration, and I will give a definition of them.

Bipolarity exists when the higher latitudes in the northern and southern hemispheres resemble one another in positive characteristics and diverge by the same characteristics from the lower latitudes situated between them. This is bipolarity in its widest meaning. It comprises both biological and non-biological phenomena, and among the biological ones also those which do not appear as discontinuity of distribution. These have also been called amphipolar.†[597] A certain discontinuity is shown in every case of bipolarity in that the tropical region interrupts the resemblance between the two surrounding zones. Within this bipolarity in its widest meaning it is possible to distinguish two subdivisions, a biological and a non-biological one, and among the former there are two kinds:

(1) *Taxonomical bipolarity with a gap in distribution.* In this case the term bipolarity is applied to taxonomic units (species, genera and so on) whose distribution is interrupted in the lower latitudes.

† Amphipolarity will be called below "the bipolarity of analogous parallel phenomena". The words bipolarity and amphipolarity mean exactly the same from the linguistic point of view. Add to this that the compound member "amphi-" according to some zoogeographers, contains the notion of discontinuity (for instance "amphi-Atlantic" instead of the more accurate "discontinuous amphi-Atlantic"), while the term "amphipolar" on the other hand is meant to exclude the idea of discontinuity. This possibly may cause confusion.

The same species occurs on both sides of the tropical belt but not within it; the same genus has various species on either side of the tropical belt but is missing in it. This is what is usually meant by bipolarity. A less pronounced case of this kind of bipolarity occurs when the gap in distribution is not quite complete, for instance when a genus has a species in the tropical belt but the majority of its species north and south of it.

(2) *The bipolarity of analogous parallel phenomena.* This kind of bipolarity may be simply characterized by saying that *it expresses itself by other features than taxonomic relationship,* for instance a greater number of individuals, greater body size, greater capacity for brood protection and so on, on both sides of the tropical belt than within it. In the typical case the similarity between the northern and southern populations is not caused by descendence from a common ancestral form but by the influence of a similar environment, particularly as regards climate. Borrowing the terminology of comparative anatomy, we may say that we are here concerned not, as in the case of taxonomical bipolarity, with homologies but with a *bipolarity of analogous phenomena.*

We shall now proceed to give some examples and in this confine ourselves to the type of bipolarity which is zoogeographically by far the most important one: taxonomic bipolarity.

EXAMPLES OF TAXONOMIC BIPOLARITY

A very large number of bipolar species and genera was described during the first years of the discussion on bipolarity. Since these two systematic categories come partly under different headings, we will treat them separately and start with the species.

A more accurate knowledge of the tropical and abyssal fauna has shown that some of the species contained in the older lists of bipolarity had to be deleted because they were found to be fairly cosmopolitan. Under these circumstances we might ask whether equatorial submergence, which has often been observed in the different taxonomic groups and animal associations, is closely connected with this question, that is whether those species which are still considered bipolar are only apparently bipolar and are in reality continuously longitudinal or cosmopolitan. Nothing definite is known in most cases. We should bear in mind the deeper shelf and the archibenthal region of the West African and West American coasts and not neglect the possibility of a communication between the northern and southern hemisphere along these coasts. We may recall two facts: firstly the low temperature to be found on the lower shelf of the tropical West African and West American regions and

secondly the fact that we must possess a very detailed knowledge of a region in order to be able to decide whether a species which is found in the northern and southern regions is in fact missing from the intermediate zone in question or whether it does not occur perhaps regularly although with only a few individuals. These circumstances counsel great caution. The west coasts of Africa and South America are still very incompletely investigated. Bipolarity seems doubtful in cases where the species belong to animal groups which are little known or if they themselves have also been found archibenthally or abyssally. The question whether bipolarity exists in purely abyssal animals is premature because of our incomplete knowledge of the abyssal fauna.

For the reasons given above we should do well to be cautious when faced with statements about bipolarity of certain species, if they are regarded by the specialists in question as not wholly unobjectionable, or if their statements give grounds for doubt. We give here a few examples.

Among Radiolaria, eight to nine species and subspecies of the Tripylea are said to be fairly certainly bipolar.[203, 410] Whether the subspecies are genotypes or possibly only phenotypes of cosmopolitan species, seems undecided, and some of the species at least are also found in abyssal depths. Equatorial submergence and continuous distribution may be suspected also for several seemingly bipolar Spumellaria and Nassellaria.[418]

The supposed examples of bipolarity among the sponges must be considered doubtful because of taxonomical difficulties[224] or because the distribution is still imperfectly known.

Among Actiniæ, the only bipolar species given is *Bolocera tuediæ*. It is, however, also found in the abyssal zone (eurybath cosmopolitan?). No bipolar species are found among hydroids; earlier surmises were found to be due to wrong determinations. There seems to be no certain example to be found among the whole group of the polychætes, which are so rich in species, although several have been mentioned. According to a more critical view[155] we may assume continuous distribution by equatorial submergence. Because of abyssal occurrence or because of too few known habitats a supposed bipolarity is also uncertain in the case of several other species, for instance several echiurids and sipunculids[496] and a number of isopods (*Paramunnopsis oceanica* and *Munnopsurus giganteus*). There are no bipolar species known among amphipods.[459]

There are several species among the molluscs which may possibly be regarded as bipolar. *Puncturella noachina*, which in northern regions does not go further south than Spain and Japan, has a subspecies in the Magellan region and another near Kerguelen. Among

opisthobranchs the only species concerned here is *Retusa truncatula* but it is considered doubtful.[392] Both the pteropods *Limacina helicina* and *Clione limacina*, which are well known to scientists investigating northern plankton, are confined to the higher latitudes but occur in the two hemispheres in separate races.[332] Among the squids we find the arctic-boreal *Rossia glaucopis*, which in the Atlantic is not found south of the Kattegatt, Ireland and South Carolina but is to be found in an identical or very closely related form in Patagonia near Magellan's Strait, and *Ommatostrephes sagittatus*, which in the north is found from the Barent Sea to the Mediterranean and in the south again occurs in the Magellan region with the race *hyndesi*.[191]

Among the crustaceans we must mention the northern and southern *Thysanoëssa gregaria* (Euphausiacea), which in the southern hemisphere is not found north of the region of the West Wind Drift, and the common northern acorn shell *Balanus balanus*, which in northern waters does not go further south than 41° N. but has long been known from New Zealand and more recently from Tierra del Fuego. Specimens from the latter locality have on examination by two experts on cirripeds been found to differ in no way from typical specimens of the boreal waters. The well-known ascidian *Botryllus schlosseri* is, apart from the North Atlantic, only known from New Zealand, and *Didemnum albidum*, which in the north is not found south of New England and northern Norway, occurs in the south also in New Zealand.

Apart from those examples among the fishes which will be given below for the genera, there are also several species mentioned by L. S. Berg,[42] for instance *Lamna cornubica*, which is found in the North Atlantic and the Mediterranean, in the North Pacific, in New Zealand, Tasmania and Australia, but is said to be missing in the tropical belt; further the two pelagic species *Stomias boa* and *Nassorhamphus ingolfianus*, possibly also the flying fish *Cypsilurus lineatus*,[67] as far as we can be certain that these fishes, which are not very frequently observed, really do not occur in the equatorial region.

Bipolarity is somewhat more common among genera and higher taxonomic groups than among species. Apart from the examples already given when discussing the fauna of South and South-west Africa and the longitudinal distribution along the extensive west coast of America, we may also point out some others.

Fig. 80 shows the distribution of two *Priapulus* species. *P. caudatus* is entirely northern, partly arctic and high arctic, and has not been reported south of Belgium, Cape Cod, the American side of the Bering Sea and northernmost Japan, while a southern species, *P. tuberculatospinosus*, inhabits the Antarctic Continent shelf and has

its most northern outposts in the Magellan region, the Falklands, South Georgia, Kerguelen, Macquarie Island and New Zealand's southern tip. These species are not found below 650 m. depth, the finds of the northern species are very numerous and the gap in distribution comprises the whole of the tropical and warm-temperate belt. Here the present-day discontinuity may be regarded as proved. The morphological position of the southern species with regard to the northern one has been investigated by Theél[542] in great detail. He found the differences between the main races small but constant and it is doubtful whether the southern form is to be regarded as a race of the northern or as an independent species. Later on, however, it was shown that the two forms are different species.[295a] Apart from these the genus contains only the arctic-boreal species *bicaudatus*, a

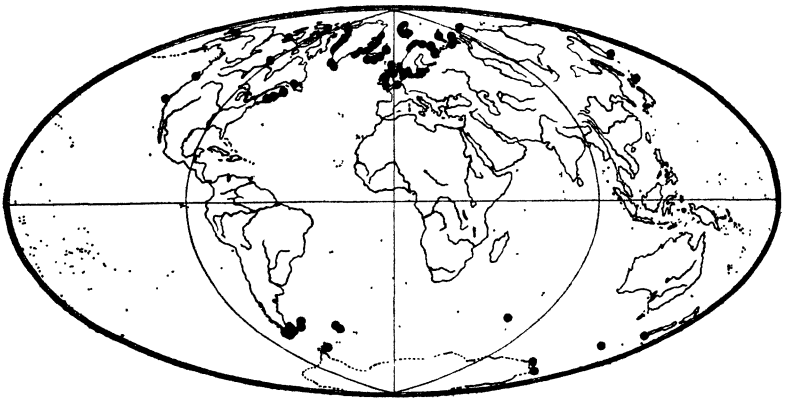


FIG. 80.—Distribution of the two closely related species *Priapulus caudatus* (in the North) and *P. tuberculatospinosus* (in the South). (After S. Ekman, 1935.)

variety of which was described in 1888 from South Shetland and Patagonia but has not been found since, and one Argentine species.

The genus *Lithodes* and possibly the whole family Lithodidæ with its 14 genera and 30 species in the North Pacific and four genera and seven to eight species in the North Atlantic both are in some degree bipolar although *Lithodes* also occurs abyssally and the family Lithodidæ also contains other abyssally occurring genera and has a species in India. It seems however improbable that these large crabs would remain unnoticed in the whole tropical belt (apart from India) if they really occurred there. *Lithodes* has, apart from its eight northern species, one species, *L. antarcticus*, in the Magellan region.

One ascidian genus may also be pointed out as bipolar: *Agnesia*,[18]

which possesses four North Pacific species off northern Japan, in the Bering Sea and off British Columbia and three species in the Southern Ocean, namely two in the Magellan region and one in antarctic Graham Land.

The whole order Lucernariida provides one of the best examples of bipolarity in that the southernmost occurrence of the northern population is off the Canary Islands and in the Mediterranean while the most northern locality of the southern population is between 40° and 50° S. off New Zealand.[292] With the exception of one other find (almost 1000 m. depth) these animals were only found within the shelf region, at least previously to 1925. Of the 10–12 genera three are found both in the northern and southern regions and it is possible to distinguish in each one of them one or two twin-pairs of a northern and a southern species. These genera are *Craterolophus*, *Haliclystus* and *Lucernaria*.

The great fish genus *Sebastodes* (including *Sebastichthys* and others), which has about 60 species in the North Pacific but is missing from the tropical belt, occurs again south of it.[42] Four species have been described from Peru, Chile, the Magellan region, the Falklands, South Africa, Tristan and Gough, but they are all so closely related that they could perhaps more correctly be regarded as the same species.[386] L. S. Berg has also drawn attention to the distribution of the genus *Engraulis* (anchovy), *Spratella* (sprats, a subgenus of *Clupea*), *Sardinops* (*Sardinia*, sardines). Whether the latter is missing in the tropical belt seems to be dependent on the definition of the sardine genera, about which the taxonomists do not agree. Both the first-mentioned genera have a discontinuous distribution with different species in the northern and southern temperate regions. Other examples are provided by the cyclostomes. This whole group is missing in the tropical belt with one exception, *Myxine circifrons* which is found in the Gulf of Panama at a depth of 1335 m. Bipolarity is, therefore, not quite proved for *Myxine*, although the genus is, with the exception of this latter species, confined to the northern parts of the Atlantic and Pacific (four to five species), southern South America (three species, one of them also in the Antarctic) and possibly also in South Africa. The genus *Bdellostoma* (Myxinidæ) has four species in the North Pacific, three off South Africa, two off Chile and one off New Zealand. The other family of the cyclostomes, the Petromyzontidæ, possesses five northern and three southern genera, the latter with eight species in southern South America, South Australia and Tasmania, and New Zealand. The Petromyzontidæ are anadromous or purely fresh-water fish, but they must have migrated by means of the sea.

The above is not a complete collection of examples (compare for

instance Derjugin[121]). The following doubtful cases may be given to illustrate the reasons for hesitation.

The amphipod genus *Haploops*, known for its existence in self-made mud-tubes, has five species in the Arctic of which three also occur boreally; it also has one species in the Mediterranean, three in the North Atlantic in abyssal regions and one off South Georgia and the Antarctic Continent. It is, however, doubtful whether this represents bipolarity, partly because of the established facts of abyssal occurrence among the species mentioned and partly because the amphipod fauna of the tropical belt is very incompletely known both as regards the abyssal and the shelf region.

Caution is also indicated as regards the possible bipolarity of the genus *Pontogeneia* and the family *Pontogeneiidæ*, since both the genus and the family for the rest also contain tropical species (two species of *Pontogeneia* in the Bermudas and Cape Verde and one species of *Bovallia* at Ceylon and the Tuamotu Islands).

Certain echinoderm genera occupy a similar position, as for instance *Porania* with four southern species (two of them in the Antarctic, and one North Atlantic species, and *Solaster* (including *Crossaster*) with five North Atlantic, 10 North Pacific and eight southern species (five of these in the Antarctic). Both genera occur also abyssally but have hitherto not been found between 35° N. and 30° S.

In the above-mentioned genera of Lucernariida and in other bipolar genera so close a relationship between the northern and southern species has been found to exist that it is possible to speak of twin-pairs. Such pairs may also be distinguished among genera with continuous north-southerly distribution. We give below a few examples of the large numbers which exist:

	Northern species	Southern species
(Hydromedusæ)	*Bougainvillia superciliaris*	*B. koellikeri*[544]
(Trachymedusæ)	*Ptychogastria polaris*	*P. opposita*[63]
,,	*Botrynema ellinorœ*	*B. brucei*[63]
(Ascidiacea)	*Cæsira bacca*	*C. crystallina*[211]
(Cephalopoda)	*Bathypolypus arcticus*	*B. valdiviæ*[191]
(Pisces)	*Myxine glutinosa*	*M. australis*[386]
,,	*Squalus acanthias*	*S. lebruni*[386]
,,	*Raja batis*	*R. flavirostris*[386]
,,	*Clupea harengus*	*C. fuegensis*[386]
,,	*Merlucius merlucius*	*M. hubbsi*[386]

Bipolarity does not exist in these cases in a species and need not necessarily exist in the genus; it does, however, exist in the twin-pair. Whether two species must be considered twin-pairs, and so as more closely related with each other than with a tropical species (if the genus possesses one), is a question which must be answered by taxonomists, yet another example of the dependence of zoogeography

on taxonomy as a basic science. The bipolarity of twin-species is in one respect of great interest. Our taxonomical experience tells us that twin-pairs are fairly common among most of the larger groups of animals, particularly if twin-races of the same species are included. There are certainly many cases of twin-pairs which are not specifically designated as such. Often an equatorial gap in distribution may be found between two twin-species or twin-races without any bipolarity being claimed for this reason, since the genus possesses other species within the equatorial region. In such cases we may speak of *masked bipolarity*. But in such a case, too, there is still bipolarity because whether the equatorial gap divides the distribution of a species, a twin-pair or a genus, etc., is naturally unimportant from the essential point of view of bipolarity.

Some scientists have denied the existence of bipolarity altogether.[133, 520] They have narrowed down the conception to apply only to the arctic and antarctic fauna, or attention has been paid mainly to the bipolarity of species. If, however, bipolarity is applied also to temperate regions and to higher taxonomic units than species, too, bipolarity is by no means a hypothesis but a fact. If, as is very often the case, a genus has various species on each side of the equatorial belt but none within it, one would have to suppose that the genus has an as yet undiscovered species in the equatorial belt in order to be able to deny the existence of bipolarity. For to deny bipolarity one would have to deny the possibility of a discontinuous north–southerly marine distribution, an untenable point of view considering the particularly numerous cases of discontinuity in the distribution of the fauna and flora as a whole.

We have seen that bipolarity may be found in animal groups of different taxonomic rank: morphologically uniform species, twin-pairs of races, twin-pairs of species, subgenera, genera and so on. In other words: the splitting off of the northern and southern populations from a common ancestral form, that is the beginning of new taxonomic types, has in the case of bipolarity taken place both during the Quaternary and the greater part of the Tertiary, possibly still earlier; which amounts to saying that the climatic and possibly also other causes which brought about the equatorial gap in distribution have been at work at various times. In cases where a species has a bipolar distribution we may assume, with Regan[429] and L. S. Berg,[42] the deterioration of the climate during the glacial period as such a cause, which, as Berg points out, had already been assumed by Darwin. But for the higher taxonomic groups we must go back still further. During the Tertiary Period we cannot assume glacial periods as a cause, but perhaps geographical changes influenced the course of the cold ocean currents or there

may have been other causes. And the more millions of years have been available for development, the greater is the chance for exceptional and favourable combinations of factors to occur; this may possibly also have played its part.

THE CAUSES OF TAXONOMIC BIPOLARITY

In the discussion of the causes of bipolarity we have one fixed point from which to start: the present discontinuity must be a secondary condition which is derived from a primary continuity.

There are in the main two attempts at an explanation. They have been called "the relict theory" and "the migration theory".

The Relict Theory of Théel, Pfeffer and Murray. It was first put forward by Théel.[541, 542] He, like most of the older scientists, confined himself to the faunas of polar latitudes and considered a present-day communication between them as unacceptable. He therefore assumed that certain species of a former cosmopolitan warm-water fauna became extinct in tropical regions for unknown reasons, thus leaving behind the northern and southern parts of these species as relicts. He considered the view (now abandoned) that at the beginning of the Tertiary a uniformly warm climate was found all over the earth as a support of his theory. Théel himself called this attempt at an explanation the relict theory.

This idea was further developed by Pfeffer[413]: in the two polar regions the same similar "relicts" remained behind. The equatorial relatives of these relicts were exterminated in the tropics either in the struggle for existence or by replacement through new forms, and thus they became dissimilar from the old universal fauna. In a slightly altered form John Murray[365] followed much the same train of thought. These relict theories are to-day mainly of historical interest. They have lost their former palæo-climatic mainstay and in other respects, too, encounter objections.

Théel, however, had postulated as early as 1886 an alternative to his theory of the extinction of the tropical population: he assumed that it could instead have developed into a new species while the northern and southern populations were arrested in their development or changed in a parallel way at a similar morphological result. This idea was purely speculative but actual cases were later discovered (p. 261).

The migration theory. The famous Polar explorer James Ross in 1847 mentions in his report on his travels in the Southern Oceans (1839–43) that he obtained animals from abyssal waters in the south which he thought he had seen on the shores of northern seas and he assumed that these animals had migrated between the two Polar seas by means of the cold abyssal regions. But a basis of established

zoological facts was first given to this migration theory by Ortmann [396-399] for the littoral and by Chun[78] for the pelagic fauna. According to Ortmann the similarity between the northern and the southern fauna is due to migrations along the coasts of the continents in a north-southerly direction and across the abyssal depths. He also ascribed great importance to these migrations at the present time and he was almost inclined to deny bipolarity, especially the bipolarity of species. This critical attitude towards the lists of bipolar species, which were formerly too liberal, was very useful. But since bipolarity was acknowledged to exist in certain rare cases, the theory of migration developed into an explanation for bipolarity. Ortmann himself admitted that an originally continuous distribution along the coast of West America may suffer an interruption and thus may become bipolar.

These two theories need not necessarily exclude one another, although they have long been regarded as incompatible. This is due to the fact already mentioned, that in the beginning the migration theory was used to deny bipolarity itself; it maintained that this was only apparent and in actual fact was a masked longitudinal distribution of eurybath species. But if one admits that longitudinal distribution in some animals took place formerly but has now ceased in the equatorial latitudes, the migration theory turns into an explanatory hypothesis for bipolarity so that we have two relict hypotheses. If, for instance, a warm-water barrier is formed in the tropical belt or another obstacle to continued communications develops after the migrations from north to south, the southern secondary region of distribution becomes isolated from the northern, and a relict formation takes place.

Bipolarity according to the above definition is thus only to be explained as the formation of relicts. But there are, as has already been mentioned, two relict theories which may be briefly characterized as follows: the original centre of distribution was, according to one theory, situated in the tropics, and according to the other in one or other of the temperate or cold regions. According to the former hypothesis we should have the somewhat peculiar occurrence that the species or genus in question possesses in recent times only relict populations but no main region of distribution. Without denying the possibility of such a situation altogether we may state that the other hypothesis is more probable for the majority of cases: a centre of development in the northern or southern hemisphere, distribution by crossing of the equatorial region to the other hemisphere and subsequent extinction in the tropical region and thus the formation of relicts.

To the examples of bipolarity already given we shall add a few

more which illustrate one of the two attempts at explanation. They also illustrate the occurrence of twin-pairs of races and species.

V. Haecker[202, 203] seems to have been the first to mention such a case. There is among the Challengeriidæ (Radiolaria) a deep-water form, *Protocystis sloggetti*, which is mainly domiciled in the equatorial oceanic regions of the Atlantic and Indian Ocean between 40° N. and 40° S. and may be caught most frequently between 400 and 1500 m. In cold seas, in the north as well as in the south, it is replaced by the distinctly bipolar *P. harstoni*, which is common in these seas and which prefers the upper layers of water, although it has also been found alive at a depth of 4000 to 5000 m. *P. harstoni* has probably developed in both the cold-water regions by adaptation to similar environmental conditions from an equatorial ancestral form, closely related to or perhaps identical with *P. slogetti*, (for the causes of this variation cf. Rensch[437] p. 182 and [531]).

Further examples of a similar taxonomical parallel development were published later. H. Lohmann[306, 311] in his studies on the antarctic plankton pointed out the development of varieties of the appendicularian *Fritillaria borealis*. This species is interesting because it is a cosmopolitan species which occurs in all warm-water regions as a certain variety (f. *sargassi*), while it occurs in both polar regions in the form which is called f. *typica*. This phenomenon is apparently to be explained in a similar manner as the development of the forms of the hydroid *Plumularia pinnata*. This species, too, is represented in the southern as well as in the northern temperate regions by the same var. *typica*, while the intermediary tropical oceanic regions contain another form (*elegantula*) characterized by smaller hydrothecæ. The same is the case in another species of the genus, *P. setacea*, and in *Lafoëa gracillima*. We are here doubtlessly confronted with the first steps in an evolutionary series which must lead to a development of bipolar species, as was stressed by Broch.[61] This naturally presupposes that these morphological changes are genotypical. Schellenberg[458] has been able to show a similar splitting off of new forms for the amphipod species *Ampelisca brevicornis* along the west coasts of Europe and Africa. A parallel case also occurs among the pelagic Foraminifera in that *Globigerina pachyderma*, characterized by its thick-walled shell, is found in the Arctic and Antarctic and cannot be separated as a separate species from the tropical *dutertrei* but is connected with it by intermediary forms (quoted from Hesse[232]). A similar explanation may, according to Michaelsen,[340, 341] be given for the position of two independent although very closely related species of ascidians, namely *Botryllo-ides leachi* and *B. nigrum*. The former occurs in the North Atlantic

(Norway to Mediterranean) as well as in the southern hemisphere off South Africa, West Australia, New Zealand and the Aucklands, while *B. nigrum* lives in the tropical part of the East and West Atlantic, the Indian Ocean and the West Pacific.

The process of development shown in the above examples may be called *bipolar taxonomic parallel development.* In this case a common parent species in the warm-water region serves as an intermediary link between the bipolar races† and species. If parallel development increases still further, the two cold-water populations will perhaps become so unlike the form which has developed by continuous evolution of the common warm-water species, that the close relationship of this form with the cold-water forms cannot be seen in their morphology. It is probable that such cases actually occur in nature. We observe how closely this process of development conforms to one of the two theories which Théel as early as 1886 had put forward as an explanation of bipolarity.

It is clear that the phenomenon of bipolarity is only one aspect of a larger problem, namely that of discontinuous distribution as a whole. This extensive zoogeographical problem has long been the subject of discussion (on the earlier history see v. Hofsten[238]). There is no fundamental difference between bipolar discontinuity and discontinuity as a whole; the former only concerns longitudinal distribution, while, for instance, the amphi-Atlantic boreal and the North Atlantic-North Pacific discontinuity concerns latitudinal distribution.

We cannot leave the problem of discontinuity without discussing the question of the polytope and polyphyletic origin of species. Some investigators have attached too much importance to it since, because of the possibility of such an origin, the postulate of a primary continuity has been thought to be unnecessary. But this is a mistake. If a species has developed newly in two different regions, the distribution is of course discontinuous and cannot be deduced from a former continuous state *for this particular species.* But this species must have developed from a parent species with a continuous distribution (cf. above-mentioned cases of taxonomic parallel development). The same is true of di- and polyphyletic origin; this too, must be traceable to a splitting off, some time previously, from a common ancestor. Nothing else has been so far proved in any case. Polytope or diphyletic development of species therefore, in the few cases where it really seems to exist, cannot dispense with the postulate of an original continuity of distribution; it only

† If the differences mentioned are only phenotypical, they naturally cannot represent the beginning of a new species. In that case they come under the heading *bipolarity of analogous forms.*

projects this postulated continuity further back into an ancient epoch.

* * *

Before we leave the question of the relationship between the shelf faunas within the non-tropical regions of the northern and southern hemispheres we should cast a brief glance at a zoogeographical phenomenon which touches upon the question of bipolarity. This is the fact that within practically every animal group having a considerable number of species there is a relatively large number of genera, and not seldom also of species, which are common to both regions and at the same time are known or assumed to be members also of the colder deep water of the tropical latitudes which lie in between. In these cases therefore no discontinuity exists, but the situation is nevertheless of interest for the question of bipolarity, since it throws light on the whole subject of faunistic communications which have existed during previous geological periods (Tertiary), and partly also exist in the geological present, between the two hemispheres. Foremost in this respect are the polychæts, which, as we have seen already, are animals with a widespread distribution. Of 101 genera found in the Antarctic (South Georgia and the Graham region) not less than 62 are also represented in the boreal fauna of Europe,[344] and the same is true for a comparatively large number of species, for instance of the following more generally known species:

Brada villosa
Flabelligera affinis
Maldane sarsi, var.
Capitella capitata
Notomastus latericeus
Scalibregma inflatum
Eunice pennata
Onuphis conchylega
Melinna cristata
Amphicteis gunneri, var.
Streblosoma bairdi, var.
Thelepus cincinnatus
Artacama proboscidea
Lysilla loveni, var.
Serpula vermicularis
Sternapsis scutata.

Most of these species occur with identical morphological development in both hemispheres, but some (designated with "var.") differ in the Antarctic in the form of varieties from the northern type-species.

In the East Antarctic, too, species of many other genera which are represented in the North Atlantic and Arctic have been found; for instance *Aricia, Scoloplos, Nereis, Lumbriconereis, Nephthys, Phyllodoce, Glycera, Syllis, Harmothoë, Lætmonice, Terebella.*[41]

Similar examples are quite common also in other animal groups. We will only mention a few here. Among molluscs we find *Saxicava, Puncturella, Nacella* and *Trophon*,[217] among amphipods *Lysianassa,*

Tryphosa, *Orchomenella*, *Ampelisca*, *Lilljeborgia*, *Epimeria*, *Jassa*[375]; among isopods *Gnathia*, *Cirolana*, *Aega*, *Limnoria*, *Munna*[204]; among decapods *Crangon* and *Munida*; among pycnogonids *Nymphon*[314]; among ascidians *Styela*, *Molgula*, *Pyura*, *Corella*, *Ascidia*, *Macroclinum*, *Amaroucium*.[18, 205] Other examples have been given previously in the discussion of longitudinal distribution and bipolarity. As an example of a species which is cosmopolitan in the fullest sense of the word we mention the solitary coral *Caryophyllia smithi*, which has been found both in the arctic, boreal and antarctic seas and possibly is also found in the intermediate abyssal regions. No morphological difference between the arctic and antarctic specimens is demonstrable.

CHAPTER XII

BOTTOM FAUNA OF THE DEEP SEA

As we pass from the fauna of the shelf to that of the deep sea we encounter a new main division of the world's fauna. It is true that the deep-sea fauna has much in common with the animal world of the upper water layers, but it is nevertheless for the most part a different world and lives under different conditions.

HISTORY OF DEEP-SEA EXPLORATION

The securing of material in deep water makes greater demands by way of vessels and apparatus than investigations in shallow water and the truly abyssal depths have been explored only by expeditions equipped with special ships. The history of the exploration of the deep sea is thus for the most part a history of expeditions. Consequently even the fact that an abyssal fauna exists has been established at a comparatively recent date.

The old conception that in the abyssal regions of the world's oceans no animals could exist seems to have derived its scientific basis from temperature measurements undertaken by Péron, who circumnavigated the world and found a progressive decrease of temperature with increasing depth. He thus drew the conclusion that the abyssal sea floor was covered with eternal ice. The well-known explorer of the marine fauna, Edward Forbes, also searched without result for an abyssal fauna in the Mediterranean (a fact probably due to local lack of oxygen) and he therefore in 1839 expressed the view that depths below 300–700 m. were void of life (azoic). Such a view seemed very plausible at the time; continuous darkness, lack of plant life and a water pressure of several hundred atmospheres were naturally considered to be extremely unfavourable for animal life.

But even earlier John Ross had collected animals from a depth of 800–1000 m. in Baffin Bay, and James Clark Ross who, together with J. Hooker, in his antarctic voyage of 1839–43 had obtained animals from the mud on the lead at a sounding of 1800 m., voiced the view that, contrary to the prevailing opinion among naturalists, the oceans of the world were inhabited even at their greatest depth. This correct opinion, however, had no influence on contemporary

science, since Ross' collection were never described and his statements therefore doubted. Deep-sea animals were first scientifically investigated and described by the Norwegian pastor and zoologist, Michael Sars, who published in 1851 a list of 13 species found on the Norwegian coast at a depth of about 550 m., which he had collected himself with the help of simple apparatus. Almost simultaneously or a short time afterwards, Bailey and Thomas Henry Huxley described foraminifera and other protozoa found in abyssal sea-floor samples which were fetched up during the laying of the telegraphic cable between Europe and America; but the ability to live abyssally thus proved was cautiously ascribed to the lowest organisms only. The idea that higher animals could not exist abyssally was still so firmly held that Wallich's assertion (1860) that he had recovered starfishes from a depth of 2220 m. was doubted and it was supposed that pelagic starfishes were caught during the winding-up of the rope. But very soon the unbelievable had to be admitted. In the year mentioned a telegraphic cable broke between Sardinia and Africa at a depth of 2160 m. and during its repair it was found that it was profusely covered with hydroids, alcyonarians, corals, worms, mussels and bryozoa, which were described by Allman and Milne-Edwards. In 1861 the Swedish Polar explorer O. Torell, by dredging between Greenland and Spitsbergen at a depth of 2500 m., caught sponges, phascolosomas, holothurians, polychætes, crustaceans and molluscs which he demonstrated in the same year to the Congress of Natural Scientists at Oslo, and after that finds of abyssal animals increased fairly rapidly. Pointing to the promising finds of M. Sars and G. O. Sars in Norway and convinced, as he said, that the promised land of the zoologist lay at the bottom of the sea, Wyville Thomson, together with W. B. Carpenter, fitted out the first special deep-sea expedition, which he led to a region north-west of Scotland on the "Lightning" in 1868. On this expedition he examined also the region of the still unexplored Wyville-Thomson Ridge, which later became so important from a zoogeographical point of view.

These expeditions and those which followed in the next few years, ("Porcupine", etc.) proved that the earlier finds of deep-sea animals were by no means exceptions and that a rich abyssal fauna exists, made up of the most divers animal groups. These expeditions were planned as trials or preliminaries for a greater deep-sea expedition.

This circumnavigation of the globe took place on board the famous "Challenger". The leader was Wyville Thomson, at whose instigation it was undertaken. This expedition is the most important and successful zoological expedition ever undertaken. It lasted three and a half years, from December, 1872, to May, 1876; more

than 1500 species of animals living below the 500 fathom line were discovered and described; a pelagic abyssal fauna was also found and the scientific results, which were collected in 50 great volumes (among them 40 zoological ones), opened up a new epoch not only with regard to the abyssal fauna, but also for zoology in general, and for oceanography.

Two other expeditions started at the beginning of this epoch. At the same time as the "Challenger" returned home a Norwegian expedition set out on the "Vöringen" to explore the Norwegian Sea for two years under the zoologist G. O. Sars. A year later (1877) Alexander Agassiz began his deep-sea explorations on the "Blake" in the Gulf of Mexico and the Caribbean Sea, which he later continued in many voyages on the "Albatros" both in the Atlantic and Pacific. Of other expeditions after the return of the "Challenger" we may mention those in the Indian Ocean (1885–1900) organized by the Asiatic Society of Bengal, which were led by A. Alcock on the "Investigator", the great German expedition on the "Valdivia" under C. Chun (1898–99) in the Atlantic, Indian and Antarctic Ocean, the French on the "Travailleur" and "Talisman", 1880–83, and that on the "Caudan" in 1895, the many and very remunerative expeditions of the Prince of Monaco, Albert I, on the "Hirondelle" and "Princesse Alice", 1892–1915, in the Mediterranean and North Atlantic, the Dutch "Siboga" expedition under M. Weber in Indo-Malayan waters 1899 and 1900, the Danish on the "Ingolf" in the Icelandic Sea and off Greenland, and later on the "Dana" in the Mediterranean and other seas, the Norwegians on the "Michael Sars" under J. Murray and J. Hjort in 1910, the John Murray Expedition in 1933–34 to the western Indian Ocean and the Swedish expedition on the "Albatros" under H. Pettersson in 1947–48. To these large expeditions must be added several smaller ones and also those to the Antarctic in which exploration of the abyssal regions played an important part.

LIMITS AND VERTICAL ZONES

It is impossible to fix at a certain depth a generally valid boundary between the deep-sea fauna and that of the shelf. In nature, this boundary is quite indistinct and consists of a mixed or transitional region. Its position must be determined by reference to the distribution of the animal species and not primarily with regard to physical conditions such as the temperature or illumination. It must not be placed at the lower limit for the distribution of certain shelf animals or the upper limit for certain deep-sea animals if it does not also coincide with the level for the greatest faunal change. This level has

only rarely been ascertained empirically. It lies at different depths in different regions (arctic and tropical ones, etc.). In general it would appear to lie between 200 and 400 m. depth. The fauna which has its main distribution below this boundary region we call deep-sea fauna. Within this fauna we can distinguish two faunistic zones, an upper zone on the slope from the outer edge of the shelf, containing the *archibenthal* fauna, and a lower zone, containing the *abyssal fauna.* The transitional region between the two is usually roughly placed at the 1000 m. level, and we have done so earlier in this book.

It must however be strongly emphasized that the drawing of a boundary around the 1000 m. depth is to a very high degree arbitrary and serves mainly practical purposes. Investigations into the position of the greatest faunal change seem not to have been undertaken and will have to wait until our knowledge of the deep-sea fauna is more complete. And it is an open question whether the boundary between the deep-sea sediments which hereafter will be called hemipelagic and eupelagic would not be a more scientific zoogeographical boundary than the 1000 m. depth level.

HYDROGRAPHY

As a rule the temperature decreases steadily with depth. The annual degree of variation, even at a depth of 200–300 m., is very slight and at greater depth almost nil. Table 42 presents in round figures the annual mean temperatures at various depths in the various climatic zones of the Atlantic.[470]

TABLE 42

TEMPERATURES AT DIFFERENT DEPTHS IN THE EASTERN ATLANTIC FROM SPITSBERGEN TO 60° S.

Depth in m.	Degrees of Latitude							
	80° N.	60° N.	40° N.	20° N.	0°	20° S.	40° S.	60° S.
0	2° C.	9° C.	16° C.	20° C.	27° C.	17° C.	15° C.	below „ 0°C.
200	2	6	12	15	15	11	10	„ 1
400	1	9	12	12	9	9	10	„ 1
800	0	8	11	8	5	5	4	„ 1
1000	below 0	7	9	6	5	4	3	„ 1
2000	−1	3	4	4	3·3	3	2	„ 0

Certain marine regions diverge from the normal type of temperature distribution, for instance the depths in the Polar regions, the Mediterranean and the Red Sea, to which we shall return later on.

The salinity varies in the abyssal zone in general between 34·5 and 35‰. In this, too, the Mediterranean and the Red Sea are different. The oxygen content is in the abyssal regions of the Atlantic generally fairly high (5–5·5 c.c. per litre), and in its northernmost parts extremely high (6–8 c.c.). In the Pacific, however, it is low, only 1–4 c.c. per litre, in the northern, equatorial and southern parts of the eastern Pacific, and at the most 0·5 c.c. per litre in the north-eastern part at a depth of approximately 700–1500 m., and only 0·2–0·3 c.c. per litre south of the Aleutians and in the southern part of the Bering Sea. The reason for this minimal oxygen content is the absence of a communication with the polar water. No arctic convergence is to be found in these regions. Further to the west the oxygen content is higher because of the undercurrent from the Sea of Okhotsk.[472] Whether this difference in oxygen content between the eastern and western North Pacific influences the abyssal fauna seems not to be known. The centre of the Indian Ocean in the equatorial region also has a markedly low oxygen content, at a depth of between 200 and 1500 m. not more than 1–1·8 c.c. per litre, at 2000–4000 m. depth a little higher (2·5–3·7 c.c. per litre).[472]

Currents, albeit very slow ones, have been found even at very great depths (>4000 m.) in the oceans. They are best known from the Atlantic.

From the report by Wüst[589] we learn the following facts: the two longitudinal depressions of the Atlantic Ocean, the western and the eastern, are filled in their depth with water which is derived from the Polar regions. It is mainly antarctic and only to a small degree arctic. In the West Atlantic antarctic influence of the bottom water may be found over more than 100 degrees of latitude, but traces of arctic influence on the sea floor may be recognized only for a distance comprising many fewer degrees. The dividing line between the two circulations lies approximately at 40–45° N. But in the bottom water of the East Atlantic depression antarctic influence is felt only up to the Walfish Ridge (22° S.) and arctic influence to 45° N.

The latest investigations have proved that abyssal conditions are not so uniform as has been formerly assumed. In the lowest stratum of the ocean especially the water is more differentiated with regard to salinity and temperature than in the stratum above. It is by no means stationary but in most of the deep-sea hollows in perceptible motion. Fluctuations in environmental conditions therefore also affect abyssal animals, both with regard to the water and the substratum. We now proceed to discuss the latter.

THE DEEP-SEA FLOOR

The many sessile species of animals which have been recorded from the deep sea show that even at great depths many localities possess a hard substratum. Very often it probably only consists of the shells of molluscs, etc., but there are doubtless also submarine mountain ridges which have remained uncovered because the deep-sea currents prevent their being covered with sediment. Very little is known, however, about the distribution and constitution of such hard bottoms. But the majority of benthal deep-sea animals, especially those which are truly abyssal, consists of the so-called mud fauna. Soft bottoms occupy by far the largest part of the abyssal and archibenthal regions (fig. 81).

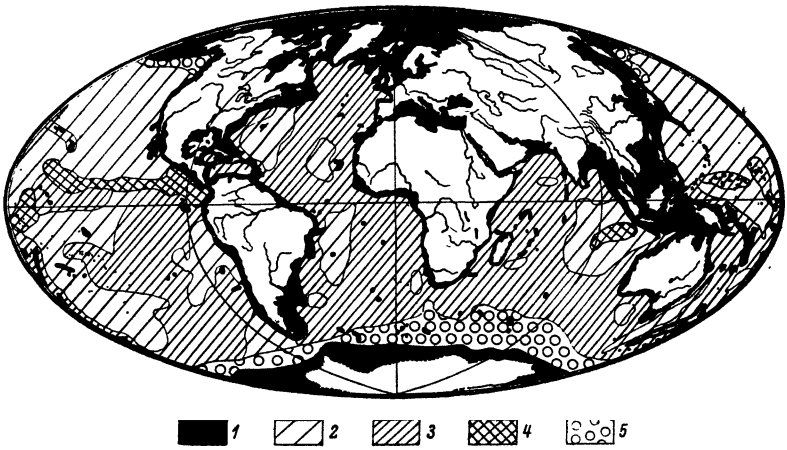


FIG. 81.—Distribution of the most important sediments of the oceans: 1. terrigenous deposits (including calcareous ooze around the coral reefs); 2. red clay; 3. Globigerina ooze (including pteropod ooze); 4. radiolarian ooze; 5. diatom ooze. (After Andrée, 1920, simplified.)

In general, marine sediments are divided into two main groups: terrigenous and pelagic, where terrigenous designates all near-shore, and pelagic all far-distant sediments. But also the terrigenous deposits are derived to a great extent from the zoo- and phytoplankton of the seawater. Andreé[7] gave a different classification of sediments into littoral, hemipelagic and eupelagic (high oceanic) ("littoral"= here on the shelf). The far-distant or eupelagic sediments (globigerina ooze, etc.) are mainly deposited by pelagic organisms, but they are also to some extent formed by fragments of or skeletal parts of bathybenthic animals, for instance spines of echinoderms, benthic foraminfera, etc. From a zoogeographical point of view we

are not so much interested in the genesis of the sediments as in their nutritional content. As a rule this diminishes from the coasts towards the open sea and for zoogeographical purposes it is therefore possible to employ a purely regional division into near-shore and far-distant sediments. We thus adopt Andrée's division into hemipelagic and eupelagic sediments.

The Hemipelagic sediments

Hemipelagic sediments are characterized by a remarkably high content of terrigenous mineral material. This is obviously of importance to burrowing deep-sea animals, the content of terrigeneous material being coincidental with a high proportion of organic material (detritus) which is derived partly from the terrestrial fauna and flora and partly from the fauna and flora of the shelf. Since, as we shall find when discussing the plankton, the coastal plankton is many times richer than the plankton of the open seas, and since the remains of dead algæ and shelf animals are carried out in profusion into the archibenthal and partly also into the abyssal zone, the nutritional conditions in near-shore sediments are generally satisfactory. Organic detritus is present in great amounts and forms the main food for the near-shore deep-sea animals which are not predatory, whether it is swallowed already sedimented by mud-eaters, or caught by seston feeders while still suspended. The naturally vague dividing line between the near-shore sediments which are rich in nutritional material and the poorer eupelagic sediments probably coincides with that between hemipelagic and eupelagic (high-oceanic) sediments. It must be noted that this dividing line does not coincide with the 1000 m. level; it lies deeper, with few exceptions (for instance in the region of Zanzibar).

The Eupelagic sediments

By far the greater part of the ocean floor is occupied by these sediments (according to the usual estimate fully three-quarters). They will be briefly discussed here because of their great importance for the abyssal fauna. Sir John Murray, together with A. F. Renard, worked on the floor-samples from the "Challenger" Expedition[367] and thus opened up a fruitful field of enquiry.

The *globigerina ooze* occupies very extensive regions, in the Atlantic more than half the surface of the sea floor. It was named after the globigerinas, mostly pelagic foraminifera of the genera *Globigerina, Orbulina, Hastigerina, Pullenia, etc.*, whose calcareous shells were sedimented after their death. The most common species seems to be *Globigerina bulloides* (fig. 82). Other pelagic organisms,

too, contribute to the composition of the globigerina ooze, especially flagellates of the family Coccolithidæ, whose small skeletons, the coccoliths, which only measure 1–28μ, are to be found in vast quantities in the globigerina ooze. The most common species is

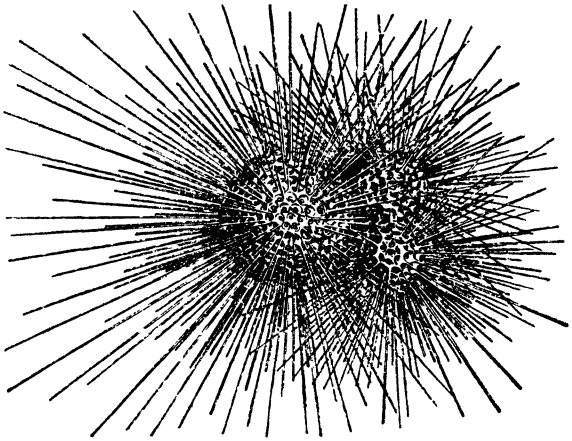


FIG. 82.—*Globigerina bulloides.*[100] (After Ziegler.)

Pontosphæra huxleyi (fig. 83). A sample of the sea floor in the North Atlantic at 2400 m. depth showed the following proportions between globigerinas and coccoliths:

Percentage of weight: globigerinas 64%, coccoliths 27%.
Number of individuals: 930, 4·5 millions.

91% of the 4·5 million belonged to the species *Pontosphæra huxleyi.* H. Lohmann, the first who appreciated the importance of these very small pelagic organisms and who worked out a method for collecting them,[305, 307] found that on each square metre of the surface of the bottom 60 milliards of shells are sedimented annually and he calculated that it needs 250 years for a covering of 1 mm. thickness to be sedimented, provided that coccoliths and globigerinas participate in a proportion by weight of 1:4. Later approximately the same slow sedimentation rate was found also for the equatorial Atlantic Ocean and roughly half the rate for the southern part of the Indian Ocean. Many scientists have studied pelagic deep-sea sedimentation during recent years

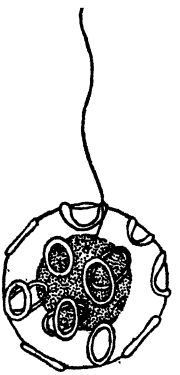


FIG. 83.—*Pontosphæra* 1902.)

(see the summary given by Sverdrup, Johnson & Flemming, 1946).

Since the globigerina ooze is largely made up of coccoliths, it is often termed coccolith ooze.

The globigerina ooze, which in dry condition is of a white, light red or yellowish colour, is usually replaced in the deepest region by the brick red or dark brown red clay of the deep sea. The dividing line between the two lies for the most part around 4000 m. depth, but the globigerina ooze has occasionally also been found down to a depth of 5900 m.

The abyssal *red clay*, which is widely distributed in the deep-sea regions is, in contrast to the globigerina ooze, poor in calcium carbonate or even free of it and it is in general poorer in organogenous components than the rest of the deep-sea sediments. According to the most plausible explanation the red clay is the end product of the break-down of the rest of the deep-sea sediments whose calcereous constituents have for the most part been dissolved out. But coccoliths have been found as well as an enormous number of the most minute fragments of the skeletons of radiolaria and diatoms. Its main mass is composed of aluminium silicate, that is clay. This clay is in reality more widespread than is represented on fig. 81, since it frequently underlies the globigerina ooze. On the surface it covers enormous distances, particularly in the Pacific. But the red clay, in its turn, is sometimes found to overlay the globigerina ooze. The rate of sedimentation of the red clay is even slower than that of the globigerina ooze.

Diatom ooze is mainly to be found in the colder seas. It has played a part in the history of deep-sea exploration, since J. Hooker nearly a hundred years ago demonstrated the fact that in the South Polar regions this ooze is formed from the shells of diatoms living in the superficial water layer. Smaller amounts of diatom shells are also found in the other sediments.

Radiolarian ooze and *pteropod ooze* is mainly distributed locally but it must be noted that fragments of radiolarian and pteropod shells also occur in globigerina ooze, the latter not, however, at the greatest depth; they consist, unlike most other calcareous shells, not of calcite but of the more soluble aragonite.

In the last sentence we have touched upon a question which is of great importance for the history of the formation of abyssal sediments, namely the decomposition of dead planktonic particles by seawater and by bacteria. Such a decomposition of the soft parts and the skeleton evidently occurs even before they reach the deep-sea bottom. Pteropod shells have not been found at a greater depth than 3000 m.; the calciferous globigerina ooze (mean depth about

2900 m.) is replaced in the greatest depth by the red clay which is poor in or free of calcite (mean depth 5300 m.); thin diatom shells are dissolved before they reach the bottom, only the thicker shells being found there; the siliceous shells of many radiolarians are also decomposed as are the skeletons of fishes. Almost the only fish remains are enamel of the teeth and the otoliths. As regards otoliths, it is probable that the decomposition of the rest of the fish skeletons took place already in the pelagic region, namely in the intestines of whales and predatory fishes.[254] The dissolving out of calcite from plankton shells seems to proceed even after sedimentation and it is supposed to depend upon the combination of high pressure and carbon dioxide content. From certain circumstances the conclusion was drawn that nearly everywhere on the sea bottom calcium carbonate is dissolved out of the sediments.

An illustration of the very slow growth of the sediment is provided by the fact that teeth of Pliocene sharks have been recovered from the abyssal bottom where they were still lying fairly superficially in the bottom material. In some places sharks' teeth collect in great masses. Thus Murray reports from the "Challenger" station No. 285 between Polynesia and South America at a depth of 4300 m. that the trawl contained at least 1500 sharks' teeth of at least 1 cm. size and a mass of smaller teeth together with about 50 petrosal bones of various whales. From the adjoining station No. 286 more than 300 sharks' teeth and 132 petrosal bones of whales were obtained from a depth of 4200 m.

The content of eupelagic sediments in nutriment must be extremely small. Analyses made reveal an average value of about 1% of organic matter.[561] It still remains to be investigated to what degree the autochthonous primary nutriment of the abyssal bottom is produced by the so-called chemo-synthetic autotrophic bacteria, which have the power to build carbohydrates and proteins out of the simple substances carbon dioxide and inorganic salts, and in so doing derive their energy from the oxidation of various inorganic compounds such as hydrogen sulphide, sulphur or ammonia.[40] Such an investigation would be of considerable theoretical importance.

During the German Atlantic Expedition on the "Meteor", 1925–27, bottom samples were obtained in the North Atlantic which showed stratification, and on the basis of changes in calcareous content and the appearance of various foraminifera in the sediments it was possible to distinguish certain strata as formed during the glacial periods and others as formed during the inter-glacial periods.[473] These results were confirmed by investigations in the North Atlantic with an improved method which permits the bringing up of sediment cores of up to 2·97 m. in length.[55] The glacial

strata are characterized by the already mentioned *Globigerina bulloides*, which is able to withstand colder water, and the interglacial strata by *Globorotalia menardi*, which is a warm-water species.[532]

THE QUANTITATIVE DISTRIBUTION OF SPECIES

The "Challenger" Expedition discovered that, apart from a few exceptions, the whole of the abyssal bottom was inhabited by animals. As far as the quantitative distribution is concerned, the deepest layers, i.e. the red clay, was, as expected, the poorest, a fact which may be seen from the following list compiled from the survey of the general results of this expedition.[365] The table shows also that this poverty of the deepest zones is not so very great if one considers that with the methods employed the microfauna was only caught to a very small extent.

TABLE 43

Depth in m.	Number of Stations	Average yield per station	
		Species	Specimens
<180	70	61	
180–900	40	47	150
900–1800	23	27	87
1800–2700	25	20	80
2700–3600	32	12	39
3600–4500	32	8	26
>4500	25	6	24

A similar reduction in the deeper zones has generally been confirmed by later deep-sea expeditions.

It is, however, not very probable that depth alone is the decisive factor here; it has been shown that distance from the shore, too, plays an important part. In this respect also Murray's survey is instructive since he compared hemipelagic with eupelagic deposits.

TABLE 44

		Average yield per station	
		Species	Specimens
Dredging	Hemipelagic deposits	25	57
	Globigerina ooze .	5	6
	Red clay . . .	1·7	4·2
Trawling	Hemipelagic deposits	32	90
	Globigerina ooze .	15	39
	Red clay . . .	9	30

The operations in the South Sea have been omitted in this calculation since they are not comparable with the rest because of their rich yield both in hemi- and eupelagic regions.

Individual stations may show a considerably richer fauna than the above mean values, for instance the following productive trawling operations:

TABLE 45

	Depth in m.	Species	Specimens	Source
Globigerina ooze .	2480	52	200	Murray[365]
,, ,, .	3340	38	100	,,
Red clay ,, .	4150	35	100	,,
,, ,, . . .	4690	30	50	,,
,, ,, . . .	5320	32	70	,,
,, ,, . . .	5600	>20	>110	Nybelin[49]
,, ,, . . .	5630	10	20	Murray[365]

Other abyssal regions, on the other hand, appear to be almost deserts. A. Agassiz[4] reports them from the Pacific between the Peru Current and Easter Island and other investigators from regions of the two other oceans. The abyssal fauna is on the whole unevenly distributed.

Qualitatively the animal communities may be divided into a hard-bottom and soft-bottom fauna. The two main qualities of the bottom are clearly related to the topography of the sea floor and the amount of movement in the water. In very calm archibenthal and abyssal troughs near the coast where organogenous detritus accumulates in quantities and a very loose, almost mucous ooze forms the contact zone between bottom and water we find an animal community which, by increased length of legs or other features, is adapted to this loose substratum. This so-called calm-water fauna is the extreme antithesis to the stone or hard-bottom fauna.

THE COMPOSITION OF THE FAUNA

After what has been said above we proceed to discuss the different abyssal animals themselves.

EURYBATHIC SPECIES

Within the deep-sea fauna animals occurring within wide limits of depth occupy roughly the same position as cosmopolitan species in the superficial strata: they are very numerous but contribute little to the zoogeographical characterization. For this reason we will mention them only briefly. We shall, however, give some

examples to show within what limits this eurybathy is found in extreme cases and we shall confine ourselves more or less to those cases where a species occurs more or less regularly on the upper shelf as well as below the 2000 m. depth line.

Porifera
Thenea muricata: 30–3440 m.
Stylocordyla borealis: 2–3000 m.
Tentorium semisuberites: 26–2970 m.
Polychæta
Lumbriconereis impatiens: at least to 3000 m.
Glycera rouxi: at least to 3000 m.
Notomastus latericeus: at least to 3000 m.
Hydroides norvegica: at least to 3000 m.
Pomatoceros triqueter: 5–3000 m.
Amphicteis gunneri: 20–5000 m.
Cirripedia
Verruca stroemia: littoral to 3000 m.
Cumacea
Diastylis lævis: 9–2980 m.
Eudorella truncatula: 9–2820 m.
Isopods
Antarcturus furcatus: 10–3010 m.
Lamellibranchiata
Limopsis aurita: 38–3175 m.
Astarte sulcata: 10–2000 m.
Scrobicularia longicallus: 36–4400 m.
Gastropoda
Neptunea curta: 8–2580 m.
Neptunea islandica: 30–3000 m.
Puncturella noachina: 8–2000 m.
Scissurella crispata: 12–2300 m.
Natica groenlandica: 3–2300 m.
Natica affinis: 0–2600 m.
Scaphander punctostriatus: 35–2800 m.
Asteroidea
Pseudarchaster pareli: 15–2500 m.
Henricia sanguinolenta: 0–2450 m.
Ophiuroidea
Ophiacantha abyssicola: 35–3500 m.
Ophiacantha bidentata: 5–4400 m.
Ophiopholis aculeata: 0–2040 m.
Ophiura sarsi: 10–3000 m.
Ophiocten sericeum: 5–4500 m.
Echinoidea
Echinocardium australe: 0–4900 m.
Holothurioidea
Mesothuria intestinalis: 20–2000 m.

THE ENDEMIC BENTHAL DEEP-SEA FAUNA

Of the great number of exclusively or at least mainly deep-sea animals only a small portion can be mentioned here. We shall select mainly the more important genera and higher taxonomic categories, while deep-sea species of genera which also occur in the shelf region and the deep-sea genera which are poorer in species will for the most part be omitted.

Porifera: an especially characteristic component of the deep-sea fauna are the glass-sponges, *Hexactinellida.* This whole order with its two suborders, 15 families, more than 80 genera and about 375 species[251] belongs almost exclusively to the deep sea, since the few finds on the upper shelf were made mainly in the Antarctic. Its main distribution is archibenthal, at a depth of from 500–1000 m.; the famous *Euplectella*-bottom in Sagami Bay (Japan) is at a depth of only 150–300 m. *Holascus* (10 species) and *Caulophacus* (12 species), on the other hand, have only been found at 3000–5000 m. depth. Well-known genera are *Euplectella* (9-15 species), *Caulophacus, Farrea* (11 species), *Rossella* (mainly antarctic), *Aphrocallistes, Monorphaphis, Hyalonema* (about 90 species, fig. 84).

Among the rest of the sponges the genera *Thenea* and *Cladorhiza* live almost entirely in the deep sea.

Hydroida. Here we may mention the enormous *Branchiocerianthus imperator*, belonging to a genus, however, which also ascends into the shallow water of the cold-water region of the Pacific.

Octocorallia. Among the Gorgonaria the genera *Chrysogorgia* (about 30 species), *Narella* (*Stachyodes*), *Thouarella*, *Caligorgia* are examples of entirely or almost entirely archibenthal genera. The Gorgonaria are generally to be found in deep water. The pennatularians, too, are very well represented here; of the 14 families only two are confined to the upper shelf, the rest belonging whole or partly to the abyssal zone. We may mention the following: *Anthoptilidæ*, a purely abyssal family (one genus, four species); *Funiculinidæ*, archibenthal and abyssal, although sometimes ascending higher: only one genus with three species, of which the well-known cosmopolitan *Funiculina quadrangularis* is distributed between 35 and 2070 m.; Kophobelenmonidæ: mainly archibenthal and abyssal but occasionally also higher, for instance *Kophobelemnon stelliferum* in 36–3600 m. (cosmopolitan); *Protoptilidæ*: purely archibenthal-abyssal family (two genera, seven species); *Scleroptilidæ*: 100–4330 m. (two genera, six species); *Chunellidæ*: purely abyssal (two genera, three species); *Umbellulidæ*: archibenthal and abyssal; *Umbellula* with 32 species (fig. 85), two other monotypical genera are purely abyssal.

Madreporaria. The two closely related genera *Lophohelia* and *Amphihelia* belong in the main to the deep sea. Most deep-sea forms are solitary; they are found in great numbers in the Sulu Sea in the Indo-Malayan archipelago.[5]

Zoantharia. Izozoanthus is the only true deep-sea genus. *Epizoanthus*, which is also represented in the littoral, contains many deep-sea species.

Antipatharia. A group which is well represented in the deep sea; only two genera are not represented there and five are purely abyssal, among them *Bathypathes*, with among others the species *lyra*, which has been found between 3700 and 5440 m.

Ctenophora. The sessile, very interesting *Tjalfiella tristoma* which forms a special order, the



FIG. 84. — The glass sponge *Hyalonema thomsoni*, with zoanthids of the genus *Palythoa* on the stalk. More than half natural size. (After F. E. Schulze, redrawn.)

Tjalfiellidea, lives in 475–575 m. depth in western Greenland at 71° N., attached to the Pennatularia *Umbellula lindahli*.

Polychæta. Most of the deep-sea species of this group belong to genera which are also represented in the shelf.

Cirripedia. The genus *Scalpellum* possesses many archibenthal and abyssal species, also *Verruca*; *Hexalasma* and *Megalasma* are purely deep-sea genera.

Cumacea. Most genera contain deep-sea species; purely abyssal genera are *Macrocylindrus*, *Bathycuma* and some monotypical ones.

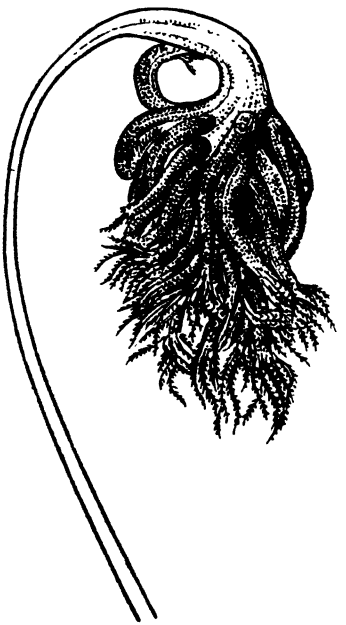


FIG. 85.—The top of the sea-pen *Umbellula antarctica*, half natural size. (After Kükenthal & Broch, 1911, redrawn.)

The *Platysympodidæ*, with two monotypical genera and the *Procampylaspidæ* with one genus and four species, are purely archibenthal and abyssal.

Isopoda. Here we must mention first of all the genus *Munnopsis*, living at a medium depth, because of its greatly lengthened extremities and antennæ which represent an adaptation to the loose ooze (fig. 86); another genus almost completely confined to the deep is *Nannoniscus*.

Amphipods. The purely archibenthal or abyssal genera are as a rule poor in species; *Trischizostoma*, for instance, possesses five to six species.

Decapod crustaceans. Among the Natantia there are some more or less pronounced bathybenthal genera, for instance *Amalopenæus*, *Benthecicymus* and *Benthonectes*, as well as the whole families *Hoplophoridæ* and *Glyphocrangonidæ*. The group Reptantia contains several deep-sea forms. The family Eryonidæ with the genera *Polycheles* and *Willemoesia* is in the main abyssal; its members have more or less reduced eyes and their morphology shows archaic traits. Among the Astacura we mention *Phoberus* and *Thaumastocheles*, which also are most closely related to extinct species, and *Nephropsis* with reduced eyes. The Anomura are rich in deep-sea forms. More than 60% of the 50 species of the *Axiidæ* live in the

deep sea. The group Galatheidea contains the preponderant archibenthal genus *Munida* and the true deep-sea genera *Uroptychus*, *Galacantha* and *Munidopsis*, which morphologically, too, are modified into deep-sea animals by having reduced eyes and greatly lengthened antennæ. The last-mentioned genus contains more than

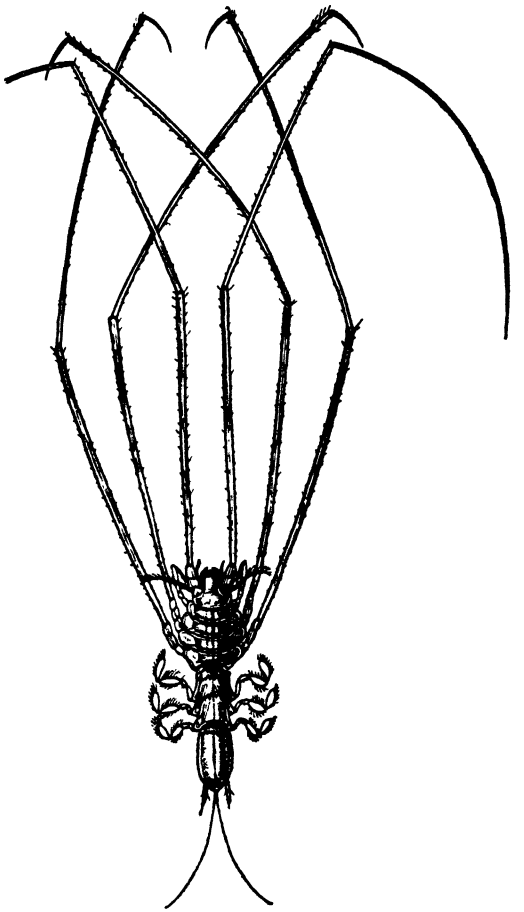


FIG. 86.—The isopod *Munnopsis typica*, fully twice natural size. (After G. O. Sars, redrawn.)

100 species, three-quarters of which do not ascend to above 400 m. depth and almost half of them not above 800 m. depth.[131] In the group Paguridea the *Pomatochelidæ*, whose species dwell mostly in Dentalium tubes, live generally in the deep sea, the *Lithodidæ* in cold regions littorally, otherwise in the deep. Finally, as far as the

crabs are concerned, the now living members of the Homolodromiidæ are deep-sea forms (*Dicranodromia* and *Homolodromia*), as are most of the Homolidæ (*Homolochunia, Latreillia*, etc., the sub-family Tymolinæ (*Cymonomus* with greatly reduced eyes) and single genera of other families, for instance *Platymaja, Geryon* etc. Several of these are calm-water types, equipped with greatly lengthened extremities. But on the whole the crabs are mainly warm-water animals and therefore comparatively little represented in the deep sea.

Pycnogonida. Most genera are eurybathic. Purely abyssal is *Pipetta* which is poor in species (Indo-Malayan and Antarctic, 2000–2450 m.).

Molluscs. For most mollusc groups, with the exception of the squids, there are as yet no lists compiled by taxonomists, which would allow a survey. However, it seems justified to suppose that deep-sea species are in general members of eurybathic genera or otherwise of genera with few species. Families which are confined to the deep sea, do not seem to exist. But among the squids we must mention the whole suborder *Cirromorpha* with its three families Cirroteuthidæ, Staurotheutidæ and Opisthoteuthidæ, who together possess seven genera and about 25 species, which may live benthally.[439] Many octopodids, too, are deep-sea species, for instance *Bathypolypus* (six species) and most of the genus *Benthoctopus* (14 species).

Crinoids. The following survey shows the inclination of this group to deep-sea life by giving the bathymetric distribution on Atlantic species (after A. H. Clark[83]).

Only on the shelf or on the shelf and archibenthal .	31	species
On the shelf to abyssal	10	,,
Purely archibenthal	11	,,
Archibenthal and abyssal, or purely abyssal . .	35	,,

Crinoids which are unstalked as adults (Comatulida) live generally on the shelf with the exception, however, of the families Atelecrinidæ (one genus) and Thalassometridæ (six genera) and single genera, which are poor in species, belonging to other families, for instance among the Antedonids *Trichometra* and *Thaumatometra*. The stalked deep-sea forms are all the more numerous. Purely archibenthal and abyssal are the families *Pentacrinitidæ* (five genera) *Hyocrinidæ* (four to five genera), *Apiocrinidæ* (two genera), *Phyrnocrinidæ* (one genus) and *Bathycrinidæ* (four genera[183]). Hyocrinus and Bathycrinus species descend deepest, as far down as 5010 m. The Bathycrinid genus *Rhizocrinus* is one of the well-known ones since *R. lofotensis* (fig. 87) belongs to the earliest discovered abyssal

animals and played an important part in the discussions of those days because of its archaic organization.

Starfishes. The following data on North Atlantic starfishes may serve as a comparison with the above table regarding the Atlantic crinoids.

Mainly limited to the shelf . .	13 species
Eurybathic	28 ,,
Purely archibenthal or abyssal . .	97 ,,

The abyssal starfishes are not so generally known as are for instance the abyssal crinoids because they do not vary greatly as a rule from the usual pattern of starfishes. Of pronounced abyssal type and also of very characteristic appearance are two families, the Brisingidæ with numerous, very long arms (genera *Brisinga, Odinia, Freyella,* etc.), and *Porcellanasteridæ* with their high marginal plates (fig. 88). Most species of the latter family are purely abyssal, several were caught in depths of over 5000 m., *Albatrossaster richardi* at a depth of 6000 m. One of the few not purely abyssal species is *Ctenodiscus crispatus,* mentioned earlier on, which ascends to 10 m. in the arctic. Two other pronouncedly deep-sea families are the *Benthopectinidæ* and *Zoroasteridæ.* Among genera which have this distribution we may mention *Dytaster, Hymenaster, Pectinaster* and *Pseudarchaster.*

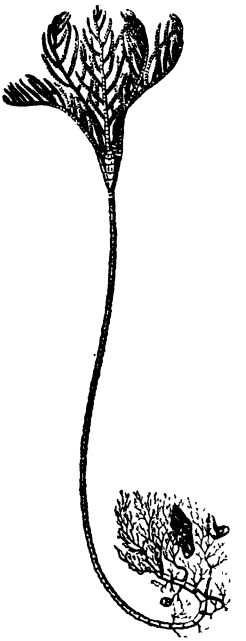


FIG. 87.—The crinoid *Rhizocrinus lofotensis,* natural size. (After Wyville Thomson.)

Ophiuroids. Here we must mention the *Asteronychidæ,* which are poor in species. The rest of the Ophioroid families usually contain both shallow-water species, eurybathic species and often also one or more deep-sea genera, with few species. One of the richer in species is *Ophiomusium.*

Sea-urchins. The order Cidaroidea is mainly archibenthal, although it also contains shelf species and several abyssal ones. Among the rest of the sea-urchins we find whole families with purely deep-water distribution. We first mention the Pourtalesiidæ, Urechinidæ and Calymnidæ, which together form a suborder, the Meridosternata. The first-mentioned family, with the two genera *Pourtalesia* and *Echinosigra,* is remarkable for its elongated body and opening of the mouth which is sunk in into a deep furrow in the

anterior part (figs. 89, 90). The family Echinothuriidæ is also noteworthy because it contains the largest of all sea-urchins (up to 30 cm. diameter); the shell is so soft that it collapses when the animal is lifted out of the water. The family contains 46 species distributed among 11 genera, of which *Phormosoma*, *Arœosoma* and *Sperosoma* are fairly rich in species. Other deep-sea families with at least 10 species are *Aspidodiadematidæ*, *Saleniidæ* and *Pedinidæ*.

Holothurioidea. Hardly any other animal group is so characteristic for the abyssal benthos as the holothurians. Two of its five

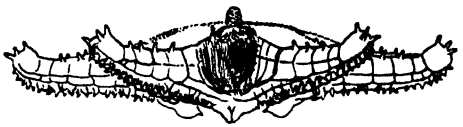


FIG. 88.—The phanerozonian starfish *Porcellanaster cæruleus*, twice natural size. (After Sladen, redrawn.)

orders are confined to deep water, mainly to the abyssal zone, and this is true moreover of one family and several genera. Mainly abyssal and only occasionally archibenthal is the whole order *Elasipoda* with four benthal families (and one bathypelagic family), i.e. the Deimatidæ (three to four genera), Psychropotidæ (four genera), Lætmogonidæ (seven genera), and Elpidiidæ (12 genera, fig. 92, p. 298). The second order of deep-sea holothurians are the *Molpadonia* containing only one family, the Molpadidæ, with few

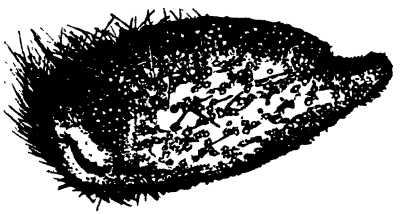


FIG. 89.—The spatangoid sea-urchin *Pourtalesia jeffreysi*, natural size. Some of the spines are missing. (After Wyville Thomson.)

genera; one species lives predominantly in the littoral. Among the Aspidochirota, most species of the *Synallactidæ* (16 genera) are abyssal, a few genera also archibenthal, and one only is eurybathic. In the order Dendrochirota the genus *Staurocucumis*, as well as the small genus *Acanthotrochus* of the order Apoda, belong to the deep sea.

Tunicata. There are three deep-sea families among the ascidians, all are poor in species, i.e. Pterygascidiidæ, Hypobythiidæ and

Hexacrobylidæ. The ascidians, listed up to 1916, are distributed vertically in the following manner (Hartmeyer):

Only in the shelf region . . .	62 genera		
Eurybathic	25 „		
Archibenthal or archibenthal-abyssal .	7 „	}	20 genera
Purely abyssal	13 „	}	

Of the 20 deep-sea genera 10 are monotypical and the rest poor in species, apart from *Culeolus* which has 14 species.

Fishes. As far as we know, most deep-sea fishes are pelagic, but the number of benthal ones is quite considerable. There are quite a number of genera and also families among them, which belong wholly to the deep sea. The following examples are taken from Brauer's,[58] Weber's[578] and Jordan's[266] surveys but they represent only a small part of the whole number of deep-sea genera and families.

Selachii. Here belong, among others, the genera *Centrophorus* and *Centroscyllium.*

Holocephali. The whole of this subclass belongs preponderantly to the deep sea as only a few species live in shallow water. *Chimæra* is archibenthal and abyssal, *Harriotta* purely abyssal.

Macrurida. This great family (approximately 140 species) is purely archibenthal and abyssal. The greater part of the species belong to the old collective genus *Macrurus*, which is now divided up into several genera (*Macrurus* proper, *Coelorhynchus*, *Chalinura*, *Nematonurus*, *Malacocephalus*, *Coryphænoides*, *Trachyrhynchus*, etc.), and to this must be added the more independent *Bathygadus.*

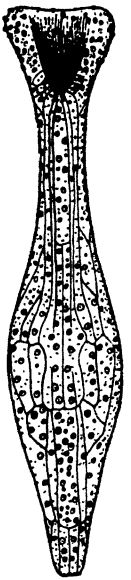


FIG. 90. — The very slender spatangoid sea-urchin *Echinosigra paradoxa*; ventral aspect, without spines. 3 × natural size. (After Mortensen, redrawn.)

Liparididæ. Of the 125 species of this family half live archibenthally and half abyssally. The two great genera *Careproctus* and *Paraliparis* are only in cold regions represented within the shelf zone. Three monotypical genera are purely abyssal.

Zoarcidæ. Only a few species of this family live in the upper shelf region. Most of the genera are completely archibenthal or abyssal, for instance *Lycodes*, *Lycenchelys*, *Neobythites*, *Dicrolene*, *Bassozetus*, *Porogadus*; the two latter are purely abyssal, which is also the

case for approximately 15 monotypical genera and several others with only a few species, among them *Barathronus* with rudimentary eyes.

Halosauridæ. This family, which some ichthyologists consider as a separate suborder, is almost wholly abyssal with its 20 species. It contains only two genera, *Halosaurus* and *Aldrovandia*. Almost purely abyssal are also the Notacanthidæ with roughly 12 species.

Pediculati. The family Ogcocephalidæ (syn. Malthidæ) contains in addition to shallow-water forms three deep-sea genera (*Dibranchus, Halieutæa, Malthopsis*).

Among the codfishes (Gadiformes) there are several genera with completely or preponderantly archibenthal or abyssal distribution, thus for instance *Mora, Antimora* and *Lepidion*.

We thus see that the bottom fauna of the deep sea is characterized by a very great number of animal forms which are more or less completely lacking in the fauna of the shelf. The most important of them are naturally those which form whole orders or other groups of a high taxonomic rank. Such groups of a higher taxonomic rank than families are, to sum up here, among the sponges the Hexactinellida with 15 families, about 80 genera and almost 400 species; among the echinoderms the Elasipoda with four families, 26–27 genera and numerous species, as well as the Molpadonia; among the ctenophores the Tjalfiellidea and among the fishes the Holocephali. The groups mentioned represent orders, the Holocephali even a class. Suborders and superfamilies are for instance among the sea-urchins the Meridosternata (family Pourtalesiidæ, etc.) and among the squids Cirromorpha. A fairly similar position is occupied by the group formed by the greater number of families among the pennatularians and the family group of stalked crinoids. To this must be added the single deep-sea families and numerous deep-sea genera and species. The whole collection is certainly not very rich if compared with the considerably larger collection represented by the fauna of the world's shelves, but in proportion to the total amount of animals found in the deep sea the specific deep-sea element is quite considerable. This is especially true for the abyssal fauna, particularly on eupelagic bottoms, since the deeper and the further from the shore, the more pronounced is the special character of the deep-sea fauna, while the number of eurybathic species decreases. Here, too, we find that the biocœnotic general principle is applicable to a certain degree, according to which the further removed the environmental factors are from the optimum of the greater number of the organisms, the more exclusive and poorer in species the biocœnosis becomes. But a second sentence of this

principle is not applicable to the deep-sea fauna, namely the one which applies to the increase in the number of individuals. This depends evidently on the fact, that one of the environmental factors, namely food, is here a minimum. The principle of an increase in the number of individuals is obviously only true if we assume that there are still optimal conditions for one or the other of the species.

CHAPTER XIII

THE REGIONAL DISTRIBUTION AND ORIGIN OF THE BENTHAL DEEP-SEA FAUNA

WE have seen that the annual fluctuations in the temperature of the water are very much less even in the upper layers of the abyssal sea compared to those in the superficial water layers, and we are thus justified in calling the deep-sea animals stenothermal both on the grounds of their bathymetric distribution and from what has been learned by keeping them in aquaria. They seem to be on the whole also stenohaline.

THE ARCHIBENTHAL FAUNA

Just as the archibenthal fauna occupies an intermediary position in the vertical distribution between the fauna of the shelf and the abyssal fauna, it also occupies such a position in the horizontal distribution, in that its species generally have a more extensive distribution than the shelf species but less extensive than the abyssal species. This phenomenon may be illustrated by the archibenthal fauna of the North Atlantic, particularly within the European region, where conditions are easier to survey than on the American coast of the Atlantic.

The *North Atlantic* contains a number of archibenthal species which have approximately the same limit of distribution northwards as the boreal fauna of the shelf since both groups of species are tied to the warmer water of the Gulf Stream (the North Atlantic Current). It would be possible to speak of an archibenthal boreal fauna but with the reservation that this archibenthal fauna is distributed further south and has there a less well defined limit than the boreal fauna of the shelf. In the Skagerak, the Norwegian fjords and on the slope of the shelf into the abyssal regions of the Atlantic on the European, American and South Greenland coasts we find this North Atlantic archibenthal fauna. It contains several endemic species. Such are for instance the calciferous hydroid *Stylaster gemmascens*, the barnacles *Scalpellum stroemi* and *Balanus hammeri*, the isopod *Eurycope phalangium*, the decapod crustaceans *Lithodes maja*, *Pandalus montagui* and *Pontophilus norvegicus*, the sea-urchins *Brisaster fragilis* and **Spatangus raschi* as well as among other groups of

echinoderms *Psolus squamatus*, **Stichopus tremulus* and *Gorgonocephalus caput-medusæ* (the asterisks denote species which are endemic on the European side). Among the fishes we may mention *Lycodes wahli*, *Lycenchelys sarsi*, *Coryphænoides rupestris* and *Glyptocephalus cynoglossus*.

The archibenthal fauna of the North Atlantic contains many species which are widely distributed also in warmer seas, for instance the two corals *Lophohelia prolifera* and *Amphihelia oculata* (cf. p. 288), the pennatularians *Funiculina quadrangularis* and *Kophobelemnon stelliferum*, the crustaceans *Geryon tridens* and *Calocaris macandreæ*, the echinoderms *Psilaster andromeda*, *Ceramaster granularis*, *Amphilepis norvegica*, *Asteronyx loveni*, *Mesothuria intestinalis*. Several of them descend into abyssal depths.

To this we must add numerous species which the North Atlantic has in common with the Arctic, where many of them also occur on the shelf, whereas in the North Atlantic they belong only to the deeper layers. This affinity with the Arctic is in the North Atlantic more marked in the archibenthal than in the shelf region, obviously due to the lower temperature in the deeper layers and the equatorial submergence caused by it. Such arctic-North Atlantic species, among them also one or more with distribution further to the south, are, for instance, among the actinians *Actinostola callosa* and *Bolocera tuediæ*, among the amphipods *Haploops setosa*, *Stegocephalus inflatus*, *Orchomenella minuta*, *Tmetonyx cicada*, *Anonyx nugax*; the isopod *Munnopsis typica*; the prawns *Spirontocaris spinus*, *S. polaris* and the generally known *Pandalus borealis* (mainly boreal but also low arctic, possibly belonging to the lower shelf rather than the archibenthal fauna); among the molluscs *Pecten abyssorum*, *Bathypolypus arcticus* and *Rossia glaucopis*. Among echinoderms we may mention for instance *Poraniomorpha hispida*, *Pteraster militaris*, *Pontaster tenuispinus*, *Lophaster furcifer*, *Ophioscolex glacialis*. The *Pontaster* species which in the arctic region occurs regularly from 60–70 m. downwards, in the boreal region from 200 m. downwards, also lives in the Bay of Biscay, where it occurs at still greater depths. It is a link with such species as *Ophiacanthia bidentata* which in the high arctic regularly occurs already at 5 m., in the low arctic at 25–30 m. but in the boreal region only at 200 m. depth and which is exclusively abyssal in the Central Atlantic, where it lives for instance off West Africa. Among fish we may mention *Cottunculus microps*, *Artediellus uncinatus*, *Icelus bicornis*, *Triglops pingelii*, *Careproctus reinhardti* and *Lumpenus maculatus*.

In the North Atlantic, and as far as we know also in other regions of the sea, it is possible to distinguish two main divisions of the

archibenthal fauna, the hard-bottom and soft-bottom facies. They are well developed and sharply divided from each other, for instance in the Norwegian fjords and the Skagerak.

The fauna of the hard bottom is greatly influenced in its occurrence by the topography, and in connection with it the hydrography of the fjord channels. The fjords are usually deepest in their central and inner parts but are bordered by a sill at the mouth towards the open sea. Such sills also exist in many places in the interior parts. They are distinguished by a great flow of water bringing abundant nourishment and oxygen and are therefore teeming with life, as are also the steep submarine mountain slopes at the sides of the fjords. Because of the flowing water these hard substrata are free from sediment and suitable for colonization by sessile animals. We find here an animal community which has sometimes been called the *Lophohelia* fauna after one of its most prominent members. It is composed of a variety of the most divers systematic groups; some of the more important ones will be briefly discussed below.

Lophohelia prolifera, the most northern reef-building coral apart from *Amphihelia* which we shall mention later, forms fairly extensive and connected reefs in the Norwegian fjords. On the west coast of Scandinavia it probably does not occur in a living state further south than on the frontier between Norway and Sweden at a depth of about 80 m.; on the west coast of Norway it occurs in some places, usually however only below 150 to 200 m. The most northerly finds of living branches were made in the region of the Lofoten Islands at 67° 11′, 68° 12′ and 68° 15′ and even at 69° 14′ N. (Andfjord) at a depth of about 350–500 m. and a temperature of 6·3–6·65° C. Still further to the north dead colonies were found at a depth of 200 to 350 m. and a temperature of 4·1 to 5° C.; the lower temperature limit seems therefore to lie at 6° C. Dead colonies have been found along the Scandinavian peninsula from western Finmark to Bohuslän in lesser depth, even above the present sea level; in the Oslo fjord, where the species is now extinct, a large area of the bottom, about 100 square kilometres at a depth of 130–150 m., is covered by their dead colonies. Another reef-building coral, *Amphihelia oculata*, also occurs just as far north but is found in fewer places. The family Stylasteridæ which, although calciferous, belongs to the hydroids and takes an active part in the building of tropical coral reefs, is represented by two species, *Stylaster norvegica* and *S. gemmascens*. The sometimes very imposing gorgonarians *Anthothela grandiflora*, *Paragorgia arborea*, *Paramuricea placomus*, *P. kükenthali*, *Primnoa resedæformis* and *Isidella lofotensis* occupy an important position in this biocœnosis. The Alcyonarians, too, are well represented by species of the genera *Anthelia*, *Clavularia*,

Anthomastus, Eunephthya, Gersemia. In similar localities there are found the sponges *Geodia barretti* and *Dragmastra normani*, the large mussel *Lima excavata* (with the same northern limit as *Lophohelia*), the barnacles *Scalpellum stroemi* and *Balanus hammeri*, the peculiar starfishes *Brisinga endecacnemos* and *Brisingella coronata*, the sea-cucumber *Psolus squamatus*; and in the branches of the gorgonarians there climbs *Gorgonocephalus caput-medusæ*.

The soft-bottom fauna consists for the most part of animals which need soft material to dig in or are mud feeders, detritus feeders, or need soft material for other reasons. Here belong the already mentioned species of the genera *Funiculina, Kophobelemnon, Actinostola, Bolocera, Calocaris, Geryon, Munnopsis* and many amphipods and other crustaceans which catch detritus, and the echinoderm *Asteronyx* which in its earliest stages is a detritus feeder but later climbs up on a *Funiculina* and from this elevated position becomes a plankton feeder. *Stichopus* and *Mesothuria* are examples of mud-eaters.

Sedimentation of the finest bottom mud takes place only in relatively calm water. Off the open coast, where the tidal and other currents have free play, there is the boundary between the harder bottom material of stone, gravel or sand and the soft mud sediment usually to be found at the outer edge of the shelf. This transition between the two kinds of bottom is doubtless a very important factor in the delimitation between the shelf fauna and the archibenthal fauna. Already in 1895 John Murray directed attention to the importance of this "mud-line", the upper limit for the soft sediment, whose position can for the most part be given as roughly 200 m. (100 fathoms) depth. But we must bear in mind that the depth is very variable as it may lie in places as low as over 500 m. (300 fathoms) and in certain Scottish fjords as high as 10–40 m. depth. The latter fact also corresponds to conditions in the Scandinavian fjords and in interior coastal waters. Thus the interior of the Gullmar fjord in Bohuslän has at a depth of 30–35 m. soft sediment with an abundant occurrence of *Funiculina quadrangularis* and *Calocaris macandreæ*, for instance, and at a little greater depth in this fjord and in the Kattegat we find for the same reason also other species which have their main region of distribution in the archibenthal zone. Only the most eurythermal and euryhaline species of the archibenthal fauna are able to withstand environmental conditions in such shallow depths. Such archibenthal enclaves in the region of the shelf are not uncommon.

The topography of the bottom of the fjords is also able to influence zoogeography. The Norwegian Sognefjord descends into the abyssal zone with a depth of more than 1200 m. and contains a true abyssal fauna although it is poor in species. The depth of the sill at the

mouth in particular exercises a decisive influence. If this sill does not lie deep enough, as is the case in the Gullmar fjord, to allow the entrance of water of 35‰ salinity, many stenohaline species are prevented from immigrating. The deep region of the Skagerak (the "Norwegian Channel") has an entrance sill which rises to 273 m. below the surface of the sea and thus permits water of 35‰ salinity to enter. The bottom slopes down from the sill in the direction of the Skagerak where it reaches its greatest depth at 700 m. The fauna of the Norwegian Channel is on the whole the same as that of the Norwegian fjords (for hydrographical and faunistic peculiarities see for instance[150, 166, 244, 278]).

The archibenthal fauna in other seas. We may regard most species of the fish family Macruridæ as typical representatives of the archibenthal fauna; the conditions of their distribution have been discussed by Brauer.[58] Although most genera and subgenera are practically cosmopolitan, the species on the other hand inhabit usually sharply limited localities. Of the 116 species of the old collective genus *Macrurus* only six to eight are found in two or three oceans, and three of these descend into depths of 3650–4840 m. The archibenthal species, which represent about a half, almost all show a limited distribution. Thus the east and west coasts of the Atlantic have, apart from the northernmost regions, not one common species. And none of the 18 species which are to be found in the West Pacific, occurs again on the west coast of America; all 30 species of this region are different, nor do they correspond to those living on the east side of Central America; the species of the Bering Sea are different from the other Pacific and polar species; and all the 19 species of the region of the islands round Hawaii are peculiar to it. In the Indian Ocean 10 of the 14 species known so far are endemic. Brauer rightly says of these conditions: it is a pattern of distribution which is usually only known from the species of the shelf and corresponds very little to the views which are commonly held on this subject. Formerly the deep-sea fauna was usually considered to be cosmopolitan.

A similarly restricted distribution is found in some other fishes and other animals of the deep sea. Weber[578] stresses the pronouncedly Indian character of the Indo-Malayan deep-sea fishes and Koefoed[281] found that among 27 Atlantic benthal deep-sea fishes only one-third was common to both sides of the ocean. Among the decapod crustaceans nearly all the Axiidæ inhabit restricted localities. The benthal decapod fauna of the Atlantic has indeed quite a different stamp from that of the Indo-Pacific or the west coast of America, at least as far as depths down to 1500 m. are concerned.[30] Roughly the same is true of the crabs.[130] It has

been calculated that among the decapod crustaceans about 80 mainly archibenthal species of the Indian Ocean do not occur outside this sea. In the Atlantic we find similar conditions: the tropical-American and European-African side have only four deep-sea species of the Galatheidæ in common, of which two are cosmopolitan, while on the American side there are about 40 and on the European side 12 endemic species. There are differences in the deep-sea zone of the East and West Atlantic also with regard to the sea-urchins and brittle stars.[345, 356] Restricted distribution is also characteristic for the *Scalpellum* species, whether they are archibenthal or abyssal, which is due to the fact that they usually lack pelagic larvæ. But among the archibenthal animals there are numerous exceptions to this rule of restricted regions.

THE ABYSSAL FAUNA

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. Koefoed[281] puts this limit for deep-sea fishes of the Atlantic at roughly 2600 m. depth. Of the fishes which live below this depth 50% are purely Atlantic, while 50% have more extensive distribution, and for the echinoderms, too, the extent of the region of distribution increases with increasing depth of occurrence.[146] Balss[30] has also shown that the East Pacific barrier has comparatively little influence on the purely abyssal benthal decapod crustaceans of the Pacific, whereas it is on the other hand a very considerable obstacle to distribution for archibenthal species, as we have also recently seen in the case of the Macruridæ. It affects even the deep-water fishes of the Hawaiian fauna.[181]

Not even for the most extreme abyssal species of the benthos can a cosmopolitan distribution, however, be considered as the rule. The lack of common species between the Atlantic and the other oceans may up to a point be due to the insufficient knowledge of the fauna, but this is only partly true. The fairly numerous deep-sea expeditions have shown that the same abyssal species are caught repeatedly in the Atlantic, and the same ones repeatedly in the Indian Ocean and Pacific, but it is much more seldom that the same species are caught in the Indian Ocean and the Atlantic, or in the Pacific and the Atlantic. Thus of the 18 elasiopods contained in the "Albatros" material from the Pacific only one species had been previously known from the Atlantic, but 10 from the Pacific.[394]

Different groups of animals seem to behave differently in this respect, as may be readily understood.

At the time of the first discovery of the deep-sea fauna its species were generally held to have a world-wide distribution. At first this view was purely speculative: it was considered probable that the climatic and other conditions of the abyssal region were completely uniform and thus it was unnecessary to divide the abyssal fauna into regions. This view, which was already criticized by J. Murray,[365] is now untenable. But it cannot be denied that the genera are usually cosmopolitan, although the species often belong to their special oceans. The opposite view with regard to species had its foundation partly in the insufficient knowledge of the fauna and partly in the fact that the bathybenthal and bathypelagic species were not sufficiently distinguished: the latter are far more often cosmopolitan than the bathybenthal ones.

MAIN REGIONS OF THE ABYSSAL FAUNA

In the following discussion of the horizontal division of the deep sea we will confine ourselves at first to the abyssal fauna of the medium degrees of latitude and then pass on to a discussion of the two polar seas.

The Atlantic and the Indo-Pan-Pacific abyssal region

Our knowledge of the abyssal fauna is still too insufficient to allow any certain division into regions. But 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, 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 the shelf fauna in that *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.*

The term pan-Pacific is here employed not only in an east–west but also a north–southern meaning. It seems probable that the deeper abyssal fauna, which is fairly uniform, reaches northwards into the southern Bering Sea and southwards to the antarctic deep sea. How far the abyssal fauna of the Indian Ocean is independent *vis-à-vis* that of the Pacific may be shown by future investigations.

Several species which are common to the abyssal regions 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.

The antarctic abyssal region

This deep-sea region probably possesses some faunistic independence. Characteristic for this region are, for instance, among the hexactinellids the genera *Aulorossella* (six species), *Gymnorossella* (two species), *Rossella* (most of its 16 species and subspecies are antarctic) and also six genera with few species. In the material brought home by the "Discovery" expeditions there were 23 purely antarctic and purely abyssal species among the starfishes, which represented several purely antarctic genera.[164] On the other hand several abyssal echinoderms which occur in the neighbouring seas are missing from the antarctic deep sea, thus for instance, among the sea-urchins, the families Echinothuriidæ, Saleniidæ and Aspidodiadematidæ, which together contain about 50 deep-water species representing 12 genera.[352] Of the 10 species of the squid genus *Graneledone* most are purely antarctic; and so on. A faunistic independence would not be surprising, if it was proved, because of hydrographical conditions: the bottom water of the South Polar basin is up to a certain height a closed unit. Wüst[588] summarizes the most recent results by saying that the South Polar basin up to a depth of 4500 and 5000 m. (considered from below) is enclosed on all sides and that the heaviest, purely antarctic bottom water of less than −0·8° C. cannot enter into the neighbouring basins. If an antarctic abyssal fauna should be found to represent an independent whole we would find the interesting phenomenon that its upper temperature limit would, as in the Arctic, lie at about 0° C. and that it, in contrast to the Arctic, had maintained its independence without topographical delimitations.

The Arctic Deep-Sea

One part of the Arctic Deep-Sea, namely the Norwegian Basin, is faunistically better known than most other deep-sea regions and it contains a characteristic fauna. We shall therefore treat it more fully than other abyssal regions.

Physical geography. The Arctic Deep-Sea has a well-defined boundary compared with the other oceans: the *North Atlantic Transversal Ridge* between Scotland and Greenland, which carries as its supramarine parts the Shetlands, Faroes and Iceland, is nowhere lower than 560 m. below the surface; between West Greenland and Cape Walsingham on Baffinsland, which lies opposite, there runs another transversal ridge in the Davis Strait at a depth of at the most 700 m.

The greatest depth of the threshold of the Bering Strait is not even 50 m. and the strait is surrounded by a very wide sea of at the most 100 m. depth. As regards the bottom topography this deep sea

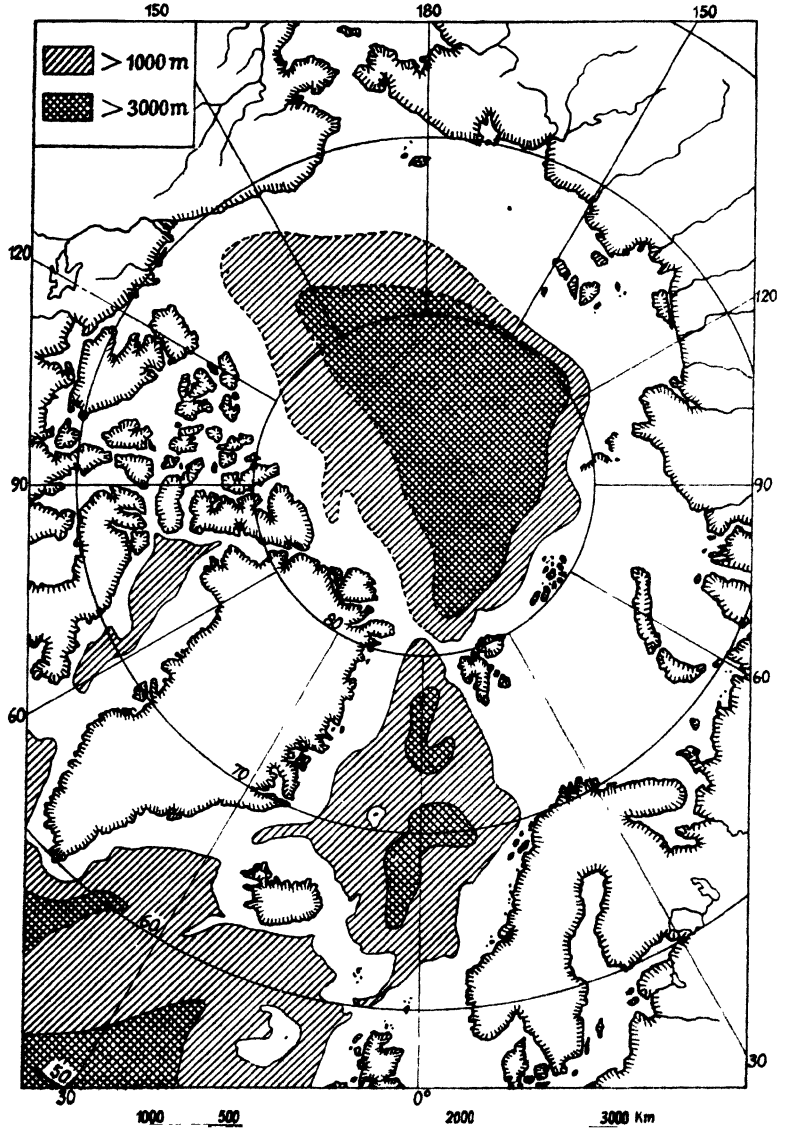


FIG. 91—The deep isolated basins of the Arctic Region. (After G. Schott, 1926, simplified.)

around the North Pole which is delimited in the above way forms a very independent part of the world's deeps: the *Arctic Deep-Sea.* We can distinguish three subdivisions in it: (1) the central *North Polar Basin* between America and Siberia, north of Spitsbergen, Franz Josef Land and Greenland, mostly at least 3000 m. deep with a maximal depth of at least 4300 m., possibly more than 5000 m.; (2) the *Norwegian Basin* between Norway and Greenland which is connected by a channel of about 1500 m. depth across the Nansen Ridge between Spitsbergen and Greenland with the North Polar depth and is delimited in the south by the North Atlantic Transversal Ridge; the maximal depth is about 3700 m.; (3) *Baffin Bay,* 2200 m. deep, which is delimited by the above-mentioned 700 m. deep transversal ridge against the Atlantic and against the Polar Basin by shallow straits.

Hydrographically the independence of the Arctic Deep-Sea is well defined, since its temperature reaches +1° C. only in a few places, where the Gulf Stream still makes itself felt, otherwise it is 0° C. or possesses negative degrees only. On the abyssal bottom of the Norwegian Basin and in a thick layer above the temperature is at the most −1° C. and the salinity remains constant at 34·93‰. On the southern boundary of the Polar Sea, too, on the northern slope of the North Atlantic Transversal Ridge, the temperature below 600 m. is 0° C. or less. The Arctic Deep-Sea therefore comprises abyssal as well as low-archibenthal zones.

The bottom deposits of the Arctic Deep-Sea diverge partly from conditions in the North Atlantic. In the Norwegian Basin the globigerina ooze forms only a thin layer on the glacial clay below, which may be due to the fact that the Atlantic Current was unable to penetrate into the Polar Sea during the glacial period because of a barrier of ice on the North Atlantic Transversal Ridge. Therefore no globigerina ooze could be deposited at that time north of the ridge in question.[411] In conformity with this Nansen found that the sediment in the North Polar Basin was almost devoid of fossils and almost purely minerogenous. The archibenthal boundary regions of the Arctic Deep-Sea are covered with an ooze which has as its main constituents the benthal foraminifera *Rhabdammina* and *Uvigerina.*

The fauna of the Arctic Deep-Sea. The special zoogeographical position of this fauna was already recognized on the first expedition, which was undertaken with a view to the investigation of the abyssal fauna in general. This was the British expedition on the "Lightning" in 1868. It investigated the sea around the later discovered Wyville-Thomson Ridge between the Faroes and Shetlands. Carpenter[75] was the first to point out the faunistic differences between the two

sides of the submarine ridge and he distinguished a "warm area" to the south and a "cold area" to the north of the ridge. Jungersen[272] finally demonstrated the purely arctic character of the deep-sea fauna of the Norwegian Basin which he called the domain of the Lycodidæ (from an ichthyological point of view) and he contrasted it with the domain of the Macruridæ within the Atlantic fauna. A more detailed investigation of the Norwegian Basin was undertaken by the great Norwegian expedition on the "Vöringen" (1876–78) under the direction of G. O. Sars and Mohn. The relation of its fauna to the Atlantic abyssal fauna was investigated by the Danish "Ingolf" expedition (1896). Apart from this, Sweden, Norway, Denmark and other countries have sent arctic expeditions to investigate the abyssal fauna of the Norwegian Basin, and to a lesser extent that of the North Polar Basin. The latter was made the object of a special investigation by the Russian expedition on the ice-breaker "Sadko" in 1935.

Stephensen[497] first discovered that Baffin Bay, in spite of its shallow connection with the Polar Basin, harbours an arctic deep-sea fauna and this result was later fully confirmed by the Danish Godthaab expedition (1928).

The table below is based on an examination of all the data, comprising more than 600 metazoa, which have been found below the 550 m. zone in the Arctic Deep-Sea, i.e. at a temperature of 0° C. or less.

The majority of the species, 560 of them, belong to the benthal fauna. They are distributed among the different zoogeographical groups in the following manner:

1. Endemic species of the Arctic Deep-Sea		
(*a*) Mainly archibenthal . .	80 species = 14·2%	
(*b*) Mainly abyssal, found in the archibenthal zone . .	62 species = 11%	
(*c*) Purely abyssal, not found above 1000 m. . .	83 species = 14·8%	
		225 species = 40%
2. Purely arctic eurybathic species (shelf to abyssal) .		70 species = 12%
3. Arctic-boreal or widely distributed deep-sea species		
(*a*) Purely archibenthal or partly abyssal	150 species = 27%	
(*b*) Purely abyssal . . .	40 species = 7%	
		190 species = 34%
4. Eurybathic and also eurythermal species . .		75 species = 14%
		560 species = 100%

The benthal abyssal-archibenthal fauna (below 550 m.) of the Arctic Deep-Sea thus contains about 40% endemic Metazoa species and it may therefore be regarded as well defined. Within the purely abyssal fauna the endemic Arctic Deep-Sea element is even more independent, as may be seen from the following table.

Purely abyssal species	.	123
purely arctic species	.	83=67·5%
also Atlantic species	.	40=32·5%

The figure mentioned, 67·5%, is very high. *The purely abyssal benthic fauna of the Arctic Deep-Sea possesses a very high degree of independence.* Before going into the relationships of the arctic deep-sea fauna with the others we must first become acquainted with its most important species. The following survey contains only purely arctic, that is to say endemic, deep-sea animals.

Porifera. The two almost purely abyssal *Cladorhiza* species, *gelida* and *tenuisigma*, are worth mentioning. *Hymedesmia* possesses some abyssal species. *Chondrocladia gigantea* is known from many archibenthal and abyssal localities. *Trichasterina* (two species), a hexactinellid genus, has been found only in the abyssal zone.

Coelenterata. The imposing Pennatularia *Umbellula encrinus* (cf. fig. 85) has been found in many archibenthal and abyssal localities and the same is true of *Izozoanthus bulbosus* and *Epizoanthus glacialis.*

Cirripedia. Scalpellum hamatum and *S. striolatum* are found not infrequently in the deeper archibenthal and in the abyssal.

Isopoda. The following are some of at least 20 endemic species: the purely abyssal *Mesidothea megalura* (fig. 59, p. 172), *Eurycope hanseni, Heteromesus frigidus* and *Macrostylis subinermis* and the mainly abyssal but also archibenthal *Gnathia stygia* and *Haploniscus bicuspis.* Endemic are, further, the monotypical genera *Notophryxus* and *Pseudomesus.*

Amphipoda. Among the 40–50 endemic species the purely abyssal *Bruzelia dentata* occurs generally, as well as the archibenthal-abyssal *Harpinia abyssi, Halirages quadridentatus* and *Byblis minuticornis.*

Mysidacea. The genus *Pseudomysis* with the single species *P. abyssi* is purely abyssal. This is also the case with the commonly found *Boreomysis scyphops. B. nobilis, Parerythropus spectabilis* and *Erythrops glacialis* are also worth mentioning.

Decapoda. Two prawns of the genus *Bythocaris* are among the most characteristic elements, namely *B. leucopis* and *B. payeri* (the latter occasionally also in positive degrees of temperature up to 1·5° C.), *Sclerocrangon ferox* is very common in the archibenthal zone but it also ascends into the upper shelf zone in the high-arctic regions (fig. 62, p. 177.)

Pycnogonida. The same position as the last-mentioned species is occupied by *Colossendeis proboscidea.* Purely abyssal are *Ascorhynchus tridens* and *A. abyssi.*

Mollusca. Of the fairly numerous gastropods confined to the

Arctic Deep-Sea we will mention only the purely or almost purely abyssal *Bela ovalis* (from at least seven localities), *Nattca bathybii* (seven localities), *Neptunea mohni* (10 localities) and the opisthobranch *Cuthonella abyssicola*. Among the lamellibranchs we must mention in the first instance *Pecten frigidus* which has become known from 30 localities at depths varying between 1050 and 2800 m. and which has never been encountered in warmer water than −1° C.; in some localities the number of individuals is considerable. At a depth between 550 and 2340 m. a squid, *Cirroteuthis mülleri*, has been found.

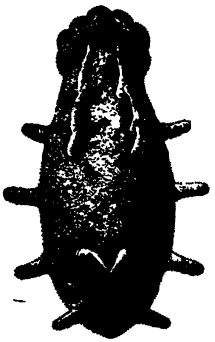


FIG. 92.—The elasipod holothurian *Elpidia glacialis*; dorsal aspect. Nearly twice natural size. (After Stuxberg.)

Crinoidea. Bathycrinus carpenteri is purely abyssal.

Asteroidea. Tylaster willei is found at 590–2400 m., *Solaster squamatus* at 90–1600 m., but most frequently below 500 m. *Poraniomorpha bidens* seems to exist only in Baffin Bay.

Echinoidea. The only endemic species in the Arctic Deep-Sea is *Pourtalesia jeffreysi* (cf. fig. 89).

Holothurioidea. Purely arctic abyssal are *Acanthotrochus mirabilis, Myriotrochus théeli, Irpa abyssicola* and *Kolga hyalina*. The genera *Acanthotrochus* and *Irpa* are monotypical and thus also endemic in the region. But even more characteristic for the arctic deep-sea fauna is *Elpidia glacialis* (about 20 localities; fig. 92), although it occasionally ascends in high-arctic regions to the lower shelf; most finds, however, come from abyssal depth down to 2800 m.

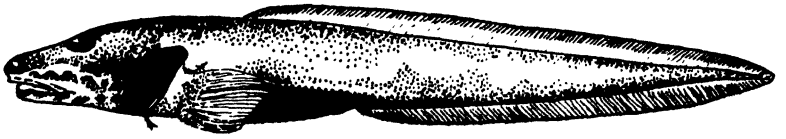


FIG. 93.—*Lycodes frigidus*, half natural size. (After Ad. S. Jensen, redrawn.)

Fish. About half of the roughly 15 endemic arctic deep-sea fishes belong to the sub-family *Lycodinæ* of the *Zoarcidæ*. The three genera *Lycodes, Lycenchelys* and *Lycodonus* are an important part of the fauna under consideration. We must mention especially *Lycodes frigidus* (fig. 93) from at least 25 localities, 22 of them abyssal (down to 2750 m.) and found only once in a temperature a little above 0° C.,

otherwise always in negative degrees; *L. eudipleurostictus* from 17 archibenthal localities (only two of them above 470 m.) and *Lycodonus flagellicauda* from nine abyssal (down to 1800 m.) and two archibenthal localities, always in water below 0° C. The most common fishes besides the Lycodinæ are *Raja hyperborea* (abyssal and archibenthal up to 200 m.), *Paraliparis bathybii* (exclusively abyssal and in negative degrees of temperature, from at least 10 localities) and first and foremost the red-coloured *Rhodichthys regina*, belonging like the last-mentioned species to the Liparididæ (fig. 94), which forms a separate genus and is purely abyssal (from 13 localities, between 1150 and 2340 m.).

There are thus some endemic genera among the deep-sea animals of the Arctic, namely the hexactinellid genus *Trichasterina* with two species and some monotypical genera, the isopod genera *Notophryxus* and *Pseudomesus*, the Mysidacea genus *Pseudomysis*, the holothurian genera *Acanthotrochus* and *Irpa* and the fish genus *Rhodichthys*. Only the latter and *Pseudomysis* can be regarded as certainly established endemic genera; the others have been found so infrequently that their true distribution is not sufficiently known.

So far we have only considered the endemic arctic deep-sea fauna. But as we have already said the Arctic Deep-Sea contains in addition about 335 species of which some must be regarded as occasional visitors but others occur regularly and with a large number of individuals. Among these we must mention especially the genuine arctic eurybathic species. Their occurrence in the upper shelf zone is mainly confined to the high-arctic region. We name the following:

Priapulida: *Priapulus bicaudatus*
Cirripedia: *Scalpellum nymphocola*
Isopoda: *Arcturus baffini*
Eurycope gigantea
Mumnopsurus giganteus
Amphipoda: *Cleippides quadrangularis*
Pycnogonida: *Boreonymphon robustum*
Chætonymphon macronyx
Chætonymphon hirtipes
Nymphon sluiteri
„ *grossipes*
Gastropoda: *Buccinum hydrophanum*
Neptunea curta
Rissoa wyville-thomsoni
Lamellibranchia: *Lima hyperborea*
Asteroidea: *Poraniomorpha tumida*
Hymenaster pellucidus
Ophiuriodea: *Ophiopleura borealis*
Gorgonocephalus eucnemis
Gorgonocephalus arcti-

Species which belong to the Atlantic as well as the arctic abyssal region are considerably less numerous. The animals found in both regions are as a rule either mainly Atlantic animals which live in the Arctic Deep-Sea only at its southern boundary, for instance the northern slope of the North Atlantic Transversal Ridge, or they are arctic and occur in the Atlantic only on the southern slope of this

ridge or in the Labrador Current, that is to say even within the Atlantic region in arctic waters. But some are equally at home in both abyssal regions, among them a few fishes.

Guryanova[200] has given a valuable survey of the abyssal fauna of the central North Polar Basin with regard to amphipods and isopods. At a depth of between 600 and 3300 m. there are found in the Polar Basin, the Norwegian Basin and Baffin Bay altogether 174 species of these two animal groups and it appears from their distribution that the endemic arctic deep-sea element is represented in all three regions by the same species.†

The Arctic Deep-Sea also contains a *bathypelagic fauna*. We shall

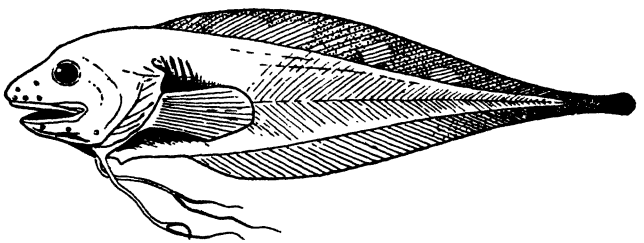


FIG. 94.—*Rhodichthys regina*. (After Ad. S. Jensen, redrawn.)

† Guryanova draws far-reaching conclusions from the distribution of the amphipods and isopods in the deep zones of the Polar Sea, which also concern important aspects of the ancient geography and topography of this sea. We shall therefore examine them here briefly. The fact that several species, which are endemic in the Arctic Deep-Sea, belong to genera with a distribution apart from this in the abyssal Atlantic south of the submarine North Atlantic Transversal Ridge obviously shows that there must have been an ancient communication between the two abyssal regions. Guryanova considers that this "confirms the connection of these two basins in the glacial period, i.e. the absence of a continuous land-bridge in the place of the present-day W. Thomson ridge", such as geologists have assumed. This criticism is, however, not justified. The Quaternary Period was, as far as we can judge, too short for the development of new species. It is thus a communication during the Tertiary Period which must be postulated and the communication in the Quaternary which Guryanova postulates, is unnecessary. Further, from the fact that the arctic abyssal fauna lacks endemic genera of isopods and amphipods—as we have seen above, there are a few of them in other animal groups—the authoress concludes that "the depth of the Polar Basin originated probably not before the very end of the Tertiary and, perhaps even in the beginning of the Quaternary Period". This conclusion, too, is based on the false assumption that present species have originated during the Quaternary Period and genera at the end of the Tertiary, while we must, as a matter of fact, put the origin of species a good way back into the Pliocene and that of the genera considerably further back into the Tertiary Period (p. 200–202). And for the rest, the absence of endemic genera in the arctic abyssal region cannot prove anything about the time of appearance of this abyssal region, because such an absence may perhaps be due to the fact that although an arctic abyssal region perhaps was present during the earlier part of the Tertiary Period it was not topographically or hydroclimatically isolated from the Atlantic abyssal region.

discuss it at this point in order to connect it with the previously discussed arctic abyssal environmental factors. The arctic bathypelagic fauna is rather meagre. It contains only some 50 metazoa, half of which are copepods. Most species occur also outside the arctic deep sea, partly as arctic surface plankton, partly as eurybathic or cosmopolitan plankton organisms and partly also as Atlantic deep-sea plankton. The latter group is richest in species. To this must be added as a fourth group an endemic arctic deep-sea plankton. It consists of seven to eight species and represents 14–16% of the total. The most common species is *Cyclocaris guilelmi*, an amphipod which is occasionally found at only 100–130 m. depth in high-arctic regions, but is otherwise bathypelagic and especially abyssal, and has been caught in many localities. Gran[188] even designates this deep-sea pelagic region as the *Cyclocaris* region (figs. 95, 96). Another fairly frequent amphipod is *Eusirus holmi* (archibenthal and abyssal), while a third, the purely abyssal *Cleonardo appendiculata* is only known from two localities. Apart from the amphipods it is mainly the medusæ which contribute to the endemic arctic deep-sea plankton, the three species *Atolla tenella*, *Trachynema arctica* and *Botrynema ellinorœ*. They are all exclusively abyssal, the first two are however only known from one and the third from two localities. Finally we must mention a pelagic nemertine, *Dinonemertes alberti*, which has been caught four times in the depth of the Polar Sea.

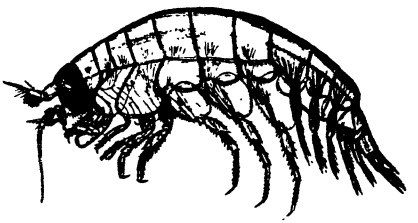


FIG. 95.—*Cyclocaris guilelmi* ♀, 3 × natural size. (After G. O. Sars, redrawn.)

None of the genera mentioned is genuinely arctic-abyssal. *Botrynema* occupies an isolated position within the northern fauna because this genus contains apart from the arctic species only another one which is antarctic (*B. brucei*).

A RETROSPECT ON THE MAIN REGIONS OF THE DEEP-SEA FAUNA

It has just been emphasized that the temperature of the Arctic Deep-Sea below 500–560 m. depth (the greatest sill depth of the North Atlantic Transversal Ridge) lies at 0° C. or below. The endemic species of the Arctic Deep Sea are therefore confined to water of this low temperature. Only in rare exceptions are they found in a somewhat higher temperature, for instance at +1° C. This temperature of 0° C. is the upper limit of temperature not for the arctic,

but for the high-arctic species of the shelf fauna. If we want to employ the same terminology for the deep-sea fauna as for the shelf fauna, which is very desirable, we are able to state that the endemic fauna of the Arctic Deep-Sea is not only arctic but high-arctic and that this high-arctic fauna borders immediately at its southern limit, the North Atlantic Transversal Ridge, on an abyssal fauna which

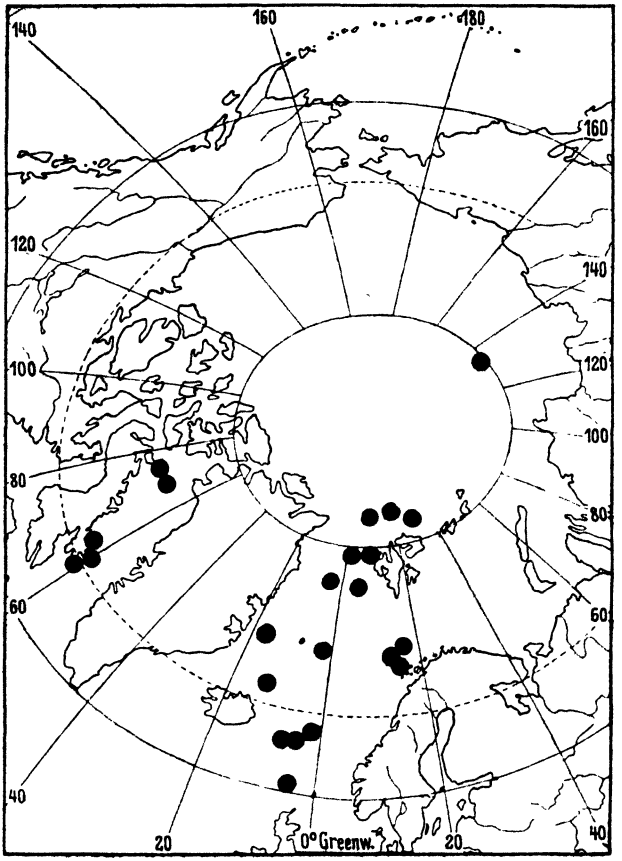


FIG. 96. Distribution of the pelagic amphipod *Cyclocaris guilelmi*.

continues uninterruptedly even through equatorial regions. This is evidently connected with the well-defined topographical and hydrographical boundary mentioned above, but also with the fact that this Atlantic abyssal fauna lives at a temperature which is closely related to that obtaining in the Arctic Deep-Sea. South of the Denmark Strait between Greenland and Iceland the temperature is at the most

3–4° C. from 800 m. down to abyssal depths, and this temperature continues uninterruptedly southwards in deeper layers and at 2000 m. depth reaches further than the equator. At these degrees of temperature we find northwards up to the coasts of Greenland quite a different animal world from that of the Arctic Deep-Sea. This Atlantic abyssal fauna lives even in equatorial regions at a temperature which would be considered arctic (low arctic) if applied to the shelf fauna. But for purely geographical reasons it is obviously not practicable to call this fauna arctic; it is unfortunately unavoidable that a terminology based on temperature has to be sacrificed in this case. Southwards this Atlantic abyssal fauna reaches to the borders of the antarctic abyssal fauna.

If we assume similar conditions for the Pacific as for the Atlantic—and we know nothing to the contrary—then the open-sea abyssal can be divided zoogeographically into only three or four main regions: an Atlantic, Pacific, arctic and perhaps antarctic region. But for the coastal abyssal and especially for the archibenthal we have to postulate a greater number of main regions.

Another peculiarity of the benthos of the abyssal as compared with that of the shelf must be mentioned. The view that abyssal genera are very widely distributed and often cosmopolitan is on the whole true. The oceans are distinguished not by special genera but by their species, if we disregard certain exceptions. *The main regions of the abyssal benthos are thus less strongly characterized taxonomically than the regions of the shelf benthos.* This is only another formulation of the law of the wide distribution of species. The reason for this phenomenon may be found chiefly in the uniform abyssal environment and partly also in the less frequent abyssal barriers to distribution.

THE DEEP-SEA FAUNA IN THREE INLAND SEAS

A few inland or marginal seas deviate both as regards hydrography and fauna from the general picture just drawn of the deep-sea fauna. We will discuss three of them which have been more closely investigated. Topographically they are similar in that they are cut off by high submarine sills from the neighbouring ocean deeps. This is also the main reason for their hydrographical and zoogeographical pecularities.

The Mediterranean

It is well known that the Mediterranean is separated from the Atlantic in the west of Gibraltar by a submarine sill whose deepest ridge lies only 320 m. below sea level. The deeper water of the ocean

is therefore debarred from entering the Mediterranean. This is, however, due not only to the sill mentioned above but also to the currents through the Strait of Gibraltar (fig. 97). Here, a superficial current enters the Mediterranean and an undercurrent leaves it. The level of the boundary between upper and lower current is here the critical depth.[261, 471] The water of the ocean is debarred from the Mediterranean already at a depth of about 160 m. This barrier conditions the special character of the deep water in the Mediterranean; it prevents the supply of relatively weakly saline, cool, fully-oxygenated Atlantic deep water into the Mediterranean, whose deep water is characterized by low oxygen content, relatively high and almost constant salinity and high and fairly constant temperature. The difference in temperature compared to the ocean may be seen from the following table.[470]

TABLE 46

THE WATER TEMPERATURE IN THE MEDITERRANEAN COMPARED WITH THAT OF THE ATLANTIC OCEAN

Depth in m.	Temperature	
	Atlantic south of Azores	Mediterranean between Sicily and Palestine
Surface (annual mean)	19–20° C.	19–21° C.
100	15–18	15–17·5
200	14–16	14–14·7
400	12–14	14–14·5
600	10·5–11	13·5–14
800	8·5	14
1000	8	13·8
1500	5	13·5–13·9
2000	3·8	13·5–13·7
3000	2·7	13·6–13·7
4000	2·5	13·5

The decrease in temperature towards the deep is thus much less, the temperature of the deep water much higher in the Mediterranean than in the ocean. It may be supposed, therefore, that the Atlantic stenothermal abyssal fauna cannot flourish in the Mediterranean. This is actually the case. Already in 1882 P. Fischer was able to demonstrate for the western part, and v. Marenzeller in 1895 by his investigation of the "Pola" material, that *no purely abyssal fauna exists in the Mediterranean.* These results, at first obtained from molluscs and echinoderms, were confirmed by later investigations on polychætes by the latter author, and other investigators, too, obtained on the whole similar results by investigating decapod crustaceans[2]

and fishes.[67] It was also found that the abyssal regions of the eastern Mediterranean are poorer than those of the western.[533]

However, the Mediterranean possesses a deep-sea fauna, namely an archibenthal-abyssal one; for in the archibenthal zone which is supposed to have its upper limit at about 200 m. depth where annual fluctuations in temperature stop, we find a fairly well-developed fauna which reaches down into abyssal depths. Even at the greatest depth in which dredging has been performed (3620 m.) eight specimens of the deep-sea holothurian *Pseudostichopus occultatus* were fished up.

That these peculiarities of the Mediterranean deep-sea are due to the distribution of temperature also follows from the fact that littoral

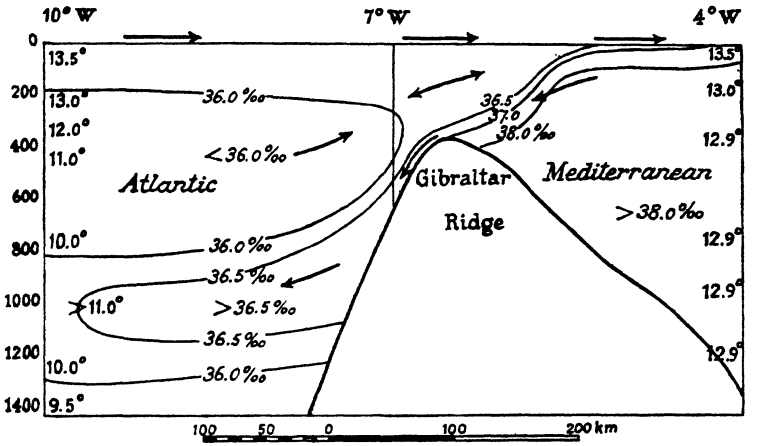


FIG. 97.—Currents and salinity on either side of the Gibraltar Ridge. (After G. Schott, redrawn.)

animals descend more generally into the deep than they do in the ocean.

The Red Sea

The geological history of the Red Sea has already been discussed above (p. 88). Hydrographically the sea shows the same characteristics as the Mediterranean, but they are intensified. The Red Sea, whose greatest depth is 2800 m., is divided from the Indian Ocean by a sill whose lowest point lies only about 100 m. below sea level[551] (the highest point is not in the Bab-el-mandeb Strait but in the Red Sea near the Hanish Islands). The deep water of the Indian Ocean is therefore excluded from the Red Sea. Hydrological conditions

may be seen from the table below, which also contains the temperature of the open sea to facilitate comparison.

TABLE 47

TEMPERATURE, SALINITY AND DISSOLVED OXYGEN IN THE RED SEA, AND TEMPERATURE IN THE INDIAN OCEAN OFF THE MALDIVE ISLANDS.[550, 470]

Depth in m.	Temperature, ° C.		Red Sea	
	Indian Ocean	Red Sea	Salinity, ‰	Oxygen, c.c./litre
0	28–29	25–30	37–40	3·99
100		25	39	3
200	13–15	21–25	40·1	2
400	10·2–11	21–22	40·3	0·53
600	9	21·4–21·8	40·5	0·52
800	7·5–8	21·5		
1000	6–7	21·5		
1500	4	21·5		2·04
2000	2·5–3	21·5		

The deep water is thus abnormally warm. From about 300 m. down, the Red Sea is warmer than any other marine region at a corresponding depth. This must, of course, influence the faunal zones.

The best known among the inhabitants of the deep-sea region of the Red Sea are the decapod crustaceans which have been investigated by Balss.[31] Of this animal group the otherwise often widely distributed abyssal species of the Indian Ocean are missing, evidently because they cannot support the high temperatures or were unable to overcome the high entrance sill. But the decapods which in the Indian Ocean are confined to the upper shelf descend in the Red Sea into the deep which conforms well with the thermal peculiarities of this sea. Among the rest of the animal groups the molluscs (mainly gastropods) are the main colonizers of the deep sea, but even these molluscs are not abyssal in other seas and generally also not littoral, but archibenthal,[173] which makes their appearance in the warmer deep-sea regions of the Red Sea remarkable. It is noteworthy that several animal groups occur only in the shallower regions of the coastal water, or they disappear sooner than in other seas below the 2000 m. level, so for instance sponges, echinoderms and ascidians. The latter have only been caught from the shore but have not been found in any of the 60 dredging hauls in varying depths[337, 338]; Spandl[490] reports that all the species of amphipods which are known from the Red Sea have been collected in pelagic regions, while the dredging operations at different depths did not produce a single species. It is still an open question how this peculiar

distribution of the several animal groups can be explained. The material investigated so far comes almost entirely from the Austrian "Pola" expedition of 1895–98.

The Sea of Japan

The Sea of Japan has a peculiar history. According to a summary of relevant investigations which was given by Lindberg[303] in his account of the fish fauna, this sea is assumed to have been a shallow brackish basin at the end of the Tertiary Period. During the first Ice Age a considerable raising of the land took place to the extent of more than 700 m. and this united the Japanese islands in the north and south with the mainland, so that the region was transformed into a fresh-water lake. But during the first interglacial period a still greater subsidence took place, to the amount of 1200 m. During a second Ice Age another elevation took place, followed by a lesser subsidence in the post-glacial period. If this history corresponds with the facts, the Sea of Japan has been subjected to changes of peculiar violence. The great interglacial subsidence seems, however, not to have left behind any deep-sea relicts. This is regarded as due to the fact that the bottom of the Sea of Japan did not reach its present depth of about 4000 m. until comparatively recent times. The present sills between this sea and the Pacific are nowhere deeper than 165 m. and the deep regions of the two seas are thus not in communication with each other.

This is the reason for the fact that the Sea of Japan, despite its considerable depth, lacks a specifically abyssal fauna, although such a fauna, rich in species, exists off the outer parts of the Japanese islands. Since this was first pointed out by Derjugin & Kobjakova in 1935 for the decapod crustaceans[122] the facts have been confirmed by investigations on other groups of crustaceans[199] and fishes.[303] On the other hand there is found in the abyssal region a fauna of eurybathic species, of which some have descended from the shelf down to a depth of 3500 m.

THE PROVENANCE OF THE BENTHAL DEEP-SEA FAUNA

If we turn our attention first to the question of the provenance of the arctic deep-sea fauna, we are confronted with two possibilities and two interpretations, either of which in their way may be true.

In his investigations on the fishes of the Arctic Deep-Sea Jensen (1905) came to the conclusion that all its endemic species derive from arctic or at least far-northern littoral fishes. Thus *Cottunculus subspinosus* is to be derived from the arctic littoral *C. microps*, and *Raja hyperborea* from *R. radiata*. Jensen was able to show further

that for the liparids the transition from littoral to archibenthal and abyssal life was connected with a reduction of the sucker formed by the abdominal fins, since the soft deep-sea bottom did not provide the firm objects necessary for attachment by this means. At the same time the lower radials of the pectoral fins developed downwards and acquired, as for instance in *Rhodichthys*, the appearance and the position of abdominal fin radials. The morphological modifications show very clearly in these cases that littoral species must have been the ancestors of the abyssal species.

For certain members of the non-arctic deep-sea fauna there are also reasons for supposing that they derive from cold regions of the shelf. The equatorial submergence, so common among arctic and antarctic species, shows of course how the deep sea is still colonized from the shelf region, since it cannot be doubted that they spread in most cases initially from the shelf. The Polar connection of the abyssal fauna were also strongly emphasized by the earlier zoogeographers and taxonomists, e.g. Wyville Thomson,[553] Ortmann,[395] Locard,[304] v. Martens & Thiele[327] and Michaelsen.[335] The examples given by them could easily be increased by many others.

Yet the shelf regions of the cold zones cannot have been the main source of the abyssal fauna, since the fauna of these shelf regions is for several taxonomic groups considerably poorer in species than the abyssal fauna, or even lacking in species related to this fauna. Examples of this are the gorgonarians, pennatularians, antipatharians, madreporarians, several groups of crustaceans, stalked crinoids, the spatangoid sea-urchins and most fish families with abyssal representation. That the abyssal fauna in the last resort derives from the shelf fauna is indubitable, but the shelves of the warmer coasts have obviously played a more important part than the more polar shelf regions.

ARCHAIC TYPES WITHIN THE DEEP-SEA FAUNA

At the beginning of deep-sea investigation, the great interest which was taken in this new sphere was combined with the hope of discovering especially archaic forms in the deep sea. This was prompted by the occurrence in some early finds of types which were otherwise known only from remote geological periods; among these types *Rhizocrinus lofotensis* (fig. 87, p. 281), discovered by Michael Sars, and several corals which had grown on the above-mentioned telegraph cable in the Mediterranean, are especially well known. It soon showed itself, however, that such "living fossils" do not play so dominating a role in the deep-sea fauna as was at first supposed. Still they are by no means few in number, and we shall first

briefly discuss the most important ones, among them also some pelagic examples.

The Radiolaria, according to Haecker,[203] provide excellent examples of great geological age. Of the so-called Microradiolaria (Sphærellaria and Cyrtellaria) it can be shown that almost all are represented themselves or by closely related forms in Jurassic, Cretaceous and Tertiary deposits. The Radiolaria mentioned belong, to use Haecker's apt expression, to the category of enduring types (Dauertypen). According to him it would, however, be premature to draw from that the conclusion that the surface forms are not equally ancient.

Of living hexactinellid genera, 10 were formed as early as the Cretaceous.[222] *Pleurochorium* was known only from the Upper Cretaceous until the "Siboga" expedition revealed that it still lives in Indo-Malayan waters, and the likewise Indo-Malayan *Tretorete* belonging to the same group is up till the present the only known living representative of the otherwise fossil family Craticulariidæ.[251]

The decapod crustaceans contain several archaic types as Doflein[130] and Balss[29, 30] have emphasized. In the first place we may mention the Palinurid family Eryonidæ, most representatives of which we know in a fossil state and whose recent species formed one of the greatest surprises of the first deep-sea expeditions. In this family, both genera *Polycheles* and *Willemoesia* are recent. By their claws on all four anterior pereiopod pairs and by a pointed telson they strongly recall the Jurassic genus *Eryon*. In the Triassic and the Jurassic the Eryonids were littoral animals with well-developed eyes, whereas in modern forms a reduction of these organs has taken place, a good indication that their life in the deep sea is secondary. In the Astacura group the Homaridæ provide similar examples in both the genera *Phoberus* and *Thaumastocheles* in that they are most closely related to littoral genera of earlier geological periods, which are now extinct. Among the crabs, the most primitive, the lower Dromiacea (*Homolodromia, Dicranodromia*), which are related to the Prosoponidæ of the Jurassic and the Cretaceous, are inhabitants of the deep sea. Among the prawns, the deep-water group Aristeæ belonging to the Penæidæ has relations as early as in the Jurassic.

During his investigation of deep-water molluscs, Locard[304] found that a relatively large number of these are identical with Tertiary species, for instance 119 with Miocene and 288 with Pliocene species. Kr. Bonnevie[51] remarks that the deep-water pteropods (thus pelagic forms) *Peraclis diversa, Limacina helicoides* and *Clio falcata* have a more archaic structure than the surface forms. (The well-known likewise pelagic squid genus *Spirula* is, according to the

latest investigations, and contrary to earlier views, by no means an archaic form.[274])

The stalked Crinoids of the deep sea have been especially regarded as archaic types. Many of them go back to ancient geological periods, e.g. *Rhizocrinus* (Eocene), *Bathycrinus* (Eocene), *Millericrinus* (Jurassic until Lower Cretaceous), and five genera of the Hyocrinidæ which were formed as early as the Upper Jurassic.[81]

On the other hand, the deep-sea fauna also contains types which are more differentiated than their nearest relatives among the species of the shelf. Thus, among the decapods of the family Galatheidæ, the more primitive genera *Galathea* and *Munida* are shallow-water forms, while the real deep-sea genera *Uroptychus* and especially *Munidopsis* are the most differentiated, that is to say, the last developed genera.[26] Similar examples could be quoted also from other animal groups, especially from the fishes (cf. for examples p. 308), and J. Murray was undoubtedly correct when in 1895 he pointed out that the fauna of the shelf is at least as rich in archaic forms as the deep-sea fauna, e.g. *Heliopora*, *Limulus*, *Lingula*, *Nautilus*, *Branchiostoma*, *Cestracion*. It is, however, not improbable that the deep-sea fauna is relatively, in proportion to the total number of deep-sea forms, richer in such forms and so has become a refuge for more conservative types, which have elsewhere become extinct. In any case, it can be regarded as established that a deep-sea fauna has existed for a very long time. This also follows from the existence of groups, rich in species, of high taxonomic rank, such as the Hexactinellida and Elasipoda which apparently have been genuine deep-sea animals since the remote time when their ancestral forms have split off from their then relatives.

CHAPTER XIV

THE UPPER PELAGIC OR EPIPELAGIC FAUNA

WE have so far occupied ourselves with the fauna of the firm substratum, that is the benthic fauna. Turning now to the pelagic fauna we are concerned with a completely different marine biotope, namely the "free" water found at a lesser or greater distance from the bottom and the coast. The faunistic difference between the biocœnoses of the two biotopes is, of course, dependent on ecological circumstances, as is any other faunistic difference. Pelagic organisms have been able to master the free water only by perfecting their swimming or floating powers, which enabled them to leave the bottom for a considerable time or during their whole lifetime. This is another example of the fact that zoogeography has to have continual recourse to ecology if it wants to explore the deeper causes of its phenomena. But the purely ecological aspects of adaptations to planktonic life will not occupy us to any great extent in this regional zoogeographical account. We shall consider it only in so far as it explains the differences in the regional distribution and the number of individuals.

The planktonic fauna of the seas has been investigated by many minor and major expeditions, among which we instance the following: among the major expeditions an American one in 1838–42, the copepod material of which was described by J. D. Dana, who thus became the pioneer of research into the geography of plankton; the English "Challenger" expedition of 1873–76, which concentrated primarily on deep-sea research but also greatly enriched our knowledge of the plankton; the German plankton expedition of the Humboldt Stiftung (1889); the German deep-sea ("Valdivia") expedition (1898–99); the "Siboga" expedition in the Indo-Malayan region 1899–1900; the German Atlantic "Meteor" expedition (1925–27); the several American expeditions on the "Albatross" and the "Carnegie" in the Atlantic and Pacific; the expeditions in the Atlantic and Mediterranean of Prince Albert of Monaco; the arctic and antarctic expeditions of several nations at the turn of the century and later; the Atlantic expeditions of the Norwegians on the "Michael Sars"; the Danish on the "Ingolf" and "Dana" and the British John Murray expedition of 1933–34; and soon. We must add to these expeditions the many investigations undertaken by

marine biological stations especially in Europe and North America and the many years' work of the International Council (Conseil permanent international pour l'éxploration de la mer) in the North Atlantic. By all these expeditions extensive material was collected. For instance, pelagic copepods were examined from between 1500 and 2000 stations.

GENERAL REMARKS

Terminology

Among the many technical terms of the planktonic literature we are here concerned only with the following:

The *pelagic* fauna is the animal biocœnosis (community of organisms) of the free water. The pelagic fauna is not quite the same as the planktonic because it comprises *plankton*, the community of organisms which drift passively in the water, as well as *nekton*, the freely swimming animals.

The term *epipelagic* denotes the upper water layers and their organisms. Its lower limit is very variable in nature (see p. 352) and different investigators have placed it at different levels. In the present work it will only comprise the upper 150–200 m. Its organisms are called *epiplankton* and *epinekton* respectively. Below this epipelagic layer lies the deep water with its *bathypelagic* fauna.

A further division is made according as the organisms are more or less completely adapted to pelagic life. *Holopelagic*, or *holoplanktonic* is a term denoting organisms which remain during their entire lifetime, that is during all stages of development, pelagic or planktonic; *meropelagic* or *meroplanktonic* are those which, on the other hand, temporarily belong to the benthos, for instance during one stage of their development, be it only in the egg stage.

As regards the position relative to the coast, the coastal organisms, which are dependent upon the coast or the shelf, are termed *neritic* and they are contrasted with the open-sea organisms; the latter are often simply called oceanic, but this term is less exact; *high-oceanic* is more unambiguous.

Finally, terms denoting the size of plankton organisms are often used. Plankton organisms of a size between about 5 and 60μ are called *nannoplankton* or dwarf plankton; with reference to the technique used for collecting it, it is also called *centrifuge plankton.* the still smaller plankton, the *ultraplankton*, does not concern us in the following account. The larger plankton which can be caught in nets is called *net plankton*, and it may itself be divided according to size: we distinguish the *microplankton* (individual size 60 to 500 or 1000μ), and *macro-* or *megaloplankton* (still larger specimens).

Nutritional conditions and quantitative distribution

It is well known that the most minute plants, because of their ability of photosynthesis, constitute the primary source of food for plankton animals. Wherever this plant nannoplankton is to be found most abundantly we should, theoretically speaking, expect the richest zooplankton. After the technique of nannoplankton investigation had been perfected, especially by the pioneer work of H. Lohmann, it has been possible to gain more detailed information about the composition of the plankton, and chemical investigations have largely established the dependence of the nannoplanktonic algæ on dissolved mineral nutrients.

Among the dissolved mineral substances nitrates, and perhaps to an even larger extent phosphates, play an important part, because, according to Liebig's minimum law, growth is limited by that essential factor which is present in a minimal quantity. This law was first applied to plankton research by K. Brandt.[56] The content of mineral nutrients in solution in seawater derives from two sources: first, an allochthonous source, of external origin, the rivers bringing dissolved substances from the land and lakes into the sea, and then an autochthonous source, since the organic substances which are produced in the sea itself and for the most part are found near the coasts are largely decomposed after death by chemical processes due to bacteria; they combine again in different ways and finally produce inorganic substances (phosphates, nitrates, etc.) which can be used as plant food. This process of mineralization takes place to a certain extent in the open water but mostly at the bottom. Autochthonous as well as allochthonous mineral nutrients thus collect in coastal water, and to a certain extent on the deeper sea-bottom, but only a small fraction of them is found in high-oceanic water. The important connection between the concentration of dissolved salts, mainly phosphates and nitrates, and the amount of plankton has been investigated particularly by Nathansohn,[372] and Hentschel & Wattenberg.[229] The activity of nannoplanktonic algæ diminishes the mineral content of the water and at the same time continually builds up organic compounds with the result that the seawater is the poorer in plant nutrients, the longer it has been exposed to plant assimilation at considerable distances from the coast. Consequently, the quantity of high-oceanic nannoplankton becomes proportionally less and the quantity of the animals which use this plankton is affected to the same degree. In this respect, the small oceanic islands act, although to a lesser extent, as coasts.

This originally theoretical consideration has been borne out by observation, as may be seen from investigations undertaken in the

Atlantic during recent years. South of the equator there is a gigantic vortex of currents between 10–15° S. and 25–30° S., the central water of which, the halostase, has been exposed to the assimilatory activities of the nannoplankton for a very long time. Here is a minimum region (fig. 98) where the water contains only 2000–5000 cells per litre, while the number of cells near the coast of Africa

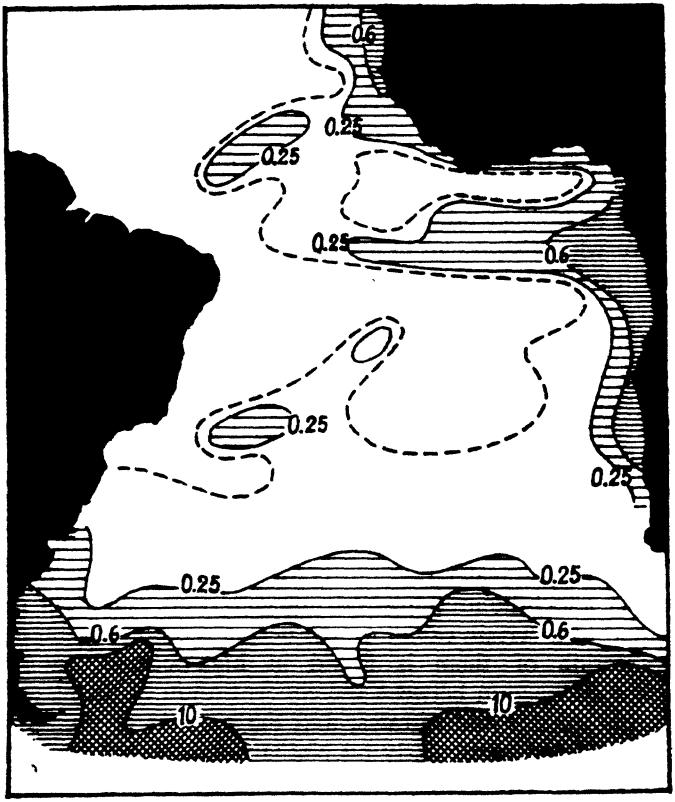


FIG. 98.—Distribution of phosphates in the South Atlantic: mg. P_2O_2/m (After Wattenberg and Sverdrup *et al.* Reprinted by permission from Sverdrup, Johnson & Fleming, *The Oceans*. Copyright, 1942, by Prentice-Hall, Inc., New York.)

reaches 50,000, in places more than 200,000. In this halostase the surface water sinks down slowly with the result that the deep water here is on the one hand warmer, but on the other much poorer in plankton than the deep water of neighbouring regions. North of the equator the Sargasso Sea represents a similar vortex of currents (halostase). For the central part of the Arabian Sea, too, similar

conditions have been proved,[523] and A. Agassiz, as early as 1906, found conditions like these in the south-eastern Pacific north of the West Wind Drift, west of the Peru Current and south of 10° or 20° S. The halostases are also termed central minimum regions.

Similar differences are often found when the non-halostatic tropical parts of the Atlantic are compared with its cooler regions. Lohmann[308] has compared the European coastal waters, the North Atlantic open sea and the tropical Atlantic open sea concerning their

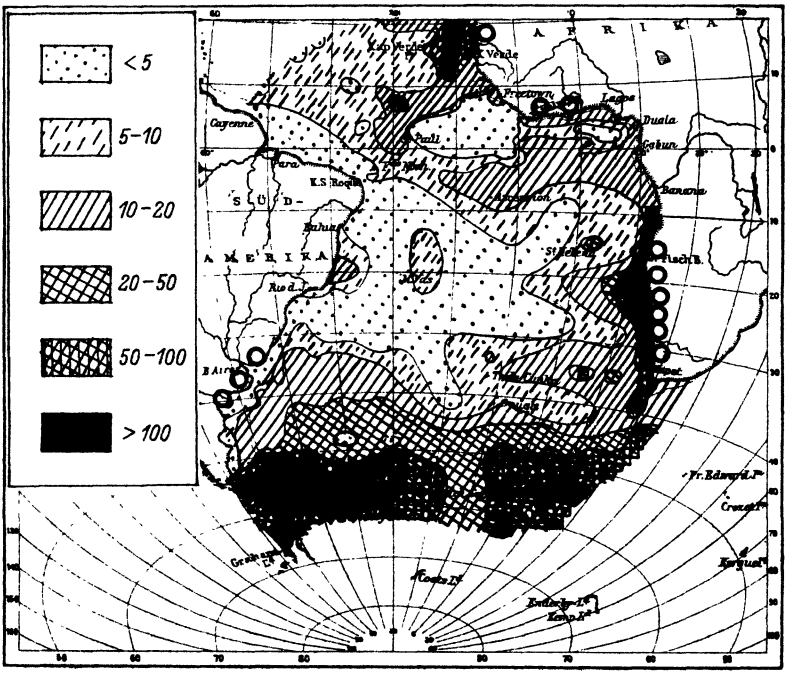


FIG. 99.—Quantities of the entire plankton at 0–50 m. depth in different regions of the South Atlantic. The figures indicate thousands of individuals per litre. The circles indicate upwelling water off the coasts. (After Hentschel, 1933, modified.)

content in nannoplankton. He arrived at the conclusion that the density of population of the upper 15 m. in these three regions approximates 1000:20:2. If these calculations are not confined to the surface layer, the corresponding figures are 1000:120:25. It will thus be seen how greatly the plant content of the sea diminishes if one turns from the coastal water to the open sea. Net plankton and nannoplankton show a similar behaviour in this respect[258] which is easily comprehensible in view of the dependence of the

animals on plants. Similar conditions are found if we compare the tropical and southern warm-temperate Atlantic with the adjoining Southern Ocean.[223, 225] In the Pacific, too, we find the same[187]; the Peru Current which is rich in plankton and the open sea to the west, which is poor in plankton, are good examples of this phenomenon. It is obvious that the low temperature in itself is not the primary cause of the rich plankton. The primary cause is rather the content in plant food, mainly phosphates, and where the unused stores of this food are brought up by a vertical circulation into the illuminated upper water layers, abundant phytoplankton can develop. Such an abundance develops more occasionally in tropical regions because of the weakness of the so-called convection currents. These vertical currents, caused by the cooling down of the water during the winter so that the surface water sinks and the bottom water rises, play an important part in the north.

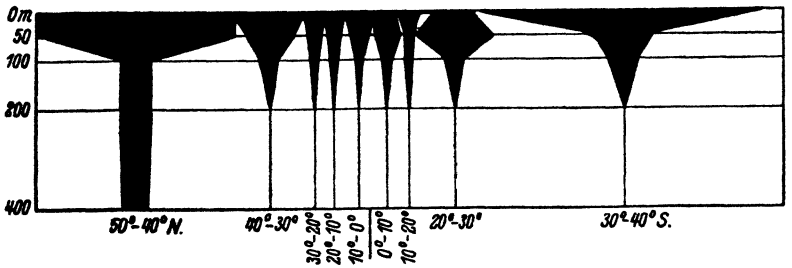


FIG. 100.—Quantities of Phytoplankton in different depths and regions of the Atlantic between 50° N. and 40° S. 1 mm. width=580 cells per litre. (After Lohmann.)

The main categories into which water is divided in limnology also hold good for the oceans. These are *eutrophic* water, rich in nutrients, and *oligotrophic* water, which is poor in nutrients. Eutrophic water is clearly preferred by most plankton animals. Species seem to occur, however, among the appendicularians which are better adapted to oligotrophic water, a phenomenon which is difficult to understand because nannoplankton is the characteristic food of appendicularians (p. 313).

The wealth of the cooler and coastal parts of the sea compared with the tropical open-sea regions holds good, however, only for the number of individuals and not the number of species. The latter is considerably greater in the tropics and it is also much greater in the more saline oceanic water than in the brackish water outside the estuaries, although the number of individuals is greater here.

Reproduction area and sterile expatriation area

H. Lohmann has in several publications given figures which show that we have to distinguish between regions where the pelagic fauna flourishes and those where it barely manages to exist. In the former the number of individuals is a thousandfold greater than in the latter areas. Similar conditions prevail also among the littoral fauna, but they are more marked in the pelagic fauna.

It is clear that such less favourable regions may be open to a different interpretation from the point of view of zoogeography. In some cases where a species occurs in a region as a dwarfed variety or with very few individuals, it may nevertheless reproduce itself to a sufficient extent and thus have its home there. But in other instances it remains questionable whether the species is able to exist independently in the unfavourable region or whether it would not die out there if it were not continuously reinforced from the more favourable regions. This would naturally happen if reproduction cannot take place at all, or only to an insufficient extent. In such a case the unfavourable region is obviously outside the real home of the species, and it would be possible to contrast the autochthonous main mass of the species which lives in the reproductive area with an allochthonous sterile expatriated contingent in an *expatriation area* ("steriles Zerstreuungsgebiet"[146]; cf. p. 176).

This question is not only of ecological but also of zoogeographical interest, since the expatriation area does not belong to the region of distribution in the proper sense. Examples may, for instance, be quoted from the North Atlantic. Störmer[528] (the article is known to me only from a quotation in[479]) has drawn attention to the fact that the Gulf Stream, which at the beginning has a mean temperature of 27° C. whereas it becomes colder and colder as it continues as the North Atlantic Drift, until at its farthest north it is little warmer than 0° C., as a consequence successively loses one species after another during its course. As each species passes out of the temperature range within which it can reproduce, its final disappearance becomes a certainty, the actual place depending on the length of life of the individual and the rate of the current. *Lepas anatifera* and *L. fascicularis* regularly occur off the coasts of Scandinavia. They do not reproduce here but have been transported by drift-wood from warmer seas.[62] The same is true of several siphonophores in the Arctic Sea and of the well-known prawn *Pandalus borealis* in high-arctic regions (fig. 57) and probably of several copepods which are transported by the warm Kuroshio Current to the Bering Sea.

The notion of "expatriation" may be able to supply the answer

to an old zoogeographical problem. It seemed remarkable to several investigators of plankton that, for instance, species in the Atlantic which seem to have their optimum at 25–27° C. can also occur at a considerable depth of the tropical or subtropical seas at a temperature of only a few degrees above zero, although they do not occur in the same low temperatures in the cold seas. Their occurrence in this cold deep region seems to show a eurythermal character and in order to explain their absence in the cold sea resort was had to the assumption that it might be due to unknown biocœnotic circumstances.[179] An expatriation zone in the deep sea is a more probable explanation, particularly if it lies in one of the two halostases where there is exceedingly little transport in a horizontal direction. There clearly a sinking down to abyssal depth may occur more easily than a horizontal spreading to arctic or antarctic regions which are at least a thousand times farther away (2000–3000 km.).

Wolfenden[585] has mentioned almost 40 copepods which may serve as examples for this phenomenon. They were caught in the Atlantic between 35° N. and 35° S. and normally belong to the surface water (0–400 m.), but have also been found at about 3000 m. depth. Between 20° and 50° N. the North Atlantic intermediate water is sinking down. "There can be little doubt that as this water mass sinks down and then flows southwards it carries with it numerous species that normally are to be found inhabiting the warm, tropical and subtropical surface layer."[479]

It would certainly be desirable if in data on the temperature requirements of animals the important distinction were made between the region of reproduction and the expatriation region, or, what amounts to the same thing, if a distinction could be made between the purely individual need of the adult animal and the requirements for maintaining the species. This is, of course, true not only for the copepods but also for other plankton animals, not only for the pelagic fauna but also for the benthos, and not only as regards temperature but also other living conditions. That a difference in this respect exists between the various stages of the animal's life is particularly clearly seen in the researches undertaken during the last decade on economically important fishes (cf. p. 112–114).

The passive transport of pelagic animals

The faculty of floating which the plankton organisms possess carries with it the possibility of unobstructed transport. This is the case more especially with holopelagic animals. There is no time limit to their pelagic life, it continues during the whole of the individual's lifetime and also during the whole of the life of the species, generation after generation. Some of the most important barriers

for shelf animals, the open spaces of the ocean, thus have no effect, and as all oceans are connected by ocean currents a barrier of land masses means little. According to Wüst[590] water of intermediate depth flows from the Northern Atlantic southward and eastward through the Indian Ocean and Pacific and again into the Atlantic. The distribution of the holopelagic animals is therefore mainly dependent on their own physiological behaviour, especially with regard to temperature.

Connected with this much less pronounced isolation of the various pelagic regions is another difference from the shelf fauna. While the main regions of the latter are in the first instance characterized by special genera, families and sometimes higher taxonomic groups, the main regions of the pelagic fauna are characterized rather by species whose genera also occur in other main regions. In other words: *the main faunistic regions of the high-oceanic pelagic fauna are more weakly characterized taxonomically than the main regions of the shelf.*[146] This is even more apparent if we compare it with the terrestrial fauna. The pelagic fauna in this respect recalls the abyssal benthic fauna.

COSMOPOLITES

Before we go into details of the pelagic fauna of the special regions we shall briefly consider a group of species which has no importance for the division into regions, but is very interesting from other points of view, namely the "cosmopolites". This expression may naturally be used in a wider or a narrower sense and has a different meaning for different authors. Here we shall term cosmopolites those animals which live in the Atlantic as well as in the Indian Ocean and the Pacific, in equatorial as well as in both cold-water regions, even if they should happen to avoid the high-arctic or high-antarctic regions.

These cosmopolites may be divided into two main groups which, however, cannot be sharply distinguished: an eurythermal and a more or less stenothermal group. Since stenothermal warm-water cosmopolites are an impossibility because the warm water itself is not cosmopolitan, the stenothermal cosmopolites are cold-water animals which have the widespread distribution mentioned above, but which avoid the warm surface water of the Tropics and Subtropics by submergence.

Eurythermal Cosmopolites.

There are not many species in this group. Several among the Atlantic species which were previously considered to belong here

have been found, according to the latest investigations in the Atlantic sector of the Polar Sea, to belong in reality to the North Atlantic Warm-water Drift, which transports them as far as Spitsbergen and the Barents Sea, while they are missing from the arctic currents flowing in a southerly direction at Labrador and Newfoundland. This seems to indicate that these species are situated in an expatriation area in the North Atlantic low-arctic region. More pronounced eurythermal cosmopolites are, for instance, among the siphonophores *Lensia conoidea* (syn. *Galeolaria truncata*), among ctenophores *Beroe cucumis*, which "is cosmopolitan in the widest sense of the word",[287] among polychætes *Tomopteris ligulata*, which is found at temperatures between −1·78° and 25·9° C., and among the copepods *Oithona similis*, which, from the Northern Polar Sea, is distributed throughout the warm region (Mediterranean, Red Sea, Indian Ocean, Pacific) to the high-antarctic sea, where several thousand specimens have been taken from water colder than −1° C. The maximal depth at which the species is found is 4000–5000 m. Another copepod with roughly the same distribution is *Scolecithricella minor*, which, from the North Polar Sea and the Labrador Current, is found throughout the whole of the Atlantic, where it also occurs in the tropical surface water, down into the West Wind Drift and to South Georgia, where it is one of the three quantitatively most important copepods, besides which it is also known from the East and West Pacific and from the Indian Ocean. A more careful survey of the types of distribution of the copepods would certainly increase the number of the eurythermal cosmopolites. Sewell[479] (p. 513) has, among his many lists of species, one which contains no less than 96 arctic and North Atlantic species that have been taken in antarctic and subantarctic waters. Several of them may, however, belong to the deep water of the non-arctic latitudes.

It is often difficult to decide whether a species should be included among the eurythermal or the cold-water cosmopolites; these groups merge into each other in nature without any sharp boundary. An example of this is *Sagitta maxima*, which is found in the Atlantic at various stations in the surface layers of the equatorial region, but which, however, occurs with a greater number of individuals within the cold-water regions north and south of it.[546] It is tempting to regard the species as mainly a cold-water form. This would be correct only if the temperature was the only factor which governed the number of individuals within the species. But we must take into consideration another factor which in this case probably has a greater influence than the temperature, namely the food supply, which, as we have seen earlier, is considerably more abundant in northern regions. Nannoplankton abundance, of course, does not

influence directly a predatory animal (*Sagitta*) but doubtless it does so indirectly by an increased supply of prey, for instance copepods. *S. maxima* may in this respect be regarded as the type of a whole group of plankton animals which is rich in species.

Cold-water cosmopolites

Since cold-water cosmopolites, because of their preference for cold water, occur in equatorial regions only in the cold deep water, they are partly bathypelagic and constitute a transitional group between the epipelagic eurythermal cosmopolites and the bathypelagic species. They are distinguished from the latter by their regular occurrence in the surface water of the Arctic and Antarctic, or at least in that of the boreal and antiboreal regions.

As example of this group we choose *Calanus finmarchicus*, one of the most often described of all marine invertebrates, and the most important copepod ecologically, since it constitutes the food of several whalebone whales and fish. The species is the first marine copepod which was described (fig. 101).

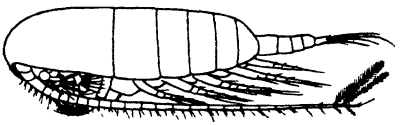


FIG. 101.—*Calanus finmarchicus*, ♀, 10 × natural size. (After G. O. Sars, simplified.)

In the North Polar Sea *Calanus finmarchicus* occurs also in high-arctic regions (north-east and north-west Greenland, 78° N.), it is very common in the most northern parts of the Atlantic and is found also in the subtropical and tropical latitudes of this ocean but as a rule in the deep water, it lives in the Mediterranean, in the deep water of the Indian Ocean and in the temperate and subantarctic regions of the southern hemisphere. In the Pacific its distribution is similar: it occurs both in surface and deeper water in the north, in the Bering Sea as well as the North Pacific, and shows submergence in warmer latitudes, as for example in the Gulf of California, off the west coast of South America, the Fiji Islands, south-east of Australia, the China Sea and the Red Sea.

Within the wide limits mentioned *C. finmarchicus* does not occur, however, at all uniformly. By far the greatest number of individuals is found in cold-water regions, particularly in the northern. Here it is, even to the south-west of Ireland, incomparably more prolific than any other planktonic copepod and in the north-western North Sea it is in some seasons by far the most important constituent of the food of the herring. The greatest numbers, however, are found in the

Norwegian Sea in its more eastern parts which are warmed by the Gulf Stream. Off the north-west of Norway it occurs in huge masses during the spring and early summer and it forms here a monotonous *C. finmarchicus* plankton ("Kril" of the Norwegian fishermen) as well as off Newfoundland, where it has been observed as red swarms in the sea. The maximum abundance is situated at about the middle of the Gulf Stream north of Cape Stat at 62° N. and at a fair distance from the coast. The numbers diminish near the coast. In the very populous regions the species serves almost exclusively as food for the blue whale (*Balænoptera physalus*). The most populated spawning grounds extend from the Faroes along the northern slope of the North Sea and the Norwegian coast from 62° N. northwards to Spitsbergen, where even in the northern fjords breeding still goes on. Breeding has also been found to take place even in north-eastern Greenland at a negative temperature; but as a rule it is supposed to take place at +4° C. and may occur even at 10° C. and still higher temperatures. The eggs are pelagic.

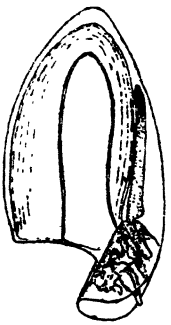


FIG. 102.—The siphonophore *Dimophyes arctica*, 3 × natural size. (After Chun.)

Bathymetrically *C. finmarchicus* behaves differently in the different oceanic regions. It daily undertakes migrations in a vertical direction. As has been mentioned earlier on, it is common on the surface of the Norwegian Sea, but it is here, too, fairly frequent in intermediate layers and in the arctic and high-arctic regions it prefers to live in the intermediate layers, probably because the water here is a little warmer than on the surface. The difference from the arctic *Calanus hyperboreus* is striking in these regions. To the west of Ireland it ascends to the surface during the night but remains in considerably deeper layers during the day and it shows the same habit in southern California. According to the relevant surveys it is supposed to be a purely deep-water form in the tropical and subtropical Atlantic, where it avoids the surface layer altogether. But if the numerous finds of *C. finmarchicus* which were made over a number of years by Prince Albert I of Monaco in the East Atlantic[453] (over 200 stations) are examined, it will be found that the species also ascends fairly frequently to the surface in southern latitudes (30–40° N.).

As a species of mainly cold-water character we may also regard the siphonophore *Dimophyes arctica* (figs. 102, 103), which is distributed from the Bering Sea and the high-arctic regions of

Greenland, Spitsbergen and the Kara Sea as far as the Antarctic Ocean, but in the warmer intermediate regions only in colder deep water.[286] The polychæte *Tomopteris septentrionalis* has a similar distribution.

Among other species of this kind we may mention the amphipods *Hyperia galba, Hyperoche medusarum, Primno* (*Euprimno*) *macropa* and *Themisto* (*Parathemisto*) *gaudichaudii* (=*T. compressa*), the first of which, although also high-arctic in the North Polar Sea, does not seem to overstep the antiboreal region to the south, while the rest occur generally also in the Antarctic. All are for the most part submerged in tropical latitudes, partially rare.

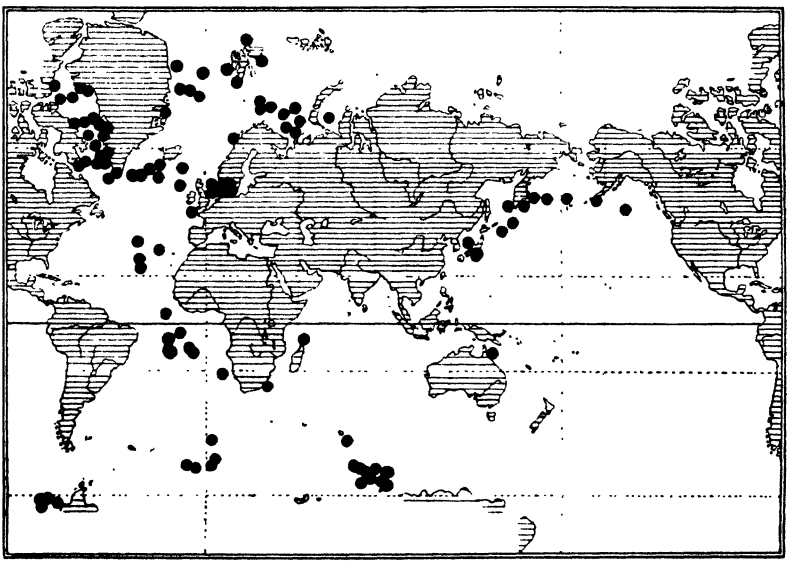


FIG. 103.—Distribution of the siphonophore *Dimophyes arctica*. (After F. Moser, 1925, and P. L. Kramp, 1942.)

One of the best examples of a cold-water cosmopolite is the chætognath *Eukrohnia hamata*.[546] It is frequent in the high-arctic part of the North Polar Sea of north-eastern Greenland and Spitsbergen, is found regularly in low-arctic, temperate and tropical latitudes in the Atlantic, but it has fewer individuals there and is confined to deeper water layers (fig. 104); south of the tropical belt it becomes again more numerous and has its frequency maximum in higher water layers. We find therefore an equatorial submergence which is clearly connected with the susceptibility for temperature. It lives in both polar seas in water of negative degrees of temperature; the upper temperature limit seems to lie between 10° and 15° C.

Limacina balea represents a borderline case. It is mainly boreal in the Northern hemisphere, and antiboreal, and to a certain extent antarctic, in the southern hemisphere. It may well occur also in the intermediate deep regions.

The *Calanus finmarchicus* type, to which several other species could be added, confronts us with a special problem. The wealth in individuals of this species in the north is particularly apparent when compared with the dearth in the tropical Atlantic. It seems therefore tempting to regard the species as in the main cold-loving, living in warm water under unfavourable climatic conditions. But is this really true? *C. finmarchicus* is not less frequent in warm-temperate regions than other species which occur there exclusively. But it is eurythermal and since it is therefore able to live also in northern regions it can make use of the enormous amount of food

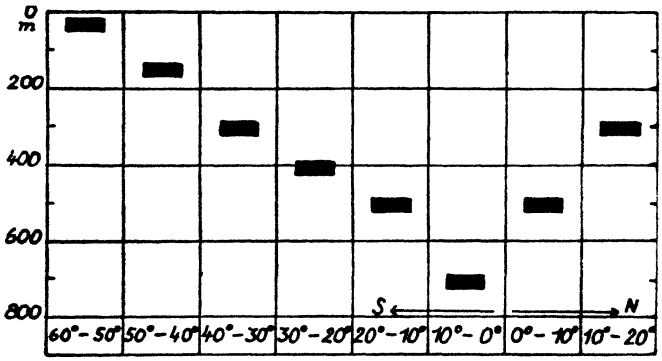


FIG. 104.—The greatest frequency at different depths of the chætognath *Eukrohnia hamata* in various parts of the Atlantic. (After Thiel, 1938, "Meteor" Expedition.)

of the northern coastal waters which is about 500 times richer than that of the tropics (cf. p. 315). It is, therefore, presumably able to produce considerably more eggs, and this is possibly the reason for the fact that it occurs in such masses in these regions. The colder water has perhaps not a direct influence on the mass occurrence in the sense that the species is particularly partial to cold. We do not know for certain (cf. *Sagitta maxima*, above p. 320).

THE PELAGIC WARM-WATER FAUNA

Giesbrecht in 1892 drew attention to the fact that the same pelagic warm-water copepods occur on both sides of America, and he postulated three main regions of the pelagic fauna: a warm-water region and a northern and a southern cold-water region. Most

plankton geographers concurred with this view; thus as regards the siphonophores,[78, 360] appendicularians,[312] pteropods,[332] salps,[15] pelagic amphipods,[414] tintinnids[283] and radiolarians.[203] Hentschel[228] has given a survey of the most important groups for the South Atlantic. The exceptions which have been found among the copepods partly concern neritic species, partly not the main pelagic regions but some subregions within them. On the whole we can adhere to the division of the pelagic fauna into three main regions.

We have seen already, (p. 213) that there is a well-marked boundary in the Southern Ocean between a northern surface water, which during the summer is warmer than approximately 15° C., and a southern colder surface water; this boundary is the antiboreal ("subtropical") convergence. In the northern hemisphere such a temperature boundary is less marked and less continuous. Several researchers into plankton geography hold the view that the most pronounced change of fauna in the southern hemisphere within the epipelagic plankton occurs at this convergence, and in the Northern hemisphere, too, a similar change of fauna at the same summer temperature of the surface, roughly 15° C., has been noted. But the drawing of a boundary between warm- and cold-water plankton is greatly complicated by the fact that the surface water from the colder side of the convergence flows down under the warmer and lighter water of the warmer side, and thus a lower (intermediary) current which is directed towards the equator transports cold-water species in this direction. On the other hand in the Atlantic, for instance, the originally warm Gulf Stream flows far north, where it is still noticeable in north-western Spitsbergen and south of Novaya Semlya, although with a greatly reduced temperature. The same plankton animal may therefore occur in very different water layers at its southern and northern boundaries, and it is true even more for the pelagic regions than for the shelf region that a rational regional zoogeography must take into consideration the distribution of the various different kinds of water in the depth zones and cannot confine itself to plotting the known localities of finds on the surface of the ocean.

If we attempt to penetrate deeper into the causal connections it will be seen that in most cases one and the same phenomenon is due to several factors, one of which may be more important than the others but it is not always decisive by itself. The cause is seldom a single factor but in most cases a complex of factors. If we speak of warm and cold-water plankton we mean therefore the plankton which inhabits the warm- or cold-water region, whether the sensitivity to temperature among the organisms is the only or main factor (which seems to be most probable) or not.

Circumglobal distribution

A large number of the holoplanktonic species are obviously only to a limited extent stenothermal, since they have tolerated transport by ocean currents south of Africa between the Atlantic and the Indian Ocean. And since the communication between the Indian Ocean and the Pacific goes through the tropics the result has been, that they inhabit warm-water regions of all three oceans. We give some examples of such species.

Protozoa. Most Tintinnoidea seem to belong here.[283] V. Haecker[202] and K. Meyer[334] have shown for the Radiolaria that many species of this group are "tri-ozeanische Warmwasserformen", particularly among the Tripylaria, for instance *Tuscarusa bisternaria* and *T. tubulosa.* Among the Foraminifera only species of the family Globigerinidæ are pelagic. The most common and best-known *Globigerina bulloides* (p. 270, fig. 82) was formerly regarded as mainly eurythermal or occupying a medium position between eurythermal and warm-water species but according to more recent investigations[532] it is possibly a cold-water form (but perhaps not very marked). *Globorotalia menardii,* on the other hand, is a warm-water form. As has been mentioned earlier on (p.273–4), it has been possible to allocate the various sediment layers to different climatic periods because of the presence of numerous shells of these two species in the globigerina ooze and their different attitude to temperature.

Siphonophora. According to Fanny Moser[361] the warm-water region contains on the whole a uniform Siphinophora fauna and species which are confined to one or two oceans are the exception. Circumglobal are, among the better-known species, *Velella spirans, Porpita porpita, Hippopodius luteus, Abylopsis escholtzii, Diphyes sieboldi, D. dispar,* which may be regarded as tropical. Other circumglobal species are a little more eurythermal and extend a little further north, for instance in the Atlantic. Among these are *Abylopsis pentagona, Galeolaria quadrivalvis, Agalma elegans, Physophora hydrostatica*; the latter is found in the north as far as southern Greenland, Iceland and the Barents Sea but does not occur constantly even in the North Sea.[286]

Ostracoda. Species of the pelagic genera *Conchoecia* and *Halocypris* generally inhabit all three oceans.

Copepoda. Because of their great number of species and individuals the high-oceanic copepods have often been the object of zoogeographical studies. Most warm-water species probably occur in all three oceans and several genera have this distribution, either entirely so or with the exception of a few species. We can only

mention a few examples here. *Sapphirina* is almost entirely a warm-water genus, as is *Copilia*[517] and *Corycæus*. Of the 15 species of the former, at least 14 have been found in all three oceans. The same is true also of a great number of other species, for instance *Acartia clausa*, *Pleuromamma abdominalis* (which also has a deep-water form *abyssalis*; fig. 105), etc.

It is interesting that of the copepod group Harpacticoidea, whose species otherwise inhabit the bottom layer and have a restricted region of distribution, the genus *Microsetella* has adapted itself to pelagic life and thus has a considerably wider distribution for their separate species. *M. norvegica* is thus a cosmopolite in the widest sense of the word.

Mysidacea. Most of the relevant species may be regarded as

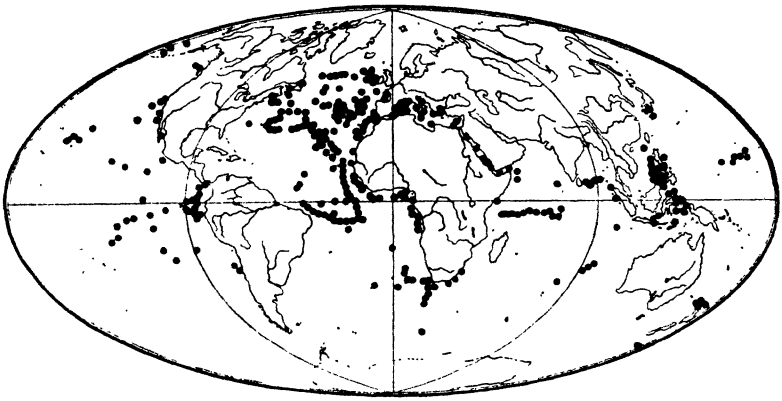


FIG. 105.—Distribution of the copepod *Pleuromamma abdominalis*. (After Steur, 1933, with additions.)

neritic, but holopelagic species exist, for instance *Siriella thompsoni*, which in contrast to the neritic species is circumtropical.

Euphausiacea. This group consists entirely of holopelagic, usually open-sea species. Among the 48 species which occur in the tropical seas at least 34, probably more, are to be found in all three oceans.[595]

Amphipoda. The subdivision Hyperiidea of this group is entirely pelagic and as a rule found in the open sea. Most species of the various families belong to the warm water and are circumtropical.[39, 491, 499, 575]

Pteropoda. All the species belonging to this group are open sea and surface forms and most of them are warm-water species. Meisenheimer has maintained in his survey of the geographical distribution of the pteropods that a great number of them are circumtropical warm-water species, for instance, to name only the better known,

Limacina inflata, L. bulimoides, Creseis virgula, C. acicula, Clio pyramidata (fig. 106), *C. cuspidata, Diacria quadridentata* and the whole genus *Cavolinia* with its six species.

Among the rest of the molluscs the group *Heteropoda*, which belongs entirely to the warm-water region, plainly contains several circumtropical species and the squids probably provide also similar examples.

Chætognatha. A group of species, among them *Sagitta serratodentata, S. hexaptera* and *S. enflata*, has its main distribution in the surface layer of the warm-water region (0–50 m.) with an annual

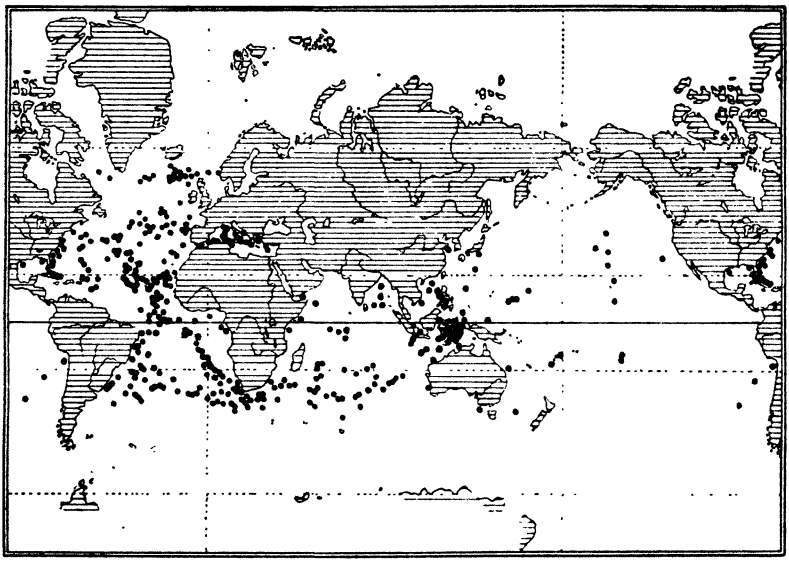


FIG. 106.—Distribution of the Pteropod *Clio pyramidata*. (After Meisenheimer, 1906, 1908, slightly modified.)

mean temperature of at least 20° C. They are also found in the Indian Ocean and the Pacific, although their distribution is only known in detail from the Atlantic.[546]

Appendicularia. According to Lohmann[312] and Ihle[250] the warm-water species of this group are for the greatest part distributed circumtropically and the centre of their region is delimited by the 20° C. isotherms, a fact which was confirmed by the detailed investigations of the "Meteor" expedition.[313] Among the species of the two main genera *Oikopleura* and *Fritillaria* there are several examples of this *O. longicauda* and *F. formica* which are mentioned as having such a distribution, are however not warm-water species, but are eurythermal.

Species of *Salpa, Doliolum* and *Pyrosoma* are generally circumglobal warm-water forms.

Finally, with regard to *fishes* the open-sea fauna plays a less important part than might be expected. Among pelagic fish the main contingent is represented by neritic species which because of their nutritional requirements or spawning habits are tied to the shelf. Among the more widely known of the high-oceanic circumglobal warm-water fish we may mention the giant plankton-feeding basking shark *Cetorhinus maximus*, the great blue shark *Prionace glauca*, the thrasher *Alopias vulpes*, the mackerel shark *Lamna cornubica*, the giant sun-fish *Mola mola*, the dolphin *Coryphæna hippurus*, the remoras and shark-suckers *Remora* and *Echeneis*, the pilot fish *Naucrates ductor*, the tunny *Thynnus thynnus*, the horse mackerel *Caranx trachurus*, the swordfish *Xiphias gladius* and several species of flying fishes. The latter, of the family Exocœtidæ, are tied to warm water; the limits of distribution for most flying fishes in the Atlantic approximately coincide with the mean annual surface isotherms for 20° C. or 21° C. according to Bruun's compilations. The best-known species, *Exocoetus volitans*, is circumtropical.

The survey we have just given may serve to illustrate the relative homogenity of the high-oceanic (holopelagic) warm-water fauna in all three oceans as far as the species are concerned. This is even more true of the genera. The holopelagic warm-water genera which do not possess species in all three oceans are relatively few. No numerical data are given for the proportions between the species and genera of the various oceans, but it may be said of the high-oceanic epipelagic fauna that the cold regions possess a higher percentage of specific cold-water genera than the percentage of genera among the warm-water fauna of the Atlantic which is not included in the warm-water fauna of the Indian Ocean. In other words: the contrast between the cold-water regions and the intermediary warm-water region is more marked than the contrast between the various warm-water regions of the three oceans. The result is that *the epipelagic high-oceanic fauna may be divided into three main zoogeographical regions: a warm-water and a northern and a southern cold-water zone.*

Minor faunal regions

In most of the surveys of the distribution of the pelagic warm-water fauna, which have been compiled by specialists, the anti-boreal ("subtropical") convergence was chosen as boundary, since the faunal change here is more apparent than in any other pelagic surface water. As the temperature at this convergence is about 14–15° C. in summer and about 12° C. in winter, the warm-water zone

thus delimited contains not only the tropical-subtropical belt but also a great deal of the warm-temperate region. The mean temperature at the surface of this tropical-warm-temperature region is, in the Atlantic, for the summer, between 15° and 28° C. and for the coldest month of the winter between 10–12° and 27° C. It would be strange if this great difference in temperature had no influence on the composition of the fauna. Changes in fauna have indeed been demonstrated. There are several examples of certain species being bound to water of extremely tropical character, such as the copepods *Corycæus gracilis* (fig. 20) and *Copilia lata*, while another number

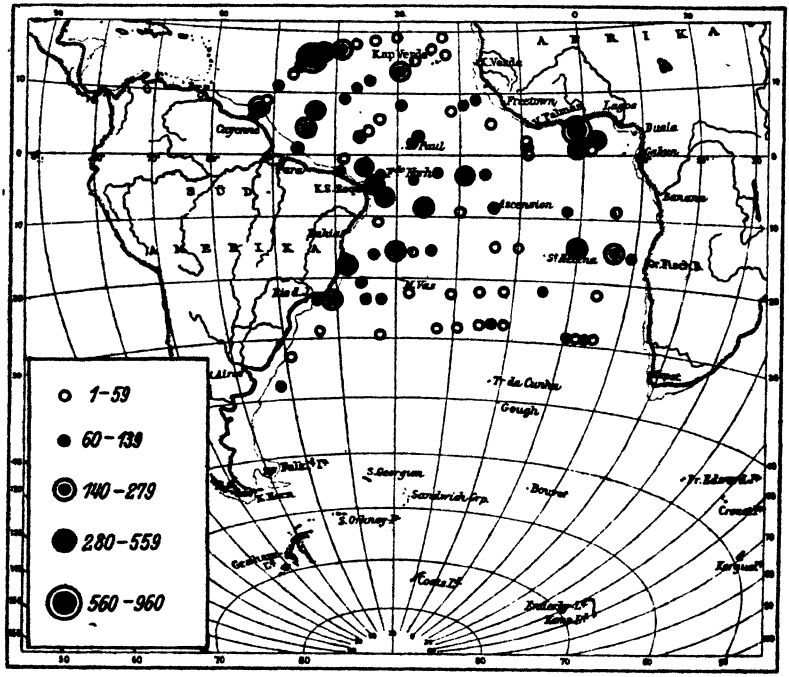


FIG. 107.—The quantitative dispersion of the copepod *Corycæus* (*Corycella*) *gracilis* in the southern Atlantic. The figures indicate number of individuals in a given volume of water. (After Klevenhusen, 1933, simplified.)

of species avoid the "warmth equator" and its immediate surroundings, as for instance the euphausiacean *Nematoscelis megalops* and the pteropod *Cavolinia gibbosa*. The latter distribution has been called bitropical and it was thought that a discontinuity existed between the northern and southern region. This, however, cannot be considered as proved, but only a weaker representation within the purely tropical regions. It is possible to go further in discriminating sub-zones, as Ruud does[448] for instance as regards the Euphasiacea.

A considerably greater contrast exists between the Atlantic and the Indo-Pacific regions, which mainly expresses itself in the fact that the latter region is richer in species, as was the case also with the shelf fauna; the West Pacific in particular is, however, only incompletely known as far as the pelagic fauna is concerned. We confine ourselves here to a few examples. Among the siphonophores the Atlantic *Porpita umbella* is represented by *Porpita pacifera* in the Pacific. As far as is known, at least 30 epipelagic species of copepods are confined to the Indian Ocean, most of which are warm-water species, while none of the 134 species (most of which are also tropical) in the temperate region of the Atlantic is missing in the Indo-Pacific. The latter region contains 88 of the 103 species of the Mediterranean. The prawn genus *Lucifer*, like some other genera, has more species in the Indo-Pacific than in the Atlantic. The pteropod *Halopsyche gaudichaudii*, which occurs generally in the Indo-Pacific, is missing from the Atlantic. Many other examples could be quoted. But there are also examples of species, which earlier were only known from one or two oceans, but were found to be circumglobal when knowledge of zoogeography increased.

The *Mediterranean* agrees on the whole with that part of the Atlantic situated immediately outside, and it also has a striking affinity to the Indo-Pacific. Of the more than 120 species of epipelagic copepods which are enumerated by Sewell[479] for the Mediterranean, 86% are thus found in the Indo-Pacific. But there are certain divergencies from the Atlantic plankton fauna. Chun pointed out as early as 1897 that several siphonophores which occur generally in the Atlantic, including the region near by Gibraltar, are missing in the Mediterranean. Several of them have since been discovered there, but for the rest their absence from this region has been confirmed, for instance for *Abyla trigona* and *Diphyes dispar*.[361] The same applies to the copepod *Pleuromamma xiphias*, the pteropods *Limacina lesueuri* and *Cavolinia uncinata* and for 46 of the 118 Atlantic Amphipoda Hyperiidea, which, however, belong partly to the deep-water plankton.[499] The Mediterranean fauna of this amphipod group is well known thanks to the Danish expeditions. A number of purely tropical species is also missing in the Mediterranean. Ruud[449] found that the six epipelagic species of Euphausiacea, which towards the north do not go beyond the isotherm for 15° C. at 100 m. depth in the Atlantic, are all missing in the Mediterranean, while the five species which towards the north go as far as the 11–12° C. isotherm at the same depth, are all found there. Among the latter *Euphausia gibba* is one of the most common.

On the other hand the Mediterranean possesses some species which as yet are not known from the Atlantic, but in several cases they are

rare species whose general distribution must be considered as not sufficiently known.

There is in the Mediterranean in certain respects a contrast between the eastern and western parts, whereby the boundary between the two may be placed in the neighbourhood of Sicily. The western part is generally quantitatively and qualitatively richer than the eastern. As far as quantity goes, this accords well with the nitrate and phosphate content of the water which diminishes from west to east[552] (even in the western Mediterranean it is lower than in the Atlantic). The following are some examples of the qualitative differences. The western part has eight species of pteropods which are missing from the eastern part, of which *Cymbulia peroni* (also in the Adriatic) and *Diacria trispinosa* are the most common,[331a] while the opposite is true only for *Hyalocylex striata*, which occurs in the eastern part.[514] Fourteen species of the Amphipoda Hyperiidea have been found in the western part, among them *Phronima curvipes* and *P. colletti*, at 23 and 15 stations respectively, while 12 species are only found in the eastern part, among them *Lycæa bovallii* at eight stations. A very good example is the North Atlantic *Meganyctiphanes norvegica* (figs. 24, 25, pp. 82, 83) which is known from many localities in the northern and western Mediterranean, where 15° C. seems to represent the upper temperature limit for this species, but it is completely missing from the south-eastern part.

The reason for this difference between the western and northern part on the one hand and the south-eastern on the other seems, in the case of *Meganyctiphanes* and probably other species, to lie in the temperature of the water of the south-eastern part which both on the surface and in the intermediate layers is higher than in the rest of the Mediterranean. The very high salinity of the south-east (38 to over 39‰) may presumably be a contributory factor, and further and not least the currents which flow in from the Atlantic, the surface ones forming a vortex skirting the north coast of Sicily, the west coast of Italy and south coast of France, while the deeper water forms an outflowing current throughout the whole of the Mediterranean.[376]

We shall return later to the Mediterranean when discussing the deep-water plankton.

APPENDIX TO THE WARM-WATER PELAGIAL: THE SARGASSUM FAUNA

We will briefly discuss the fauna of the floating Sargassum as an appendix to the high-oceanic fauna; we do so in an appendix because this is not a planktonic fauna. It is pelagic only in so far as it lives

within the pelagic region and it may be regarded as such only from a purely geographical point of view; ecologically it is rather a littoral fauna since its relation to the pelagic drifting Sargassum weed is about the same as that of ordinary littoral animals to attached seaweed. It is, as Pax expresses it, so to speak, a littoral enclave within the pelagial.

This fauna has been examined lately by Hentschel[221] and Timmermann.[559] It consists of animals which are sessile on the seaweed, as for instance species of the bryozoan *Membranipora*, and the barnacles *Lepas anserifera* and *L. pectinata*, or of those which cling to it, such as the decapod crustaceans *Planes minutus*, *Latreutes ensifer* and *Leander tenuicornis*, or of freely swimming animals which hide in the weed, such as, for instance, the fishes *Pterophryne historio* and *Syngnathus pelagicus*. In their appearance these Sargassum animals often diverge from their purely littoral relatives in being considerably smaller, a feature which has become a species character in the isopod *Ianira minuta*. This form which attains at the most a length of 2 mm. is to be regarded as a separate species which stems from the littoral *I. maculosa* whose size can reach 10 mm.

As for the origin of this fauna, there is no doubt that it is derived from a coastal fauna. But there are good reasons for supposing that they are not coastal forms accidentally displaced, but that the Sargassum fauna has lived for countless generations in the Sargasso Sea. Some of its species seem to have been transported far from the Sargasso Sea by ocean currents, so for instance the pycnogonid *Endeis spinosa*, which is common in tropical-subtropical Atlantic America and in the Sargasso Sea and which has been found also in various localities on the East Atlantic coast from north-western Africa to western Norway.[216] As most likely ancestor of the Sargassum fauna we may regard the West Indian littoral fauna. But there are some remarkable differences and the quantitatively and qualitatively richest Sargassum fauna does not live near the coast or in the western part, but in the central and eastern parts of the Sargasso Sea. It is well known that the Sargassum itself has not for the most part, as was earlier assumed, become detached from the Antilles and been swept out into the open sea, but that these algæ live a life independent of the coast and are kept together in their region by the great circular current of the Sargasso Sea.

THE NORTHERN COLD-WATER PLANKTON

We have seen that the boundary between the colder and warmer faunal zones of the pelagic region has been found to be most clearly marked at about the isotherm for a mean annual temperature or

possibly a summer temperature of approximately 14–15° C.; but we have to bear in mind that certain species are confined to a warmer, truly tropical zone. As we now pass on to the cold-water plankton we leave aside for the moment the boreal zone, which is adjacent to the warm-water zone in the north, and begin instead with the pelagic region of the Arctic.

Hydrography. In the eastern part of the Atlantic the arctic surface water does not reach far south, since the northern continuation of the Gulf Stream has pushed the warmer water northwards, but in the west the cold Greenland Current and even more the Labrador Current transports the arctic plankton a long way south. In the

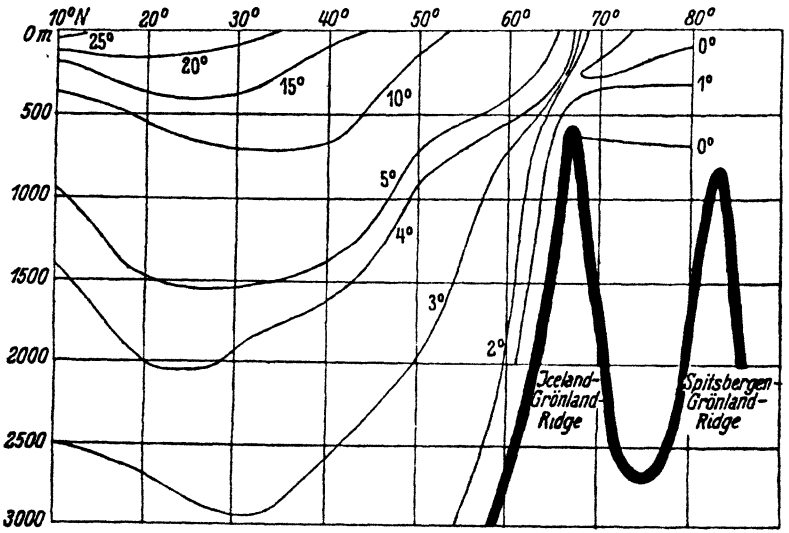


FIG. 108.—Vertical section through the northern Atlantic along 30° W., but north of 60° N. north-eastward, with isotherms; compiled according to available information.

North Pacific the distribution of the zooplankton is not known in detail, but we have every reason to suppose that an arctic plankton here, too, reaches further south on the west coast of the ocean than on the east coast, because the polar water flows south along the west side of the Bering Sea and thereafter combines with the current coming from the Sea of Okhotsk and forms the cold Oyashio Current, which reaches northern Japan. The Norwegian Sea between Norway and north-eastern Greenland is only in its eastern part boreal down to a depth of approximately 200–300 m., but it is otherwise arctic, on the surface with a temperature of at the most 5° C. in the summer and 1° C. in the winter and at a depth below

600 m. with constantly negative temperatures. Its south-western boundary is Iceland and the submarine ridges Iceland–Faroes–Scotland and Iceland–Greenland. Water of decidedly arctic temperature (roughly 1° C.) flows across both these ridges from the Norwegian Sea down into the deep of the North Atlantic, where it forms the bottom layer because of its density (fig. 108). This arctic bottom water extends a long way south. As a rule the water of the greatest density in the oceans is formed in high latitudes[537] and it thus happens that at 3000 m. and below the whole bottom layer of the Atlantic is at the most 3° C. with the single exception of the Sargasso Sea. This cold bottom water is, however, only partly arctic because in vast regions antarctic water covers the bottom even far north of the equator, namely west of the mid-Atlantic longitudinal ridge to 40–45° N., but east of it only as far as Walfish Ridge (20–33° S.). But above this bottom water there flows intermediate currents in a southerly and northerly direction, which are determined in their depth by the density of their water which varies with temperature and salinity; and to these must be added branching currents which do not flow horizontally but obliquely up or down. Thus a very complicated system of currents arises below the more superficial layers and the possibilities for transport of plankton organisms in the various directions are almost unlimited.[589, 590]

The temperature of the surface layer in the high-arctic parts of the Polar Sea is somewhat lower than 0° C. but rises in the intermediate layer to a little above 1° C. for depth between 600 and 800 m. and then sinks to negative degrees (fig. 108). This, combined with the increasing salinity as depth increases, possibly contributes to the fact that the number of plankton species has been found to grow with increasing depth. The surface layer, on the other hand, is marked by a great number of individuals. We find the same also in the antarctic region (p. 346).

Arctic species. These occur within the arctic region very often both in the surface and deeper water layers, but further south they are, as a rule, submerged. Since one and the same species thus often belongs to the epiplankton as well as the deep-sea plankton, we include both kinds of plankton in the following survey.

It has been maintained that all pelagic animals in the North Polar Sea are domiciled also outside the arctic region and that there is thus no purely arctic ("eu-arctic") plankton. This assertion is, however, false. It is due to the common but misleading method of plotting all localities of finds on the surface and thus forgetting the difference between the surface temperature and that of the deeper layers. An animal which has followed the arctic current across the North Atlantic Transverse Ridge and afterwards comes to live in

the bottom water a few degrees south of the transverse ridge has not thereby entered the boreal zone but continues to live in arctic water. The same applies to the transverse ridge of the Davis Strait. There exist thus purely arctic pelagic species and in the plankton of the Polar Sea, which is poor in species, they constitute on the whole a fairly high percentage. The poor arctic fauna has in reality relatively strong positive characterization. We give here a few examples. Three of them show that there is also an endemic bathypelagic high-arctic fauna, although poor in species, which does not live in water warmer than 0° C.

The ctenophore *Mertensia ovum* is an example from the cœlen-

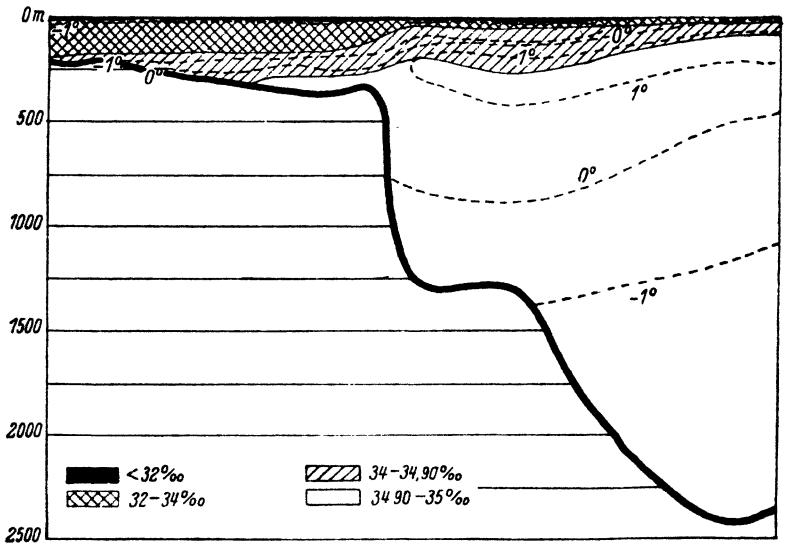


FIG. 109.—Salinity and temperature in a vertical section through the Norwegian Sea from North-east Greenland eastward. (After Damas & Kofoed, 1907, simplified.)

terates. In the far north, for instance in the sea between north-eastern Greenland and Spitsbergen, this species lives in the surface water, where it prefers to stay on the ice floes from which it strikes with its long tentacles at diatomes and other food particles. *Ptychogastria polaris*, a trachymedusa, is arctic in spite of occasional occurrences in the west Norwegian fjords. It is eurybathic. The two trachymedusæ *Crossota norvegica* and *Botrynema ellinorœ* are found exclusively in the deep water of the Norwegian Sea. Both are therefore high-arctic. The Narcomedusa *Aeginopsis laurenti* which is caught on the surface and down to 1000 m. depth, is circumpolar and is found only in the Labrador Current as far as Newfoundland

apart from the arctic and high-arctic regions. It may be seen from the survey by Kramp[287, 290] of the medusæ and ctenophores of the arctic region that of the 10 holopelagic species five are purely arctic. A purely high-arctic bathypelagic siphonophore is *Stephanomia orthocanna*. The genus *Mertensia* which was mentioned earlier is monotypical and forms alone the family Mertensiidæ which therefore is an endemic arctic family.

Among the copepods we may mention the following: *Pareuchæta*

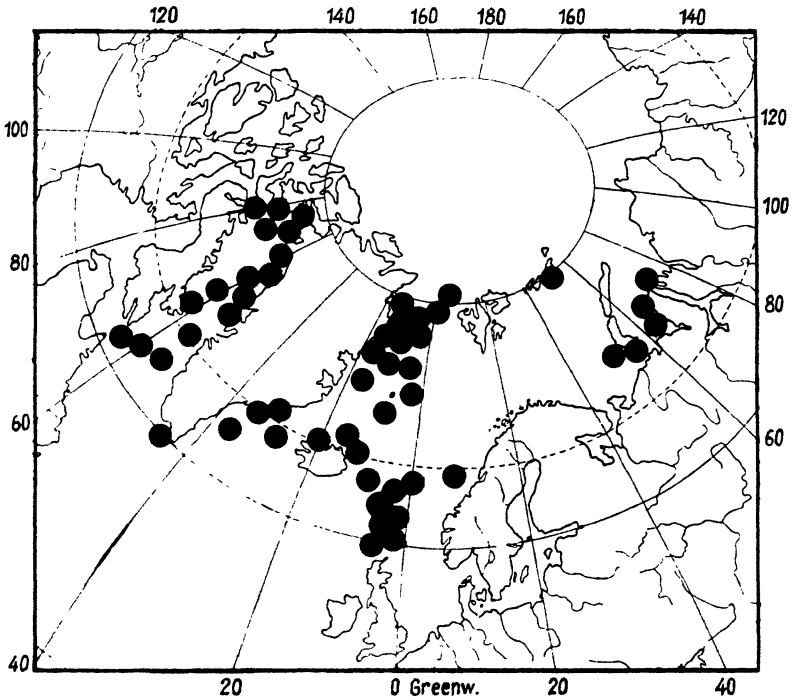


FIG. 110.—Distribution of the copepod *Pareuchæta glacialis*. (After Jespersen, 1934.)

glacialis has been caught in surface water at several localities north of Spitsbergen and Siberia, in other regions in the intermediary and abyssal layers. South of the North Atlantic Transversal Ridge and the Davis Strait Ridge it is only found in the vicinity of these ridges and, apart from this, only once off the southern tip of Greenland.[259] The same applies to *Chiridius obtusifrons* which has been transported as far as Nova Scotia by the Labrador Current. Both these species live almost entirely in water of negative temperatures.

Apart from these, only a few species seem to be endemic in the Arctic.

A characteristic species is also the amphipod *Themisto libellula* which is known from numerous finds and which is circumpolar in arctic, also high-arctic, regions, especially in the upper water layers. At the southern limit of its distribution it is most often found in deep water. The most southerly localities are two in northern-most Norway, one south-west of Iceland, two off southernmost Greenland and two in the Labrador Current as far as Newfoundland. The species usually occurs in great numbers and reaches more than 30 mm. in length, which makes its distribution well known.[500]

Arctic-bathy-subarctic species. Very like the arctic group is another which resembles it especially in that it clearly belongs to the arctic region first and foremost but is also, as far as we can judge, at home in fairly remote southern regions, namely in deep water of somewhat higher temperature than the arctic. Whereas we cannot

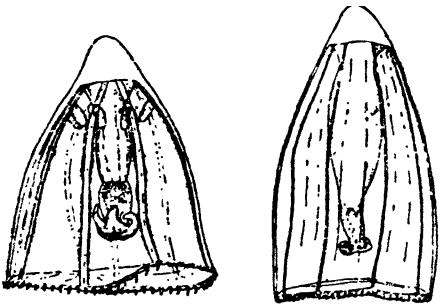


FIG. 111.—The Trachymedusa *Aglanta digitalis*, (on the right a neritic, on the left an arctic and partially bathypelagic form. (After Broch.)

avoid the suspicion that in the arctic group which we have just described the most southerly finds, for instance in the southern part of the Labrador Current, consist of individuals in an expatriation area, the individuals belonging to the group now under discussion seem to be indigenous also in certain non-arctic regions. It is hardly possible to call this group arctic-boreal or arctic-temperate, since it does not agree with arctic-boreal or arctic-temperate epipelagic species with regard to temperature requirements; and "arctic-subarctic", which would be admissible from the point of view of temperature, is not applicable to occurrence off the Azores or in the Sargasso Sea. I therefore call these species arctic-bathy-subarctic.

A distribution which is characteristic for this group is shown by *Aglantha digitalis*, a trachymedusa which is often red and up to 20–30 mm. high (fig. 111). It is extremely common within the whole

of its region, more than 1000 specimens being often caught in a single haul. The distribution has been compiled by Kramp.[290] It is circumpolar and comprises in the north both high and low-arctic regions. In the former, for instance in Baffin Bay, the species occurs epipelagically and has its main contingent at about 50 m. depth, in the southern part of the Norwegian Sea it is most numerous at about 600–1600 m. depth (4800 specimens in one haul at 1300 m. depth), and in the North Atlantic south of the transverse ridge at about 500–1000 m. depth, where it has also been caught occasionally in great numbers at a depth of 3000 m. In the Bay of Biscay it is the most common of all the medusæ. The southernmost finds have been made near the Azores, in the Gulf of Maine and Massachusetts Bay and in the Pacific off Vancouver and Japan.

The copepod *Calanus hyperboreus*, reaching 9 mm. in length, is one of the best-known invertebrates of the North Polar Sea because of its abundant occurrence. It has been found in the North Polar Basin on the surface and in very great numbers even at the northernmost stations. The following data supplied by Damas and Koefoed show the bathymetric distribution in the sea between Spitsbergen and North-east Greenland which was covered with drift ice; the samples were taken in July with the same vertical closing net.

TABLE 48

78° 05′ N., 5° 21′ W. Depth 1425 m.		75° 55′ N., 9° W. Depth 1275 m.	
20– 0 m.	1000 specimens	10– 0 m.	1004 specimens
60– 38 m.	2 ,,	100– 20 m.	2 ,,
125– 70 m.	7 ,,	400–210 m.	4 ,,
300–125 m.	89 ,,		
1350–800 m.	52 ,,		

The mass occurrence on the surface is supposed to be dependent on the enormous masses of diatoms immediately below the ice, which serve as food for this species. The most prolific propagation in the Norwegian Sea takes place in water of about 0° C. and 21–30‰ salinity during spring and summer, particularly within the East Greenland Polar Current. A second main region of the species is in the region west of Greenland, where it occurs only in scanty numbers on the coast of Greenland but much more prolifically in the western part of Baffin Bay and in the south-going Labrador Current. In the Gulf of Maine it is also very common at certain seasons.

In the open Norwegian Sea the species is clearly dependent on Polar water and avoids eastern regions where the Gulf Stream increases the temperature. But it is also at home in the deeper

Norwegian fjords and in the Skagerak. Aurivillius[22] found it in the Skagerak only in February and April and regarded it as a species which was not indigenous in these parts. Runnström[443] showed that these animals could not be found all the year round in the fjords near Bergen and said that "they are probably recruited afresh each year from the sea". But Sömme[488] found them in the fjords east of the Lofoten and also in the Romsdal fjord in West Norway at 63° N. and in the Oslo fjord in circumstances which show that they are certainly indigenous in the Lofoten and probably also in the two other fjords. In the region of the Lofoten they spawn in February and March at 6·5–7° C. and a salinity of 34·5–35‰ and all stages of their development have been found there.

In the open Atlantic *Calanus hyperboreus* has been caught between Ireland and America at a fair number of stations and in the Northern Pacific, probably however always in restricted numbers, the furthest points south being 30° N. (Sargasso Sea), the Galapagos Islands and off northern Japan.

Pareuchæta norvegica has on the whole the same distribution as *C. hyperboreus*. *Metridia longa*, another copepod, lives in the Polar Sea on the surface but further south with few exceptions in deep water, the southernmost points being the Azores and the Peru Current. It is constantly found at all seasons in the Norwegian fjords and in the Skagerak.

Themisto abyssorum may be listed here as an example among amphipods.

Arctic-boreal species. The last mentioned group merges with intermediary forms into another which may be called *arctic-boreal*, since its species inhabit the superficial boreal water layers and since on the whole they do not transgress the southern boundary of the boreal region, which in this case seem to coincide fairly well with the isotherm for about 11° C. at 100 m. depth.

The following species may be mentioned as examples:

Pteropoda. *Limacina helicina* (figs. 112, 113), a bipolar species, circumpolar in its northern region, spawns in high-arctic regions at 0° C., further south in higher temperatures. The southernmost finds are in the Skagerak and Kattegat, in the Northern Atlantic, at the western entrance to the Channel and on the American side south of Cape Cod. The likewise bipolar *Clione limacina* (fig. 112) has a distribution which for the most part coincides with the former species. Outside the Labrador Current the few finds south of 50° N. were made in deep water,[51] the most southern at 34° 44′ N. at 100–1250 m. depth. Both *Limacina* and *Clione* occur in great numbers in the continuation of the Gulf Stream off Norway and there provide a considerable part of the food for the whalebone whales.

Euphausiacea. The three species of the genus *Thysanoëssa*, *T. raschi*, *T. longicauda* and *T. inermis*, belong to this group.[449] In particular the last, which is more neritic than the two others, occurs off Norway in such great numbers that it constitutes the main food for several species of whalebone whales at certain seasons.

Appendicularia. *Oikopleura labradoriensis* occurs as far south as the southern North Sea.

There are very few, if any, purely *boreal epipelagic species*. A few were formerly so designated, for instance among the siphonophores, pteropods and euphausiids, but as our knowledge of their distribution increased, they were found to have a more extensive distribution. If one disregards a few species which in reality seem to be neritic, the cold-temperate (boreal) epipelagic region is completely, or almost completely, inhabited by cosmopolites, by arctic-North-Atlantic species or more occasionally by epipelagic individuals from the plankton community, which is living in the intermediate deep-sea zone. *The absence of an endemic boreal epipelagic fauna is very remarkable*, not least when compared with the well-defined benthal fauna of the boreal shelf. This absence makes the boreal epipelagic layer stand out as an exceptionally sharply defined boundary region which, being a field devoid of endemic elements, occupies about 15 degrees of latitude in the middle of the Atlantic, namely between 65° N. (surface isotherm for about 3° C. annual mean) and 50° N. (the corresponding isotherm for about 12° C.). In conformity with the course of the cold and warm ocean currents the northern boundary shifts along the coast of Greenland and North America considerably to the south, and along the coast of Norway to the north.

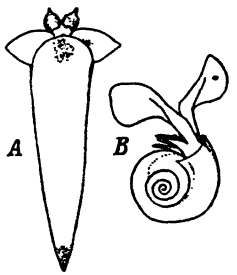


FIG. 112. — Two pelagic pteropods: (A) *Clione limacina;* (B) *Limacina helicina*; 4 × natural size. (After G. O. Sars, 1878, redrawn.)

Several northern cold-water species which occur in the North Sea, Skagerak and certain Norwegian fjords were formerly considered as proof that arctic polar water flows into these regions at certain seasons. It has, however, since been proved that this view was due to our incomplete knowledge of the distribution of the species and their temperature requirements. In actual fact these were not purely arctic species but some which are domiciled also in temperate water. It has also been proved that arctic water is never admitted into the North Sea or the Scandinavian coastal region, since the northern continuation of the Gulf Stream, like a submarine wall,

bars the way, in that its Atlantic water reaches down to the sills which at the entrance to the Skagerak and the fjords reach fairly high up (in the Skagerak 260 m. below the surface, cf. fig. 34, p. 104).

At the boundary between two different faunal regions the conditions of flow may on certain occasions bring about a change in the

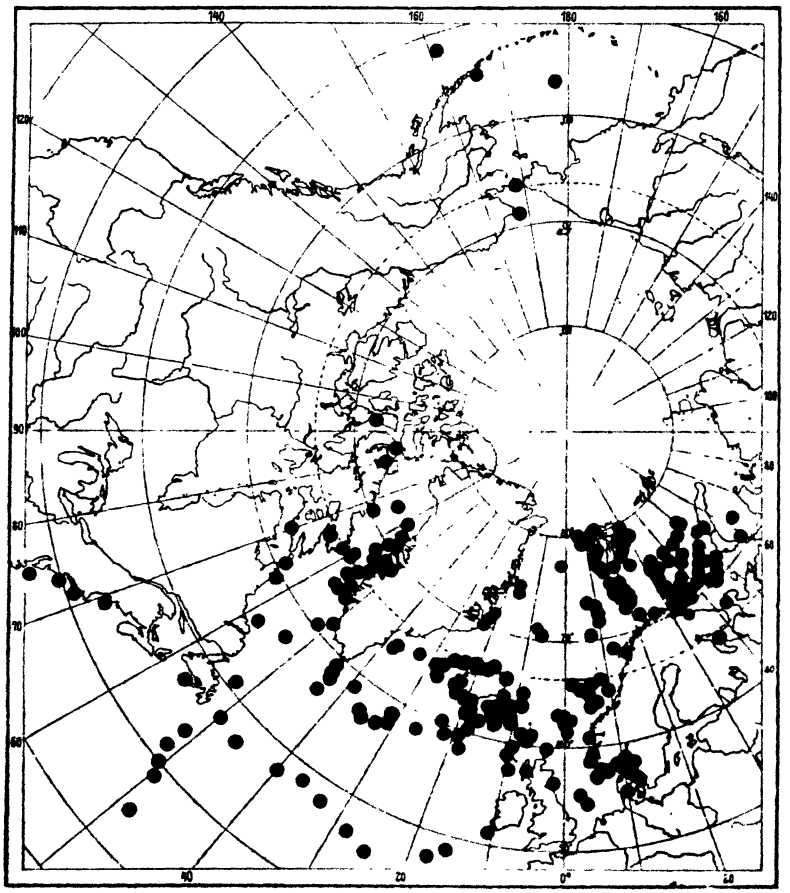


FIG. 113.—The pteropod *Limacina helicina* in the northern hemisphere. Compiled after various authors.

composition of the plankton, and certain plankton species are thus indicators for various types of water. A detailed knowledge of these is of theoretical and practical importance, for instance for the fishing industry. Studies of these indicators were made in several regions: in the North Sea and its vicinity[295, 401] (see also the survey by Russell[445]), the Gulf of Maine in North America,[48] off Iceland,[226] etc.

THE SOUTHERN COLD WATER

We have (p. 211–213) made the acquaintance of the two convergence lines of the South Sea where the surface water changes its temperature more abruptly than anywhere else, namely the Antarctic Convergence with a summer temperature of between 3·5° and 4–5° C. and the Antiboreal ("subtropical") Convergence with a summer temperature of 14–15° C. and a winter temperature of 10–12° C. We may point out how well these temperatures agree with the surface water isotherms which in the northern hemisphere we

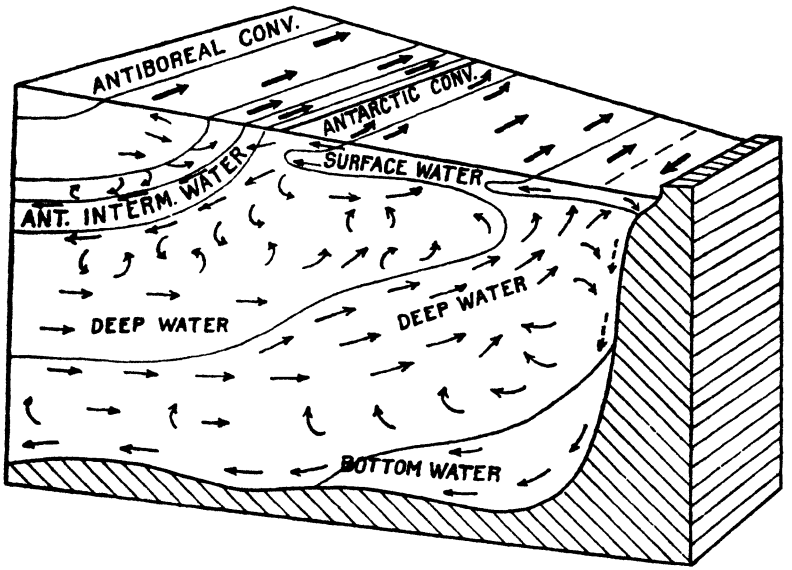


FIG. 114.—Schematic representation of the currents and water masses of the Antarctic regions and of the distribution of temperature. (Reprinted by permission from Sverdrup, Johnson and Fleming, *The Oceans*. Copyright 1942 by Prentice-Hall, Inc., New York. Terminology partially modified.)

have found to mark the approximate southern boundary for the arctic pelagic fauna and the appropriate northern boundary of the epipelagic fauna, which may be called warm-water fauna in its widest sense. In the southern hemisphere, too, the isotherms mentioned have a similar importance, the two convergence lines being the most important zoogeographical boundaries in the southern epiplankton.

In the southern hemisphere, too, the geographical distribution of the pelagic fauna is considerably more complicated and difficult to interpret than that of the shelf, since dispersion of plankton

animals within the tremendous water masses takes place not only with the help of surface horizontal currents but also by deep-water currents which go partly obliquely upwards or downwards, partly also at different depths horizontally but in various, and at times contrary directions (fig. 114).

Because the water masses of the West Wind Drift do not proceed due east but diverge somewhat to the north, the *antarctic surface water* is transported northwards until at the Antarctic Convergence it lies below the antiboreal water and continues further northwards as *antarctic intermediate water*. It occupies a layer of varying depth, the position of which, at some distance from the convergence, may be given very approximately as 800–1500 m., sometimes 2000 m. below the surface, with a temperature of between 3° and 7° C. The salinity is fairly low, less than 34·5‰. This current, which flows slowly north, even crosses the equator in the western Atlantic and sends one branch into the Caribbean Sea and another along the outside of the Antilles. In the Pacific the intermediate water reaches as far as the equator, in the Indian Ocean it does not reach far north. But very close to the Antarctic Convergence the antarctic intermediate water also separates off water which turns south and thus returns to the antarctic coast or pack-ice belt. This is the so-called *antarctic return current*. It forms the upper layer of the great water masses which are quite simply called antarctic deep water (see below).

Alongside the bottom of the Antarctic Continent the surface water also sinks down and continues as a bottom current which flows very slowly north, in the western Atlantic, as we have already seen, a good way north beyond the equator. This *antarctic bottom water* has far south a low salinity(<34·5‰) and negative temperatures, but it gets a little warmer through contact with the water above it so that in the deeps of the western Atlantic near the equator it reaches 1° C. and at 30° N. 2·5° C. The loss of water in the antarctic regions through these two northerly currents is replaced by the *deep water* which lies between the bottom water and the antarctic surface and intermediate water; it has a temperature of 1–4° C. and flows towards the antarctic coast. In the antarctic region the temperature is lower.

Within the region of the pack-ice which roughly coincides with the East Wind Drift belt (map p. 212) we thus find the following temperature layers: from the surface to a depth of 200–300 m. the temperature is throughout the whole year below 0° C., with the exception of only a few small isolated areas, and the same is true of the bottom water at greater depth. But in the pelagic region the water from about 300 m. down has positive degrees of temperature, which, however, are very close to 0° C. and hardly in any region

below the surface East Wind Drift reach 2° C. This water, which thus lies between the surface water and the bottom water, has therefore often been called intermediate. To distinguish it from the above-mentioned antarctic intermediate water we may call it the *antarctic polar intermediate.*

The conditions of flow mentioned above also have an influence on the quantity of the plankton. The antarctic coastal water, in conformity with other coastal waters, is relatively rich in phosphates, and as it proceeds north it gives rise to a rich phytoplankton and thus also a rich zooplankton, which in its turn is the basis for the profitable antarctic whaling industry. The food requirements of the plants impoverish the water of phosphates, but when it sinks below the surface at the Antarctic Convergence with its content of plankton, a number of the latter die and decompose with the result that their phosphate content becomes again dissolved in the water which, thus enriched, returns to the antarctic.[90] On the whole, the highest phosphate content and the greatest plankton abundance of the surface layers of the Southern Ocean both lie south of the Antarctic Convergence (figs. 98, 99, pp. 314, 315).

THE ANTARCTIC PELAGIC FAUNA

To begin with we must pay attention to a peculiar faunal contrast between the coldest antarctic surface water, which we have just mentioned, and the only slightly warmer polar intermediate water (cf. fig. 117, p. 358).

Popofsky[418] was the first to draw attention to this contrast. During the summer, but not during other seasons, he found in the material from the German South Polar expedition 18 radiolarians in the polar intermediate water which he considered to have immigrated from warmer northern regions, and this view was confirmed and further exemplified by Lohmann[309, 310] who showed that certain appendicularians, for instance *Oikopleura valdiviae* and *O. gaussica*, exclusively inhabit the antarctic surface water with its negative temperature, while the polar intermediate water below that contains other species which avoid the polar surface water but occur in more northern regions with warm water. Such are, for instance, *Oikopleura longicauda*, *Fritillaria formica* and *F. pellucida*. These three live in the polar intermediate water not as expatriates but they reproduce here. Their northern main region from which they were transported to the Antarctic by the deep-water current flowing south (fig. 114), comprises also the surface water of the equatorial region and this is the region where the number of individuals is greatest. This very

pronounced eurythermy (temperature limits about 27° and 0° C. or sometimes −1° C.) is remarkable.

Other animal groups, too, concur with the appendicularians in this distribution in the two water layers under discussion as do also among the unicellular plants the Peridinæ. The radiolarian family Challengeriidæ contains six species of the genus *Protocystis* in South Polar Water which are considerably more numerous in, or even exclusive to, the upper 100–200 m.[410] Among copepods, we have in *Calanus acutus* and *C. propinquus* examples of species of the cold surface water, while *Metridia gerlachei* belongs to the polar intermediate water.[207, 404, 405] This latter is generally richer in species than the coldest surface water; the number of species seems to increase steadily down to about 1200 m. depth.[207] The two *Calanus* species are not confined to the water of negative temperature furthest south, but occur in lesser abundance everywhere in the antarctic zone and nearly the same is true of *Oikopleura valdiviæ* and *O. gaussica*. The insensitivity to temperature of these species is naturally a condition for their occurrence in negative temperatures, but their greater abundance there need not be due to any predilection for the very low temperatures but may be connected with the greater amount of food in the coastal waters. The parallel with high-arctic regions is striking.

We now pass on to various types of the antarctic pelagic fauna. It is, however, not possible to draw a boundary between the fauna of the surface water and the deeper water layers, as was also the case in the arctic region, since the same species usually occur within both zones.

Siphonophora. Although the northern cold-water region lacks indigenous endemic species and only contains cosmopolites of this group, the southern cold-water region contains three to five endemic species[361] of which at least two, namely *Diphyes antarctica* and *Pyrostephos vanhöffeni*, are purely antarctic.[291, 318]

Copepoda. According to the numerous investigations which have lately been undertaken with regard to the copepods of the southern cold-water (antarctic and temperate) regions approximately 50 species may be regarded as characteristic for this region and of these 70% are regarded as antarctic. It must be pointed out here that several of them have been found in inconsiderable number and that the antiboreal plankton is considerably less well investigated than the antarctic plankton, so that 70%, the figure mentioned, seems to be too high. But it may be considered certain that the purely antarctic plankton copepods are more numerous than the purely arctic ones. Most copepods of the antarctic pelagic region are not characteristic for this region but have a very wide

distribution. The North Atlantic, for instance, has almost a hundred species with a distribution even in antarctic or antiboreal water.[479]

Only a few examples of antarctic species will be given here. *Calanus acutus*, mentioned above, has even in the antarctic intermediate water never been caught at any great distance north of the Antarctic Convergence. The numerous plankton hauls made by the British "Terra Nova" expedition 83, north of 50° S., contained no specimen of this species, and in 20 hauls between 50° and 60° S. only 27 specimens were caught, while in 99 hauls between 60° and 78° S. 87 contained this copepod, several of them thousands of specimens. At 77° 40′ S. a haul in an ice-hole produced 1760 specimens. Ottestad,[405] who studied the occurrence of the various developmental stages, came to the conclusion that *C. acutus* spawns in the surface water between the edge of the pack-ice and the convergence, after which the young stock is transported northwards, gets into the antarctic intermediate current but from there is trans-

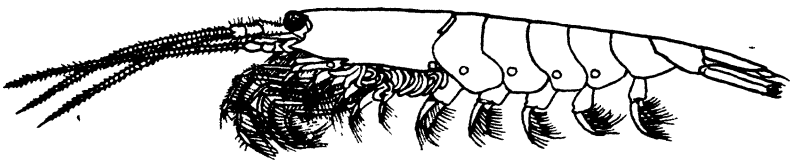


FIG. 115.—*Euphausia superba*, 1·1 × natural size. After H. Bargmann, 1937, in the "Discovery" Rep. (*National Instit. of Oceanogr.*, London); redrawn.

ported back by the antarctic return current into the region of the pack-ice finally to emerge there in the surface as fully grown individuals. *Calanus propinquus* and *Metridia gerlachei* seem to behave in a fairly similar manner. The latter's most northerly locality has been a find south of New Zealand, but only dead specimens were caught, a good example of the consequences of arrival in an expatriation zone outside the home region. Other endemic antarctic species are *Pareuchæta antarctica*, *Oithona frigida* and *Oncæa curvata* (1300 specimens in a haul from the ice, from a depth of 10 m.). All these species occur in very great numbers during the winter below the ice.

Ostracoda. While the cold-water region of the northern hemisphere contains hardly any pelagic species which are not mainly deep-water forms, the Southern Ocean contains several of them, of which some are endemic antarctic, for instance *Conchoecia belgicæ* which lives in great numbers also under the ice.[207, 362]

Euphausiacea. This group is not rich in species but it plays a very important part in the southern cold-water plankton because of the great numbers of individuals in some of its species. This is

especially true of *Euphausia superba*, a transparent red-pigmented species, measuring 50–65 mm. when fully grown (fig. 115), which more than any other plankton animal constitutes the food for the blue and fin whales and determines their occurrence in the Antarctic. An examination of the stomach contents of 519 blue and fin whales showed that 451 of them contained food and this food consisted entirely of *E. superba*.[320] An investigation of whales from the sea

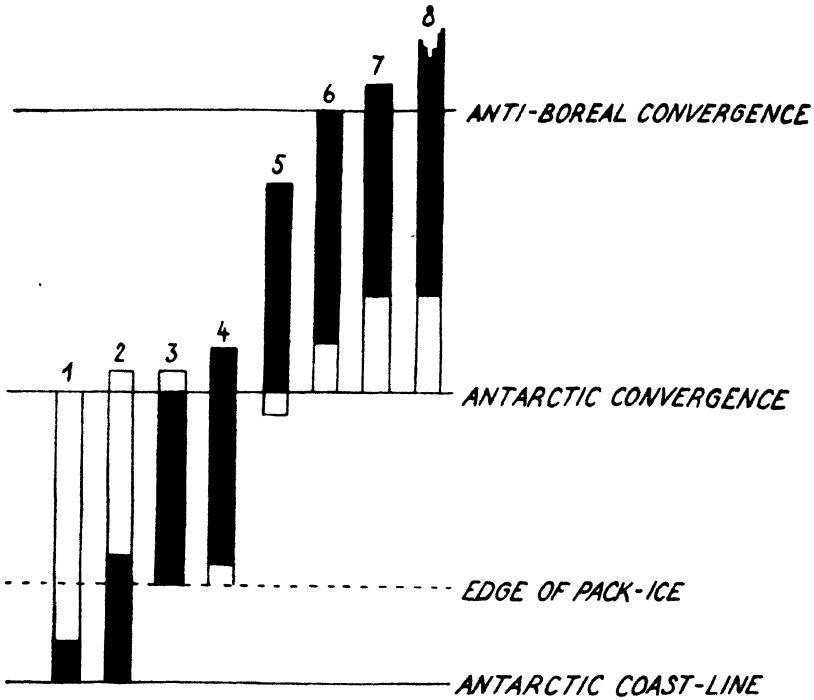


FIG. 116.—The distribution of some South Sea species of *Euphausia* in surface waters. The inked-in portion of each column shows the normal range, the entire column represents the possible range. 1=*E. crystallorhophias*, 2=*E. superba*, 3=*E. frigida*, 4=*E. triacantha*, 5=*E. vallentini*, 6=*E. longirostris*, 7=*E. lucens*, 8=*E. similis*. After D. John, 1935, in the "Discovery" Rep. (*National Instit. of Oceanogr.*, London); slightly modified.

nearer to Bouvet Island gave a similar result. *E. superba* constitutes also a considerable part of the food of the crab-eating seal (*Lobodon carcinophaga*) and the Weddell seal (*Leptonychotes weddelli*) as well as for several penguin species and for the fish of the group *Notothenii-formes*. The distribution of the more important cold-water species of the genus *Euphausia* in the Southern Ocean may be seen from fig. 116 which is taken from D. John's account of these species.[263] In these

species, as in *Calanus acutus*, the fully grown individuals live only in the surface water and are transported with it towards the Antarctic Convergence, while the younger stages are probably returned by the antarctic return current to the pack-ice where the population has its maximum concentration.[170] The other endemic antarctic species are *E. crystallorhophias*, *E. frigida* and *E. triacantha*. *Thysanoëssa macrura*, which occurs in great numbers, is also antarctic.

An antarctic pelagic amphipod is *Hyperiella dilatata*.[35, 506]

There are three antarctic species among the Pteropoda, namely *Clio* (*Cleodora*) *sulcata*, *Clione antarctica* and *Spongiobranchæa australis*.[207, 318]

Tunicata. In his survey of the appendicularians of the Weddell Sea Lohmann[309] enumerates five to six species which may be considered as belonging to the polar region. Among them are the already mentioned *Oikopleura valdiviæ* and *O. gaussica* and among the *Fritillaria* species *F. antarctica*.

An examination of all the purely antarctic species has shown that they are considerably more numerous than the purely arctic ones. Several have their most numerous occurrence in the pack-ice region with negative temperatures but whether this is due to their temperature requirements or to more abundant food supplies is difficult to determine. In certain cases the different stages of development behave differently. Only in a few cases, *Euphausia crystallorhophias* and the copepod *Haloptilus ocellatus*, does endemic high-arctic occurrence in water of temperatures lower than 0° C. seem to have been established.

THE ANTIBOREAL AND GENERAL SOUTHERN COLD-WATER FAUNA

The antarctic zone has aroused greater interest among zoologists than the antiboreal, partly because the lucrative fishing of blue and fin whales takes place mostly south of the Antarctic Convergence. So our knowledge of the plankton of the antiboreal zone is not so detailed that we are always able to say whether a species which is found on both sides of the convergence is mainly antarctic or antiboreal or possibly occurs equally in both zones. It seems however that the antiboreal plankton possesses in the three *Euphausia* species *E. vallentini*, *E. longirostris* and *E. lucens* three characteristic species.[263] Quite a number of species are common for both this region and the antarctic, that is for the whole of the cold-water region of the Southern Ocean, for instance among the copepods *Calanus simillimus*, *Rhincalanus gigas* and *Drepanopus pectinatus*, among the amphipods *Vibilia antarctica* and the genus *Cyllopus* with its two species, and among the euphausiids *Thysanoëssa vicina*

(possibly purely antiboreal). Several of them, however, avoid the high-antarctic region.

THE NERITIC PLANKTON

There is no absolute unanimity about the term Neritic among specialists. It is true that almost all seem to be of the opinion that the neritic zone should mean the pelagic region above the shelf or within a certain distance from the coast, this distance of course varying considerably in nature itself. But as to the terms *neritic plankton* and *neritic species*, opinions are divided. Some would consider a species as neritic if it occurs in greater number within the neritic region than in the open sea and consequently they designate *Calanus finmarchicus*, for instance, and certain flying fishes as neritic. In the following account the term neritic is taken in a narrower sense and applied to species which by their nature are dependent upon or bound to the neritic region and therefore do not normally complete their whole life cycle in the high-oceanic region. Even with this reservation the boundary between neritic and high-oceanic often remains uncertain. The causes for the neritic nature of a species may be various. A common cause is that the animal is not holo- but meroplanktonic, that is to say at one stage, possibly only as an egg, it is confined to the bottom of the shelf. Examples for this are most of the hydroid medusæ and many scyphomedusæ, possibly also several copepods, although not much is known about where their eggs are to be found at hatching, pelagic fish with viscid eggs, such as the herring, and so on. A number of bottom animals with planktonic larvæ are neritic during the development of the larva. In other cases a holopelagic animal may be neritic because it is tied to brackish water or oligohaline salt water. Certain holopelagic fishes, for instance the cod, need shallow bank water of certain temperature and salinity for their spawning. Other reasons, too, are possible. The group Mysidacea is generally neritic because most species live on detritus which is suspended in the water nearest to the bottom. But a holopelagic species which occurs regularly within the high-oceanic region is not considered to be neritic even if it is to be found in greater numbers in the neritic regions as a consequence of the greater amount of nutriment in such regions. One reason for such a classification is that the means of dispersion and thus the conditions for its geographical distribution are different for such a species and for the neritic species in a narrower sense.

In general, neritic species are considerably more circumscribed in distribution than are the high-oceanic species. This is clearly connected with their poorer prospects of transport by oceanic currents

and with the risk of being taken by such currents across deep-sea regions where they themselves, or their pelagic developmental stages, must perish. Several neritic genera, too, have a more circumscribed region of distribution than the holopelagic genera usually have. Among the scyphomedusæ, *Rhizostoma* is confined to the East Atlantic and Mediterranean, and *Stomolophus* to both sides of the isthmus of Panama. For both these genera the central Atlantic barrier has thus proved insuperable. In the same group of medusæ is the species *Cyanea lamarcki*, which is confined to the region of the North Sea.

Several species of *Eurytemora* among the copepods are instances of dependence on water with a low salinity and the neritic distribution caused by this is associated with small areas of distribution. Neritic species confined to the Mediterranean are found, for instance. among the genus *Acartia*. The crustacean group Cladocera, which really belongs to fresh water, has from there branched out into the sea with two genera, *Podon* and *Evadne*, of the family Polyphemidæ, and the genus *Penilia* of the family Sididæ. The most euryhaline of these species is *Podon polyphemoides*, which is able to withstand both fresh water and water of a salinity of 35‰, and is also the one most widely distributed (circumglobal).

In the deep sea, too, meropelagic animals occur, namely plankton larvæ of benthal deep-sea animals (echinoderms, crustaceans, molluscs, polychætes, tunicates, etc.). Because of difficulties of method, however, this deep-sea meroplankton, which corresponds in the deep to the neritic plankton, has not been much studied.

CHAPTER XV

THE PELAGIC FAUNA OF THE DEEP SEA OR THE BATHYPELAGIC FAUNA

OUR knowledge of the existence of a bathypelagic fauna dates from the "Challenger" expedition 1872–76 and J. Murray's investigations during it. It was supposed earlier, for instance, that all deep-sea fishes lived near the bottom. Our knowledge of the pelagic deep-sea fauna made great progress through the "Valdivia" expedition under the direction of Chun (1898–99), the Atlantic deep-sea expedition under Murray and Hjort,[366] and several others. So far as deep-sea fishes are concerned, Brauer's study of the "Valdivia" material constitutes an important pioneer work.[58]

DELIMITATION AND VERTICAL DIVISION

It has proved to be a difficult question to find the upper limit of the deep-sea pelagial. The difficulty does not only lie in the fact that there exists in nature a wide transitional zone rather than a boundary, but rather in the fact that this transitional zone or boundary lies at a different depth in the different parts of the oceans, that different species of animals or different developmental stages of the same species behave differently, and that certain bathypelagic species ascend higher than usual during the night or at certain seasons. Other difficulties are connected with our insufficient knowledge of the vertical distribution of many plankton animals, even of those which have been caught several times; we know for instance that they have been caught in vertical hauls from a certain depth to the surface, for instance at a depth of 2000–0 m., but not in which part of this layer. Only closing nets and other modern methods have opened up possibilities of a greater accuracy in this respect.

The principles of theoretical evaluation, too, have suffered change. At first certain non-faunistic boundaries were drawn and it was supposed that they also represented boundaries for the fauna, as for instance the lower limit of illumination, seasonal variations of temperature, a temperature of 10° C. or some other degree of temperature, or the lower limit for phytoplankton, and the animals were arranged in the zones thus defined. This speculative approach,

which is also to be met with in more recent authors, does not, however, lead to unequivocal conclusions. We must rather proceed empirically and first determine the actual distribution of the animals at various depths; only then is it possible to see whether and how far this coincides with one as other of the non-faunistic boundaries. This empirical procedure has yielded acceptable results with regard to certain animal groups. The first attempt of this kind seems to have been made by Fr. Dahl in 1894 when he divided the pelagic copepods of the Atlantic according to their occurrence in three layers of depth, one between 0 and 200 m., the second between 200 and 1000 m. and the third below 1000 m. Another division was proposed by Haecker[203] for the radiolarians based on their behaviour with regard to illumination.

Taking the adaptations of the animals to deep-sea life as a basis, it would be possible to select from the great numbers of deep-sea species those which are distinguished as particularly typical deep-sea animals by the development of special morphological adaptations, and to determine the upper limit of their distribution. Such investigations have been made, for instance by Hjort on the expedition of the "Michael Sars" in 1910. His results were given greater precision by the improved method of catching the animals and by their great numbers. These investigations were made with special reference to the colour of fishes.

The animals of the pelagic surface layer are as a rule light coloured or hyaline, the fishes are often silvery along the sides and underneath, sometimes mottled. The animals of medium depth are very often red but already at 500–700 m. depth black becomes the dominating colour of the fish. The prawns and many squids in this last layer are still red, the medusæ dark brown or red, the pteropods and many copepods dark purple. These colourings are clearly protective measures which render the animals invisible. A red object appears red because it only reflects red rays and since these only penetrate the water to a depth of 100–200 m., the red colour means the object below this depth does not reflect any rays and thus is invisible. The rays which strike the surface of the water obliquely penetrate less deeply than rays which hit at right angles. Thus the power of penetration of the light rests among other things on the latitude and the time of day. The greater or lesser transparency of the water due to differences in plankton content also plays a part. The fact that nearly all decapod crustaceans in the equatorial belt are red, at any rate below 750 m. depth, in medium latitudes below 500 m., and in the polar seas below 200 m., accords well with this theory.[232] Black objects do not reflect any light.

Hjort's investigations mentioned above were made on fish of

the genus *Cyclothone* which contains both black and light species. Of the two species *C. microdon* and *C. signata* 7500 specimens in all were caught. The black *C. microdon* was obtained every time a haul was made at 500 m. minimum depth, and the main contingent seems to be uniformly distributed over depths between 500 and 1500 m. Small specimens of 20–30 mm. were most numerous in the upper part and large specimens of approximately 60 mm. length in the lower part of the layer. The distribution of the red prawn *Acanthephyra multispina* agreed with that of *Cyclothone microdon* with the exception that its larvæ occur still more superficially, in a layer up to 50 m. depth. In another red prawn of the same genus, *Acanthephyra purpurea*, the adults are found in roughly the same layer, i.e. 500 m. or deeper. The light *Cyclothone* species *C. signata* lives however in a higher level, at 300–500 m. depth, and it is practically speaking absent from greater depths than a little over 500 m. This species, too, when young inhabits the upper part and as fully grown fish the lower part of the depth layer for the species.

In a comparison between a northern series of stations between Ireland and the banks of Newfoundland and a southern series in the Sargasso Sea it was shown that the level where the fully grown animals had their maximum frequency was 200–300 m. deeper in the Sargasso Sea than in the northern series of stations, and this was confirmed by earlier investigations on other light and dark *Cyclothone* species.[58] This accords well with what has been said above about the power of penetration of light at different latitudes and it constitutes a convincing proof that in this case it is illumination and not, for instance, the temperature or conditions of salinity which is the main reason for the faunal zoning.

E. Bertelsen[46a] has lately given a valuable survey of the fishes of the suborder Ceratioidea (*Ceratias*, *Melanocetus*, *Gigantactis*, *Linophryne*, etc.). The larvæ and the fully-grown fishes behave very differently. Most larvæ have their greatest frequency in less than 65 m. below the surface between 40° N. and 35° S. in a temperature optimum of 15–29° C. and are thus epipelagic warm-water animals. Metamorphosis leads to a rapid sinking down; it takes place as a rule in 2000–2500 m. depth and the full-grown fishes, which are thus bathypelagic cold-water animals, can be found everywhere in the oceans south of the arctic and north of the antarctic water.

The difference between the level at which adults and young stages live may be great also in species of other fish genera. The black fish *Gonostoma lanceolatum* and the species of *Vinciguerria*, which are equipped with large luminscent organs, live as adults in the deep (the latter genus, however, not below about 150–500 m.), but their larvæ and young live in the surface layer 0–150 m. Still greater is the

difference in level between the eel species during spawning and their *Leptocephalus* larvæ. Similar examples could be given from other groups than fish (cf. p. 362). It is therefore not always possible to include the various developmental stages of the species in one and the same bathypelagic layer. But in other species it may be possible. Thus both young and adults of *Argyropelecus* have their maximum numbers at a depth of about 300 m., and of the black species of the pronouncedly deep-sea genus *Alepocephalus* even the larvæ are equipped with some pigment and are only found at 500–2000 m. depth.[236]

Time has shown that not all fish and other animals, which originally were regarded as deep-sea inhabitants, are to be so regarded in the strict sense of the word. Not a few of them are, rather, dark or twilight animals which live during the day at medium depths but often ascend to the surface during the night. This naturally is possible only for good swimmers and this change of locality has been found therefore among fish, squids and amphipods. Brauer[58] who made a special study of this phenomenon, excluded most myctophids from the deep-sea fish because many species of the subgenera *Myctophum*, *Lampadena* and *Diaphus* (with 50 species) were observed on the surface during the night, some of them in great numbers. Some stomiatids, which have the appearance of deep-sea animals because of their black colouring, luminescent organs and skin without scales, were also caught on the surface, and Brauer therefore suspects that their relatives such as *Chauliodus* and *Stomias* which are more akin to surface fish because of their scales and colouring than to deep-sea fish, live in a similar way. This has since been confirmed, as the German South Polar expedition caught many animals which otherwise inhabit the deep sea in horizontal catches on the surface (10–20 m. depth), among them species of the two last-mentioned genera as well as several others (*Myctophum*, *Lampanyctus*, etc.). Pappenheim[406] lists 20 such finds and states that the greater part of even the most pronounced deep-sea fishes regularly visits the upper layers during the night. These vertical migrations are made easier by the fact that many deep-sea fish lack a swim bladder; this bladder is, as is well known, not adapted to quick changes in pressure. Certain types, on the other hand, such as *Melamphaës* have not been caught above 400 m. even at night.

Among crustaceans vertical migrations have been found which must be considered as relatively extensive, having regard to the size of the animals. Thus many deep-water species of prawns, Euphausiacea, Mysidacea and Amphipoda, which at midday have their maximum number of individuals at 400–800 m. depth, shift

this maximum at midnight about 200 m., or more usually 400 m. nearer to the surface.[576] In certain species, for instance in the important *Euphausia superba*, only the younger stages undertake daily vertical migrations, while the older ones remain constantly in the surface layer.[170]

It will be clear, however, from what has been said, that different bathypelagic zones actually do exist in nature. Murray & Hjort, with special reference to pelagic fish,[366] have proposed a division of the central Atlantic into a zone between 150 and 500 m. and one below 500 m. They mentioned as characteristic for the *upper layer*: *Argyropelecus hemigymnus*, *A. aculeatus*, *Valencienellus tripunctulatus*, *Vinciguerria lucetia*, *Cyclothone signata*, *Argentina* and *Gadiculus*. They are silver grey, blue or purple fishes with large, often telescopic, eyes and mostly with numerous luminescent organs. Stephensen[499] mentions the same level (150–250 m.) as a very good boundary layer in the Mediterranean as well as the Atlantic between the superficial and the deep-sea inhabitants among the hyperioid amphipods, basing himself on the great amount of material from the Danish expeditions. Sewell on the other hand found reason to postulate only one deep-water zone in his survey of the copepods of the pelagic region (p. 339), the greatest number of species occurring at about 550–1200 m. depth, at different levels in different regions. The upper bathypelagic zone of 150–500 m. which is applicable to the other animal groups just mentioned contains on the other hand fewer species of copepods than the upper and lower strata. But this survey of copepods is based solely on the number of species and is therefore purely quantitative. It remains to be seen how the different species are distributed bathymetrically. The distribution in depth of the copepods need therefore not clash with the postulation of an upper faunistic deep-water zone.

The *lower bathypelagic zone* has its upper limit at approximately 500–550 m., as has been stated. It has, however, been already stressed that the depth of this limit varies with the geographical position and the transparency of the water. Fish which are characteristic for this zone in the Atlantic are for instance *Cyclothone microdon*, *Opisthoproctus soleatus*, *Malacosteus indicus*, *M. niger*, *Gastrostomus bairdi*, *Cyema atrum*, *Gonostoma grande*, etc., and beside these many invertebrates. The fishes and also the cephalopods of this zone (*Vampyroteuthis*, *Watasella*, *Melanoteuthis*, etc.) are dark in colour. The many deep-water species of the eels (Apodes) and some others probably belong into the same zone.

It must be emphasized, however, that this division in two bathypelagic zones has regard to the full-grown fishes and that the larvæ of the same species often live in another zone.

HYDROGRAPHY AND NUTRITIONAL CONDITIONS

The hydrography of the deep-sea has been mentioned earlier on in connection with other problems (p. 343). As regards the pelagic temperature zones in particular we may supplement earlier data with the following table.

TABLE 49

TEMPERATURES IN VARIOUS DEPTH ZONES ALONG THE CENTRE OF THE ATLANTIC. THE TWO VALUES FOR THE SURFACE WATER REPRESENT THE MEAN FOR THE COLDEST AND WARMEST MONTH OF THE YEAR

Depth in m.	60° N.	40°	20°	0°	20°	40°	60° S.
0	7–12° C.	15–23° C.	23–26° C.	25–27° C.	21–25° C.	11–16° C.	−2 to −1° C.
100	8–10	15	22–23	15–19	21–23	8–10	−1
200	9	12–15	16–19	12–14	18–19	10	0
400	7–8	12–14	13–14†	7–8	9–12	5–7	0–1
1000	5–6	7–8	6‡	4–5	3–4	2–3	0–1
2000	3–4	4	3·5–4	3–3·5	3·5	3	0

† Sargasso Sea 16–17° C. ‡ Sargasso Sea 7–8° C.

Fig. 117 shows the temperature curves for several regions. We see among other things that the temperature of the warm surface water sinks rapidly down to the 80–100 m. depth. But from there, in the so-called thermocline, it sinks only slowly downwards. The thermocline is thus a bend in the course of temperature and the vertical distribution of a species or a developmental stage no doubt is often influenced by this bend.

The basic food for the pelagic fauna of the deep sea consists for the most part of dead plankton organisms, especially algæ, which rain down from the superficial water layers. Before this dead plankton has sunk down into the deepest layer several thousand metres below the surface, they are very largely dissolved in the water or decomposed by bacteria. Hentschel, who undertook a thoroughgoing analysis of the general biology of production in the sea while on the "Meteor" expedition in the South Atlantic, maintains that the greater part of the nannoplankton species of the upper water layer are a negligible factor below about 200 m. depth. The tremendous dark water masses below this level contain only an insignificant number of nannoplankton species, and among these species the Schizophyceæ in the form of the so-called *olive-green cells* are most important, followed by the protozoa (zooflagellates), the coccolithophorid *Syracosphæra heimi*, bacteria, etc. The olive-green cells are almost completely absent in the uppermost 50 m. layer, reach their maximum number at 200–500 m. depth and after this diminish slowly but occur, apart from local exceptions, right down to at least 5000 m. depth. Even at 200-500 m. depth the number of individuals is fairly small, on an average only 70–170 cells per

litre.[227] They maintain themselves probably, in common with the rest of the nannoplankton in the deep sea, by feeding on organic substances which are dissolved in the water and thus are not avail-

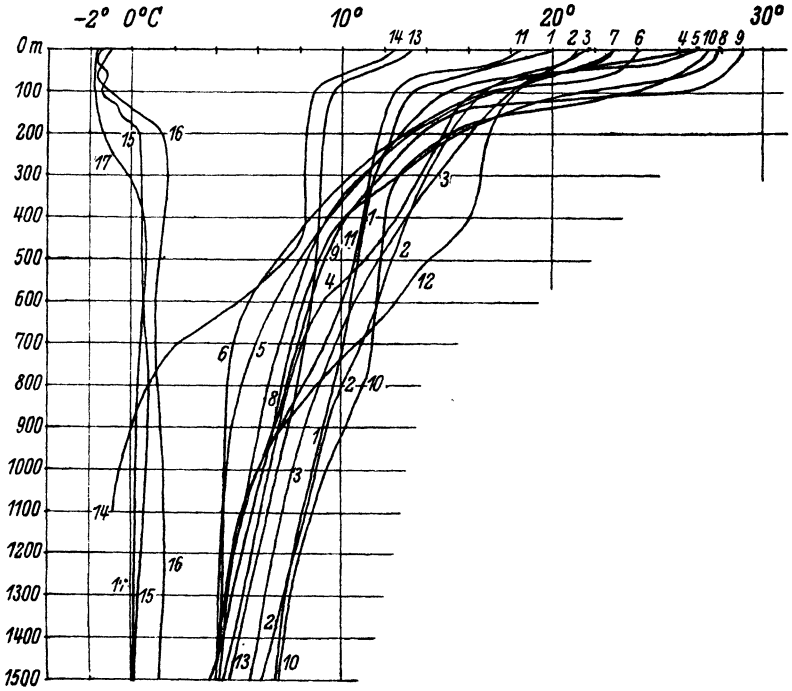


FIG. 117.—Temperature curves:

Atlantic: 1. Off Cape Finisterre.
2. South-east of Madeira.
3. South of the Canaries.
4. The Cap Verde Islands.
5. Off Freetown, West Africa.
6. Guinea Current, 10° 16′ W.
7. South Equatorial Current, 8° 30′ W.

Indian Ocean: 8. Between Chagos and the Seychelles, 2° 57′ S.
9. Between the Seychelles and Africa, 5° 42′ S.
10. Arabian Sea, 9° 6′ N., 53° 41′ E.

Atlantic: 11. North of the Azores, 46° 48′ N.
12. Sargasso Sea, 34° 44′ N., 47° 52′ W.
13. West of Scotland.
14. Faeroes-Shetland Channel north of the ridge.

Antartic: 15. The ice border of Bouvet Island.
16. Pack-ice limit north of Enderby Land, 62–63° S.
17. Weddell Sea, 72° 20′ S.

1–10 and 15–16 after G. Schott from the "Valdivia" Expedition, 1902.
11–14 after Murray and Hjort, 1912.
17 after G. Schott, 1926.

able as food for zoo-microplankton. This dissolved organic material constitutes at least six milligram per litre and is therefore greater than the content of particulate organic substances in this deep water. Any organisms, i.e. the olive-green cells, that are capable of reclaiming this dissolved organic material are important in building it into bodies of suitable size for use by filter-feeding animals.

THE COMPOSITION OF THE PELAGIC DEEP-WATER FAUNA

In the following survey we confine ourselves in the main to a mention of the characteristic genera and groups of higher taxonomic rank and in general we shall have to leave out the species of genera which occur also in the pelagic surface layer. A division into certain layers of depth (upper and lower) would have to take into account the distribution of the species and thus must in most cases be omitted, reference being made to the few examples which have already been given for the Atlantic.

Radiolaria. The results of the "Valdivia" and the later "Meteor" expedition, which the use of closing nets made more precise, showed that the family Challengeriidæ may also occur in the upper warm water but that it is represented by an incomparably higher number of individuals and somewhat higher number of species in the deep cool water and the polar cold water. *Pharyngella gastrula* in particular (and thus the monotypical family Pharyngellidæ) is a pronounced abyssal form which has been caught oftener than other species in the zone between 1500 and 5000 m. The family Tuscaroridæ is more exclusively confined to the bathypelagical than are the Challengeriidæ: it hardly ascends, at least in the warmer seas, above 400 m. depth.[54] These radiolarians belong to the group Tripylæ. The families Thalassothamnidæ and Orosphæridæ which belong to the group Collodariæ, live mainly, if not exclusively, in the medium and deep zones.

Medusæ. The group Trachymedusæ contains several bathypelagic genera, for instance *Crossota, Pantachogon* and the monotypical *Colobonema.* The group Narcomedusæ is predominantly bathypelagic. Among Scyphomedusæ only the order Coronatæ enter into this category, with for instance the genera *Nausithoë, Atolla,* and the monotypical *Periphylla.*

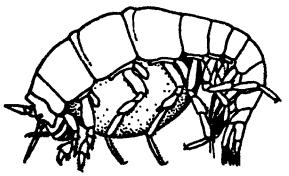
Ctenophora. The two monotypical genera *Aulacoctena* and *Bathyctena* together form the family Bathyctenidæ, which therefore belongs entirely to the deep water.[348]

Nemertini. This group contains a fairly large number of bathypelagic species which were made known specially by the works of Bürger[70] and Brinkmann.[60] They all belong to the group Hoplo-

nemertini and form a special tribe, the *Pelagica*, comprising no less than nine families with exclusively bathypelagic species. Everything indicates that all pelagic nemertines are bathypelagic.

Ostracoda. Here we must mention the purely bathypelagic genus *Gigantocypris* with two to three species, among them the largest of all ostracods, *G. agassizi*, fully 2 cms. in length. An accessory mechanism of the eye has been interpreted as an adaptation to deep-sea life (reflector?).

Copepoda. A number of species are mainly tied to deep water. Many, however, ascend to the upper layers in the higher latitudes and may therefore be regarded as eurybathic or equatorially submerged cold-water species. Certain genera, too, are wholly or almost wholly bathypelagic, for instance among those with a fair number of species *Gætanus* and *Xanthocalanus*, the latter, however, possessing three species in the surface layer in the southern cold-water region. Usually the deep-sea genera do not show morphological adaptations to deep-sea life; *Cephalophanes*, with a few species, is possibly an exception to this rule to judge from the modification of the eye.



Amphipod *Lanceola clausi*, ♀, 3×natural size. (After G. O. Sars, redrawn.)

Amphipoda. The fairly numerous pelagic species of the Gammaridea are usually strong, active swimmers with wedge-shaped modification of the head are several purely bathypelagic genera, the largest being *Cyphocaris* with five species. *Hyperiopsis* has developed in a different direction. It has a powerful, round head with large eyes and thus represents a parallel form to the Hyperidea. This bathypelagic genus forms (with two species) a separate family. The Hyperiidea, which contain exclusively pelagic species, live for the most part in the upper layers but many are bathypelagic, e.g. the fairly considerable families *Lanceolidæ* and *Scinidæ* with the exception of a few, perhaps eurybathic, species; also the Thaumatopsidæ, the Pygmæidæ and Eumimonectidæ (with fewer species), the Chuneolidæ (monotypical) and the Dairellidæ (two species). Stephensen, who has given us the most exact data, divides them into two groups. The species of one group (the Thaumatopsidæ) ascend at the time of reproduction or at other times into the upper regions, those of the other group, for instance nearly all Lanceolidæ and most Scinidæ, are not normally found at a higher level than 150–200 m., and usually much deeper, down to 4000 m. The Lanceolidæ are distinctly abyssal except for *Lanceola sayana*, which also differs in having a thicker

shell and better developed eyes than the rest. Characteristic of the abyssal Hyperidea is that they are hyaline, have thin shells, and possess more or less rudimentary eyes, which may even be completely reduced as for instance in *Vibilioides* and *Acanthoscina spinosa*. It is striking that the pigmentation of the bathypelagic Hyperiids is not red, as in other deep-sea crustaceans, but only pale hyaline, sometimes with small red speckles.

Euphausiacea. The monotypical genus *Bentheuphausia* is abyssal. It has reduced eyes and, characteristically enough, lacks luminescent organs which are found in the rest of the euphausiids whose eyes are functioning.

Mysidacea. Deep-water genera are *Gnathophausia* (with many species), *Lophogaster*, *Eucopia*, *Boreomysis*, *Pseudomma*, *Erythrops* and *Pseudomysis*. The last three have rudimentary eyes with no pigment.

Decapoda Natantia (prawns). Approximately a third of this group inhabits medium depths or deep water. It is often difficult to tell which of them are truly pelagic since several of them live very near the bottom and there subsist on detritus stirred up from the bottom. Bathypelagic are, among others, *Amalopenæus*, *Benthecicymus*, *Gennadas*, *Sergestes* (vertical nocturnal migrations to the surface are usual among this genus), *Parapasiphaë*, *Hymenodora*. Two small families, the monotypical Bresiliidæ and Stylodactylidæ with one genus and seven species, are purely bathypelagic.

Cephalopoda. The squids constitute a considerable proportion of the bathypelagic fauna. Within the group Decapoda the subdivision Oigopsida contains only pelagic species and many of them are bathypelagic, often adapted to life in deep-water by the possession of luminescent organs and by other modifications, for instance telescopic eyes. Several species ascend during the night to the surface water. Several families are wholly bathypelagic, as for instance the *Octopodoteuthidæ*, *Histioteuthidæ*, *Chiroteuthidæ*, *Grimalditeuthidæ*, *Joubiniteuthidæ*, *Bathyteuthidæ* and the giant squids of the family *Architeuthidæ*. The large family Cranchiidæ is for the most part bathypelagic. Here belong for instance the genera *Teuthowenia*, *Toxeuma* and *Bathothauma*, which have stalked telescopic eyes.

An example from the group Myopsida is the well-known *Spirula spirula* which forms by itself the somewhat isolated family Spirulidæ. The young stages are found only at 1000–1750 m. depth, the older ones up to 200, seldom at 100 m.[69]

Among the Octopoda we may mention the jelly-like transparent *Cirrothauma murrayi* which is said to have its suckers modified into luminescent organs but is nevertheless blind (a mysterious coincidence of two characteristics one of which, blindness, makes the other useless; one or the other may therefore be questionable). The

family Vampyroteuthidæ, which has six genera and nine species and by itself forms the suborder *Vampyromorpha*, is wholly abyssal and is characterized by primitive traits in its organization. The best known genera are *Vampyroteuthis* (fig. 119) and *Melanoteuthis*, both with black-pigmented species. The octopods are in general not pelagic. But the bathypelagic species are not so few as was formerly supposed. Thus an examination by S. Thore[554] of the material from the "Dana" expeditions has shown that *Japetella diaphana*, *Eledonella pygmæa*, *Amphitretus pelagicus* and *Vitreledonella richardi* are bathypelagic. The distribution of all four is confined to a region between about 40° N. and 40° S., which can hardly be due to the requirements of adult animals, since they live at 1000 m. or deeper, but rather to the fact that the eggs and young stages live mainly in the upper bathypelagic region up to approximately 100 m. depth and are dependent on a relatively high temperature in the water layer between 100–300 m. depth (fig. 121).

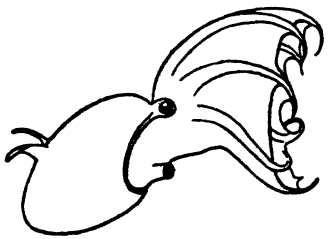


FIG. 119.—*Vampyroteuthis infernalis*, an octopod cephalopod of the Atlantic depths; 1·6 × natural size. (After Chun, redrawn.)

Holthurioidea. Curiously enough there is one family among the sea-cucumbers whose species do not live only as larvæ but also as fully grown individuals pelagically, namely the family Pelagothuriidæ with the two genera *Pelagothuria* (three species) and *Planktothuria* (one species). The few finds were made in deep water. The family forms a special suborder, the *Pelagothuriida*.

Fishes. When Brauer had published in 1906 his great work on the fish from the "Valdivia" expedition 66 bathypelagic genera which have species exclusively below the 400 m. level, were known. This number has naturally increased since this time, for instance through the rich results of the expeditions from the station on Bermuda, which are provisionally listed by Beebe in 1937. These investigations were made within a very small region approximately 15–20 km. south-east of the Bermudas, no greater than the fifth million part of the surface of the world's oceans and yet the result of about 1500 hauls was 220 species belonging to 65 genera and 46 families, which constitutes more than a third of the whole world's fauna of bathypelagic fish species. These may thus be presumed to be at least 600 in number. All the 220 species were caught below the 300–400 m. level. 66% of the species possessed luminescent organs.

Of most of the bathypelagic fish only a few specimens are known, and it is therefore in most cases difficult or impossible to state how they are distributed within the upper and the lower bathypelagic zones, unless the decision is based on colour which, according to what has been said before, may be regarded as an indicator. Many species, particularly in the upper bathypelagic layer, undertake nocturnal migrations upwards.

The fish constitute a very considerable part of the deep-sea fauna. The number of purely bathypelagic families seems to be about 40 and to this must be added a number of bathypelagic genera and species of other families. The following collection of examples comprises only a few selected types.

Selachii. Genera in question are for instance *Etmopterus* (=*Spinax*) and *Somniosus.*

Malacopterygii. In this group we must mention especially the superfamily (according to some taxonomists the suborder) *Stomiatoidei* with the family Stomiatidæ and the genus *Stomias* as main type. This superfamily contains, according to the latest classification, at least 10 families and is altogether bathypelagic. In the Atlantic, the most prolific in species are the Melanostomiatidæ, which in the Bermuda region alone has 36 species of the genera *Eustomias, Photonectes,* etc. Other families of the same superfamily are: Sternoptychidæ with *Argyropelecus,* known for its telescopic eyes, Maurolicidæ with *Maurolicus,* Idiacanthidæ with *Idiacanthus fasciola,* which has a very peculiar larva with eyes on long narrow stalks which is shortened during metamorphosis. The fully grown females are about 25 cm. long, but the males are only 3–4 cm., lack teeth and paired fins, have a rudimentary intestine but a large luminiscent organ on the cheek. They seem to die immediately after spawning and their peculiar organization seems to be adapted to the very special conditions in the deep sea (cf. Ceratiidæ below). And finally mention must also be made of the family Gonostomatidæ because of the great numbers of individuals of some species of the genus *Cyclothone.* Among the 115,740 individuals which were caught in the expeditions mentioned above from the Bermudas, 82% were represented by the two species *C. microdon* and *braueri.*

Other families of the Malacopterygii are *Bathylagidæ* (of the group Salmonoidei) with *Bathylagus* and *Nansenia,* and the *Alepocephalidæ* (of the group Clupeoidei) with at least some 50 black species of *Alepocephalus, Aleposomus, Bathytroctes,* etc., belonging to the lower deep-water layer. The latter genus has telescopic eyes. The most prolific in species, however, of all deep-sea families seems to be the *Myctophidæ* (Scopelidæ; they are at times classified as belonging to the order Haplomi). In the small region south of the Bermudas

alone there are found 58 species of which 23 belong to *Lampanyctus*, 15 to *Diaphus*, 15 to *Myctophum* and 5 to *Lampadena*. The closely related *Bathypteroididæ* have greatly lengthened upper rays in the pectoral fins, an example of adaptation to life in the dark deep-sea by development of a tactile organ to replace the optic organs. In *Ipnops* (Ipnopidæ) the reduction of the eyes goes so far that they have disappeared without leaving any trace whatsoever.

Gadiformes. The family Gadidæ contains the entirely bathypelagic genus *Gadiculus*, which is poor in species and belongs to the upper, illuminated layer, and the genera *Læmonema* and *Melanonus*. The otherwise benthal family Macruridæ has one monotypical bathypelagic genus *Lyconus*.

Apodes. Among the approximately 20 families into which this order is now divided, several are purely bathypelagic, most of these, however, possess rather few species. Among the more prolific in species are *Synaphobranchidæ* and *Nemichthyidæ*. Well known are the *Saccopharyngidæ* because of their huge mouth, this being an adaptation to the nutritional condition in the deep water with its sparse population of suitable prey and the consequent necessity for the predatory fish on occasion to store food for a considerable period of fasting. The Saccopharyngidæ are detached from the Apodes by some taxonomists and included in another order (Lyomeri). The Atlantic *Saccopharynx ampullaceus* may reach 1836 mm. in length.

Jugalares. The family *Chiasmodontidæ*, which is fairly poor in species, accords with the last-mentioned family in that its black species are adapted to the rarity of their prey by an immense extensibility of the mouth opening and elasticity of the stomach and abdominal wall. The family is entirely bathypelagic.

Pediculati. The superfamily Ceratioidea, which contains 10 families and about 80 species[46a] belongs to the deeps. Most species are black. The group is known mostly for its mode of reproduction. In several species the males are tiny dwarfs, several times smaller than the females and so firmly attached to them that their vascular system becomes fused and the heart of the male is rudimentary, a condition without parallel among the vertebrates. For these fish, which occur very sparsely in the deep sea, a parasitic mode of life contains a guarantee of fertilization for the egg. In the species *Ceratias holbœlli* which has been known longest and which is the giant of the family, being almost a metre in length while 10 cm. is the usual length for the others, the small dwarf males are only 4–5 mm. long and sit attached to papillæ of the ventral skin. In some species, however, the males are of normal size and swim free but differ from the females in possessing a well developed chemical sense organ which facilitates their search for the female. Most species have a large mouth with

big teeth and are, like many other deep-sea fishes, adapted for the swallowing of large prey. Of *Melanocetus krechi*, which lives in the southern Atlantic and Indian Ocean, a specimen was once caught which contained in its elastic stomach a *Lampanyctus* twice as long as *Melanocetus* itself.

In the survey given here of the constitution of the pelagic deep-sea fauna the intention was to bring out that this fauna contains among its endemic elements not only a number of species and genera but also a great number of families, most of which are certainly poor in species. Some, however, are quite prolific in species. This deep-sea fauna contains even some higher taxonomic groups, for instance the suborders or superfamilies *Narcomedusæ*, *Pelagica* among the Nemertini, *Vampyromorpha* among the Cephalopoda, *Pelagothuriida* among the Holuthurioidea, *Stomiatoidea* and for the greater part *Ceratioidea* among the fishes.

Taxonomically therefore, the bathypelagic fauna shows a well marked independence.

HORIZONTAL DISTRIBUTION

The open oceans

The difference in temperature between the equator and the higher degrees of latitude is considerably lesser in the deeper water layers than on the surface (table 49, p. 357) and we may presume a priori that a more extensive distribution in a north-southerly direction is more common in the bathypelagic than in the epipelagic fauna. This is confirmed by the facts. It is however quite common that deep-sea animals which normally occur in purely abyssal depths at 1000–2000 m. at a temperature of 3–7° C., do not inhabit, or at least do not regularly inhabit, the arctic and the antarctic deep sea with its temperature of −1° to +1° C. The comparatively slight difference in temperature between 3° and 0° or 1° seems in this case to be decisive, since there seems no reason to suppose a different cause than temperature (cf. fig. 117).

The bathypelagic species, which are truly *cosmopolitan* with regard to temperature, are thus not numerous. But there are some. From the Atlantic sector of the globe, where this distribution is best known, we might mention the ostracods *Conchoecia borealis* and *C. obtusata*, the hyperiid *Scina borealis*, the gammarid *Cyphocaris anonyx*, the prawns *Sergestes arcticus* and *Hymenodora glacialis*. Other examples have been mentioned from the eurythermal cosmopolites and the cold-water cosmopolites among the epipelagic species, of which several are mainly bathypelagic in lower latitudes. Some few species which are sufficiently eurythermal to occur from the Arctic to the

equatorial deep water are, however, missing in the Antarctic, for instance the copepods *Heterorhabdus norvegicus* and *Calanus finmarchicus*, etc. On the other hand, mainly antarctic copepods are to be found in deep water considerably to the north, but only occasionally, which seems to indicate that these are cases of transportation to expatriation areas. Thus *Metridia curticauda* has been caught off the Galapagos, Lower California and the Philippines, in Polynesia and even at 50° N. in the Atlantic, *Calanus propinquus* at 9° S. and 3° N. in the Atlantic and the Caribbean Sea, *Rhincalanus gigas* off South Africa and *Metridia gerlachei* at 17° N. in the Atlantic and 7° N. in the Pacific. The medusæ *Halicreas minimum*, *Botrynema brucei* and *Pantachogon hæckeli* are characterized by a regular occurrence within the whole deep-water region from the shelf of the Antarctic Continent to the North Atlantic but, peculiarly enough, are absent from the arctic region.[290]

A great number of species inhabit the whole of the bathypelagic region between the southern boundary of the arctic and the northern boundary of the antarctic region. The North Atlantic Transversal Ridge, Faroes–Iceland–Greenland and Davis Strait, represents a very effective barrier for the pelagic deep-sea fauna in its penetration to the north. This accords well with the fact that this ridge, together with the arctic water which flows south over it is likewise a barrier to that water, which below the surface layer approaches the ridge from the south. Only between Scotland and the Faroes does the water of the Gulf Stream flow further north without impediment (fig. 34, p. 104). In the Atlantic deep water immediately to the south of the ridge there lives a pelagic fauna which is rich in species and consists of members of almost all the major taxonomic groups, and the great majority of these species spread south through the deep water of the equatorial region and further into the southern hemisphere. We can only mention some of the most often reported species here. Many are found in all three oceans; these are marked by an asterisk in the examples given below.

Among the different groups of medusæ, 10 species belong here,[290] for instance, apart from the three mentioned last also **Periphylla periphylla* (fig. 120), **Colobonema sericeum*, **Aeginura grimaldii*. A great number of copepods inhabit the tropical and temperate Atlantic north of the equator, whose deep-water plankton has been more carefully investigated than any other. It is worth mentioning that this deep plankton is considerably richer in species than the surface plankton of the same region of the Atlantic. While Sewell lists 134 copepod species in the surface plankton ([479], p. 459), his figure for the deep plankton is 357 ([479], p. 498). Many of these occur in all three oceans. Among the Mysidacea we notice, for

instance **Gnathophausia gigas* and **G. zoëa*,[153] among the Amphipoda Hyperiidea **Phronima sedentaria*, **Paraphronima gracilis* and **Euprimno macropus*, among the prawns **Acanthephyra purpurea*, which occurs in the various oceans with different races, as is also the case in a number of other species. If we now pass on to fish, leaving aside several taxonomic groups, we may mention **Argyropelecus olfersi*, *A. hemigymnus*, **Melamphaës mizolepis*, **Synaphobranchus kaupi*, **Cyclothone microdon*, **C. signata*, **C. acclinidens* and *Maurolicus müller*i. It is impossible to say what percentage the three-oceanic species represent among the bathypelagic fauna as a

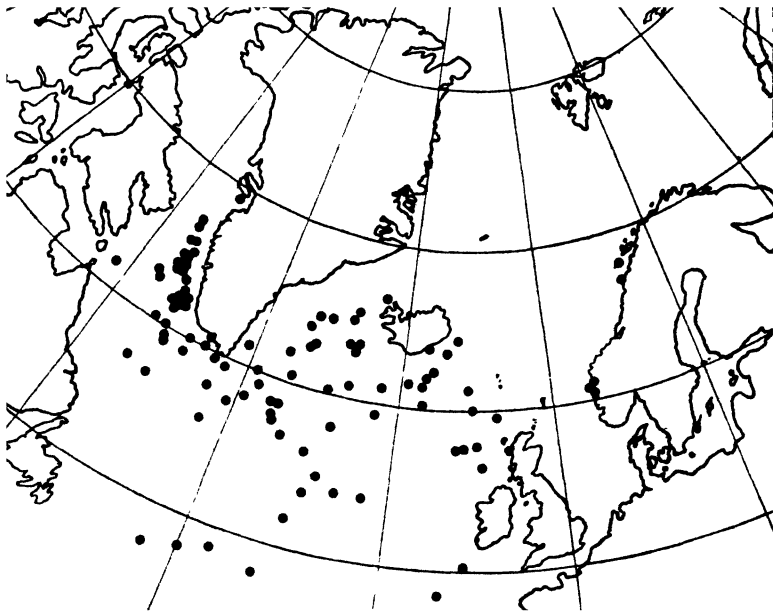


FIG. 120.—Distribution in the North Atlantic of the medusa *Periphylla periphylla*. (After Kramp, 1947.)

whole because of our incomplete knowledge of the Pacific. But we may assume that this percentage is fairly high. As an indication we may mention that on the John Murray expedition, in five collections made in various parts of the deep-sea region of the Indian Ocean, the percentage of Atlantic species varied between 71 and 94, with a mean of 84, and that of the 212 known deep-water copepods of the South-western Pacific 78% are Atlantic ([479], pp. 531–548).

This wide distribution is in complete accord with the presumable transport by ocean currents. It is true, that deep-sea currents are, of course, more incompletely known than are the surface currents but

certain facts about them are known (cf. pp. 318–319 and 353–344). The three oceans are largely connected with each other in the southern hemisphere, and with the Southern Polar Sea.[590]

But in the deep sea there are also pelagic species with a more *restricted distribution.* Limited to lower latitudes by temperature are, for instance, among the squids **Japetella diaphana* (fig. 121), which seems to have its temperature optimum in 200 m. depth at 13–15° C., and, among the fishes, **Stomias affinis*,[137] whose temperature limit on the whole does not go below 18–20° C. at 100 m. and 14–15° C. at 200 m. depth. Other species on the other hand avoid the warmest equatorial region, for instance **Stomias boa*, which occurs both north and south of this and has roughly the same upper temperature limit as the last-mentioned lower limit for *S. affinis*. The various

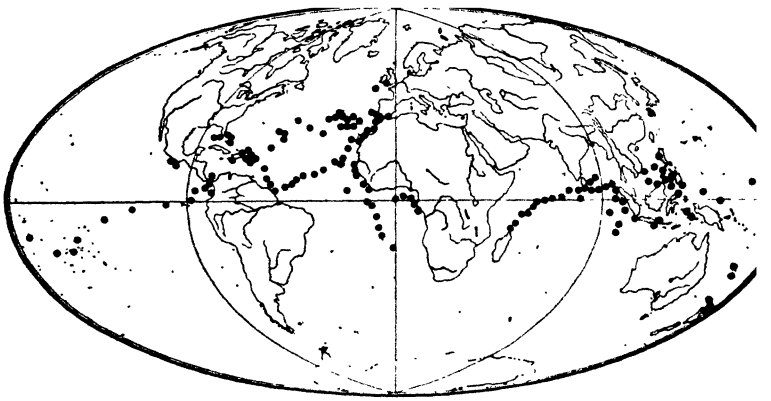


FIG. 121.—Distribution of the cephalopod *Japetella diaphana*. (After S. Thore, 1949, redrawn.)

oceans, too, possess their own special species. Although our knowledge of the bathypelagic fauna of the oceans is as yet only imperfect, it seems highly probable that species which are found regularly and in high numbers in the Atlantic and which because of their size and appearance are easily noticed, but yet are still not found in other oceans, are specifically Atlantic. Such a species is, for instance, the prawn *Gennadas elegans*.[71]

Burkenroad[71] maintained, with special reference to the Central American land barrier between the Atlantic and Pacific, that although the faunas of the prawn family Penæidæ in the shelf region of the Atlantic and Pacific coasts "are more nearly related to another than to the faunas of other regions of the world, the reverse seems to be true of the deep-water peneids. This contrast is indicated to have a possible cause in the shallow depth of post-Cretaceous Middle

American intercommunications between the Atlantic and Pacific, which, while placing the littoral populations in contiguity, left the deep-water forms effectively at opposite ends of the world."

The Mediterranean and the Sea of Japan

The *Mediterranean* is partly divided from the Atlantic by a sill immediately outside the Straits of Gibraltar at a depth of only 320 m. This is, according to several investigators, the main reason for the differences between the deep faunas of the Mediterranean and the Atlantic; several species were, quite simply, debarred from entering the Mediterranean (pp. 303–304). But there are also other causes. In the deep of the Straits of Gibraltar a strong bottom current flows out from the Mediterranean at least during the greater part of the year, which is discernible a long way out in the ocean by its higher salinity and temperature. This undercurrent is strongest at a depth of 200–300 m. in the Straits of Gibraltar and flows there with a velocity of 2 m./sec. (7·2 km. per hour[376]). This out-flowing current increases further the effect of the dividing wall formed by the topography of the bottom, so that the inflowing current of Atlantic water only occupies the uppermost 100 m. The higher temperature and perhaps also the higher salinity in the Mediterranean deep water makes it uninhabitable for certain deep-sea animals of the Atlantic. The temperature does not fall below an annual mean of 13° C. even at 2000–3000 m. in the Mediterranean and in its south-eastern part it is about 15·4° C. at 300–400 m. depth. Factors affecting both existence and distribution thus make the penetration into the Mediterranean difficult for many deep-sea animals of the Atlantic.

This is reflected in the composition of the deep-sea fauna of the Mediterranean. It contains only a few deep-sea medusæ of the Atlantic,[290] not a single one of its pelagic nemerteans,[60] and of hyperioid amphipods the Mediterranean contains only epipelagic species or those which in their vertical nocturnal migrations ascend to the surface water layer, whereas the true deep-sea families (Lanceolidæ and Scinidæ), however, are absent.[499] The same is true of many squids (*Spirula*, for instance, is missing) and fishes. The whole group of ceratioid fishes are totally missing in the Mediterranean although both larvæ and older specimens occur in Cadiz Bay.[46a] In general, the western Mediterranean's bathypelagic fauna is, like the epipelagic fauna, richer than that of the eastern Mediterranean, but the latter contains several species which are missing in the western part. Thus we find *Myctophum glaciale* only in the western and northern part, but *M. coccoi* only in the eastern, *Paralepis sphyrænoides* only in the western, while *P. pseudosphyrænoides*, and even more so *P. affinis* prefer the eastern part.[67]

That this distribution is due to the temperature of the water is shown by the fact, that the distribution of these two pairs of species in the Atlantic shows much the same variation according to temperature. *Cyclothone microdon*, *C. braueri* and *Stomias boa* have smaller individuals in the Mediterranean, or they have rather fewer vertebræ than in the North Atlantic[137]; a similar variation is also to be found in other fishes which live both in cold and tropical seas.

If thus the higher temperature in the deep of the Mediterranean has in general reduced its deep fauna compared with that of the Atlantic, it has on the other hand had the reverse effect in certain cases, in that species which because of their temperature requirements are in the Atlantic relegated to the upper water layers, descend very much further down in the Mediterranean. Such species are fairly numerous.[77] This phenomenon has its parallel in the bathybenthal fauna (p. 305).

The *Sea of Japan*, too, is shut off from the deep water of the Pacific by high sills and here the bathypelagic fauna, too, is only weakly represented (cf. p. 307). The North Atlantic Transverse Ridge and the shallow Bering Strait have a similar effect on the communication of the two adjoining oceans with the *arctic deep sea*, whose low temperature is largely due to the fact that these ridges prevent the influx of warmer water. The low temperature probably acts as a more effective faunal barrier than the ridges themselves.

THE ORIGIN OF THE BATHYPELAGIC FAUNA

A retrospective glance at the survey given of the composition of the bathypelagic fauna will show that it has a double origin. In the first place there are connections with the epipelagic fauna. From this originated the great number of species which belong to partly epipelagic genera and also the majority of endemic bathypelagic genera and families. This is fairly obvious in the case of animal groups which are purely or mainly pelagic and are well represented in upper water layers; for instance radiolarians, medusæ, ctenophores, the halocyprids and cypridinids among the ostracods, most of the copepods in question, the hyperiids, mysidaceans, euphausiaceans, decapod crustaceans, œgopsids and most fishes. In some cases it is difficult to decide where to look for the ancestral forms, whether the ancestors were epipelagic or benthal. These obscurities exist, for instance, in the case of some bathypelagic gammarid amphipods whose affinities do not clearly go back to epipelagic forms, and also in the case of the cephalopod family Spirulidæ which seems most closely related to benthal forms but occupies such an isolated position within the system that it is difficult to form a decision. Other bathy-

pelagic types show a more pronounced benthal origin, thus the group Pelagica among the nemerteans, since epipelagic nemerteans are absent; the genera *Melanoteuthis* and *Cirrothauma* and the families Bolitænidæ, Amphitretidæ and Vampyroteuthidæ among the otherwise mainly benthal octopodid squids; the Pelagothuriidæ, which represent the only pelagic type among the echinoderms, and some fish families, namely the Ceratioidea, Saccopharyngidæ and the pelagic members of the Apoda. The nearest relatives of these fish are true bottom forms which partly belong to the deep sea and partly to the shelf.

We now turn from the biocœnotic to the regional origin. Because of the cold-water character of the bathypelagic fauna we might incline to the view that this fauna derives for the most part from the arctic and antarctic pelagic fauna. But this cannot be true since the polar pelagic faunas are considerably less rich in species than that of less cold regions. It is in these latter regions that we must look for the original home of the greater part of the bathypelagic fauna. This has been borne out by phylogenetic investigations on radiolarians[203, 417] and several metazoan groups. Theoretically, a polar origin is occasionally conceivable, for instance in connection with an equatorial submergence of a polar species.

CONCLUDING REMARKS

In the course of this work I have often had occasion to stress that as a characteristic of a zoogeographical region an endemic family is more important than an endemic genus, an endemic genus more important than an endemic species, and that endemic elements are more important than those which are common also to neighbouring regions. We must now devote further attention to these methodological questions.

The taxonomic (morphological) differences between two closely related genera are more comprehensive than the differences between two species of the same genus, and palæontological discoveries show that the generic differences have taken a longer time to develop than differences between species. In general, the endemic genus of a region has thus lived a longer time in the environmental conditions of this region than an endemic species in the environment of *its* region. The same is true of an endemic family as compared with an endemic genus. There is, therefore, in general a parallel between the taxonomic rank of an endemic element and the time it has lived in the environment in question. The "environment", of course, does not apply to regions with purely geographical delimitation, for

instance by certain longitudes and latitudes, since these have often been subjected to climatical and other alterations, but to the ecological conditions to which the species (genus, family, etc.) is adapted.

The taxonomic scale contains, therefore, historical documents of great zoogeographical value. It is important in this connection that for close on 100 years taxonomy has operated mainly with phylogenetic, that is to say historical, concepts.

The surest basis for a historical zoogeography is clearly provided by palæontological, palæogeographical and palæoclimatological evidence. This is available to a certain extent and has been drawn upon in the preceding chapters. But as is well known, palæontology is by no means free from gaps and here taxonomy thus can provide a welcome complement.

Another factor which deserves special attention in the characterization of a fauna is endemism. Because of its exclusive occurrence within a environmental region a greater value must be attached to an endemic than to a non-endemic species, genus, etc., in the characterization of this region. We may imagine, for instance, an endemic genus with five species all of which are thus endemic in the same region. This genus will clearly be more characteristic for this region than another genus which likewise possesses five endemic species within the said region, but has some species in other regions as well. The same criterion must also be applied to an endemic family as compared with a non-endemic family. That an endemic species is more characteristic for a region than a species which is also found in other regions, is obvious.

The characterization of zoogeographical regions and the assessment of their relationship to one another results in a regional zoogeographical system with a graduated scale of super- and subregions. The parallel with the taxonomic system and its scale of classes, orders, families, etc., is clear. And just as the final aim of taxonomic research is not the graduated scale *per se* but the unravelling of the historical (phylogenetic) relationships between the taxonomic categories and thus the history of the animal kingdom, in the same way the final aim of zoogeography is not the graduated regional system in itself but the history which this system reflects, that is the history of the faunas. Zoogeography, like other sciences, strives to discover the ultimate causes. And the causal connections here are, as in so many other cases, to a great extent historical connections. Hence the importance of the parallelism between the rank of a region within the zoogeographical system and the position of its faunal constituents within the taxonomic scale.

To this must be added yet another factor. In the assessment of the

position of a fauna within the zoogeographical system, that is to say its greater or lesser independence as a centre of development, we may introduce mathematical values for its various elements according to age within the environmental region, endemism or other facts, and these values may be combined into more comprehensive figures by summation, multiplication and division. This offers considerable advantages. For there is a fair number of partial values, which must be graded and combined so as to arrive at a reliable estimation: the value for families, genera and species in comparison to one another, the value for endemism and non-endemism in various taxonomic elements, the value for affinity with other regions as compared with independence, etc. It is advantageous to have a statistically expressed survey in order to be able to summarize the many combinations and so reach as far as possible an objective estimate instead of a more or less arbitrary and subjective one. The basis for such a statistical estimate is, of course, a fully adequate faunistical knowledge of the group or groups of animals with which this analysis is concerned. Space precludes a detailed description of the method. For this I must content myself with a reference to an earlier paper.[147]

* * *

Like all other biological phenomena, geographical distribution is the product of an interaction between two factors, namely the physiological properties of the living entity and the quality of the environment. The organisms must distribute themselves regionally in conformity with their own genotypical nature which is adapted to certain environmental conditions. But in the geographical distribution of the various species which thus comes about, there is not stagnation but change. And this change has its cause in the same two factors which we have mentioned above. The germ plasm may change; we call such changes mutations. Through these the organism becomes adapted ("pre-adapted") to new environmental conditions and is able to take possession of new regions. And the environment may change in various ways and thus give formerly useless mutations a "place in the sun". On the other hand changes in the germ plasm and environment may become unfavourable to the species and lead in time to its extinction. As far back as we have been able to trace life into ancient times, each geological period has shown examples in plenty of changes both in the organisms and in inanimate nature. Biologists have no difficulty in regarding time as a sort of fourth "dimension" in the whole of nature.

Throughout the phylogenetic evolution species, genera, families and so on and faunas have appeared, changed and disappeared. By the events in inanimate nature mountains and the deeps of the sea,

ocean currents and climatic zones have appeared, changed and disappeared and as a result of interactions of infinite complexity between animate and inanimate nature the present biogeographical conditions have emerged in the course of the ages. Time, which is in reality nothing more than the succession of events, that is historical happenings, is a factor of profound importance for all manifestations of life. In other words: biogeography cannot confine itself simply to describing the occurrence of living forms, arranging them regionally, investigating the ecological causes of distribution. It must also proceed historically.

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