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"..... per litora spargite muscum,
Naiades, et circum vitreos considite fontes:
Pollice virgineo teneros hinc carpite flores:
Floribus et pictum, diuæ, replete canistrum.
At vos, o Nymphæ Craterides, ite sub undas;
Ite, recurvato variata corallia trunco
Vellite muscosis e rupibus, et mihi conchas
Ferte, Dææ pelagi, et pingui conchyliis succo."
N. Parthenii (Giannettasii) Ecl. 1.

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I.—*What is to be understood by the Term "Deep-sea Fauna," and by what Physical Conditions is its Occurrence governed?* By Prof. T. FUCHS*.

THE great depths of the sea are peopled by a peculiar fauna, which is characterized by the occurrence or predominance of certain species, genera, and families, and presents a very similar constitution over the whole earth, so that a collection of deep-sea animals from any given part of the earth may be immediately and easily recognized as such.

The following may be regarded as the most striking and characteristic types of the deep sea:—

Oculinidæ.	} So-called deep-sea corals.
Cryptohelia.	
Solitary corals.	
Brachiopoda.	
Vitreous sponges (Hexactinellidæ).	
Crinoidea (<i>Pentacrinus</i> , <i>Rhizocrinus</i> , <i>Hyocrinus</i> , <i>Bathycrinus</i>).	
Echinothuriæ.	} Echinida.
Pourtalesidæ.	
Ananchytidæ.	
Brisinga.	
Elasmopodia (a peculiar suborder of Holothuriæ).	
Ribbon-like fishes (Lepidopidæ, Trachypteridæ, Macruridæ, Ophidiidæ).	

* Translated by W. S. Dallas, F.L.S., from the 'Verhandlungen der k.-k. geologischen Reichsanstalt,' 1882, no. 4, pp. 55-63.

The passage of the littoral into the deep-sea fauna is not effected suddenly and without transitions, but gradually, the different littoral animals ceasing and the different deep-sea animals commencing at different depths.

In this way a number of zones of depth may be distinguished between the shore-line and the greatest depths, each of them characterized by a definite assemblage of animals; and hence at the first glance it appears to be very much a matter of arbitrary choice where we draw the boundary between littoral and deep-sea faunas.

But when we go thoroughly into the matter, and in so doing take into account not so much the distribution of individual species or classes, as the distribution of the animals in its great fundamental features, we arrive at the conviction that this apparent indefiniteness really by no means exists, but that there is rather a perfectly definite region in which a change in the fundamental features of the fauna is effected, so profound and general, that in comparison with it all other subdivisions appear to be only divisions of subordinate rank.

The facts upon which this view is based are as follows:—

It is well known that marine plants, and indeed both seaweeds and the Phanerogamia of the sea, as organisms dependent upon light, only extend down to a moderate depth in the sea; indeed we may in general fix this limit at the depth of 30 fathoms*. These submarine forests and meadows of marine plants, however, are the seat of an exceedingly rich fauna; and a great part of this has its existence dependent upon these plants, and is therefore bound to them in its occurrence.

A second prominent shallow-water assemblage of animals is presented to us in the coral-reefs. The reef-building corals attain the maximum of their development in a zone from 1 to 8 fathoms. Lower down they decrease perceptibly; and a depth of 20 fathoms is generally regarded as their extreme limit. The coral-beds, however, are also the gathering-grounds of an extremely rich fauna; and the animals composing this are at the same time often so remarkable and peculiar, and so closely connected in their occurrence with the coral-banks, that we may characterize them at once as reef- or coral-animals as, indeed, one sometimes speaks in this sense of coral-fishes, coral-mollusks, &c. The unparalleled wealth of marine animals which is displayed by the tropical part of the Indian

* Only Nullipores extend into greater depths, and are found, for example, in the Mediterranean, according to Carpenter, down to 150 fathoms.

and Pacific oceans is for by far the greater part connected with the coral-reefs. If we imagine the coral-reefs with their characteristic population to have disappeared, the Indian and Pacific oceans would at one blow lose the whole splendour of their animal life, and we should, instead of it, have before us a comparatively poor and insignificant fauna.

A third important element of the littoral fauna consists of the beds of large bivalves, such as oysters, pearl-oysters, scallop-shells, &c. These shell-beds appear generally to find the maximum of their development in from 8 to 10 fathoms, and no longer to occur below 20 fathoms. These shell-beds, however, also attract many other animals, especially Ascidians, worms, and starfishes, which likewise form a definite association of animals, and in part are specially attached to this dwelling-place.

The seaweed-forests, coral-reefs, and shell-beds with their inhabitants constitute the three most important animal-assemblages of the littoral region; and we may say, without exaggeration, that fully two thirds of the whole of the littoral marine animals are more or less intimately connected with one or other of these three assemblages. But as the seaweed-forests as well as the coral-reefs and shell-beds are confined to a depth of less than 30 fathoms, it follows directly that the great majority of the littoral animals cannot descend much below 30 fathoms in the sea.

A second point that we have to bear in mind is the fact that over the whole earth, at a depth of from 90 to 100 fathoms, almost all the important types of the deep-sea fauna are already represented, and the fauna already bears quite indubitably the character of the deep-sea fauna.

The celebrated Pourtales Plateau on the coast of Florida, so exceedingly rich in deep-sea animals, begins at a depth of 90 fathoms, from which it descends gradually to 300 fathoms, but without essentially changing its fauna in this further course; and the grounds near the island of Barbadoes, which are so rich in deep-sea animals, are also situated at a depth of from 80 to 100 fathoms. But at both these points we not only find an astonishing abundance of deep-sea corals (over sixty species have already been described), but there are already in great plenty and variety true vitreous sponges (*Hexactinellidæ*), besides deep-sea Crustacea, Arctic Asterida, *Echinothuridæ*, *Pourtalesidæ*, and no fewer than four pedunculate Crinoids (*Holopus*, two *Pentacrini*, and *Rhizocrinus**).

* Of Mollusca there are near Barbadoes at this depth:—*Cadulus sauridens*; *Dentalium disparile*; *Margarita asperrima*; *Calliostoma Bairdii*; *Mi-*

The ground upon which the *Euplectellæ* are fished near the Philippines does not lie deeper than 100 fathoms. That on the Scandinavian and English coasts, and no less in the Mediterranean, a well-marked deep-sea fauna prevails at a depth of 100 fathoms, has long been known from the researches of Sars, M'Andrew, Barrett, Forbes, and many others; and the same phenomenon has been observed wherever such investigations have hitherto been undertaken.

If we sum up the preceding statements, we find that the great mass of the littoral animals do not descend in the sea much beyond 30 fathoms; and, on the other hand, that at a depth of 90 fathoms the fauna already everywhere shows the marked type of the deep-sea fauna.

Between these two limits, *i. e.* between 30 and 90 fathoms, then, the passage from the littoral to the deep-sea fauna must be effected; and the question now arises whether we are in a position to lay down a more exact boundary within this zone. I believe that this is really possible, and, indeed, that we may find data for this purpose in the fact that, almost everywhere on the surface of the earth, the first forerunners of the deep-sea fauna are found at a depth of about 50 fathoms, consisting generally of deep-sea corals and Brachiopods.

On the coasts of Norway, according to M'Andrew and Barrett, the Brachiopoda commence in about 30 fathoms, and the deep-sea corals about 60 fathoms.

On the English coasts Forbes fixes the commencement of the zone of deep-sea corals at 50 fathoms.

On the French coast, in the Bay of Biscay, the deep-sea corals and Brachiopoda commence, according to Fischer, at about 31 fathoms.

In the Mediterranean the coral-grounds with the Brachiopoda commence, on the average, at 50 fathoms (according to Forbes at 55 fathoms in the Aegean).

On the coast of Florida, the first deep-sea corals appear, according to Pourtales and Agassiz, at a depth of about 40 fathoms; and from this point they increase rapidly with the depth, so that in about 100 fathoms, on the above-mentioned Pourtales Plateau, they are met with most abundantly developed.

On the coast of Brazil the 'Hassler' expedition found numerous deep-sea corals at a depth of 30-40 fathoms; and

crogaza rotella; *Verticordia ornata*, *acuticostata*, and *Fischeriana*; *Poromya granulata*; *Neera granulata*, *rostrata*, and *Tiffrupii*; *Crenella decussata*; *Nucula crenulata*; *Leda messanensis*, *Carpenteri*, and *vibrea*; *Terebratulina Cailleti*; *Terebratulina cubensis*; *Eudesia floridana*; *Cistella Barrettiana*; and *Thecidium Barretti*, Dall.

the remarkable deep-sea corals from the Philippines described by Semper were obtained by him from a depth of about 40 fathoms.

In this connexion the numerous lists of local coral-faunas which Studer gives, founded on the rich coral-material collected by the 'Gazelle,' are very interesting*. Whenever he cites a locality which is below 40 fathoms, we may be sure that the coral-fauna bears the character of the deep-sea Corals.

This long series of facts from different seas therefore indicates very accordantly a depth of about 50 fathoms as that critical zone in which is situated the great turning-point that separates the littoral from the deep-sea fauna; and we are therefore justified in regarding the line of 50 fathoms as an ideal boundary between the littoral and the deep-sea fauna.

It is very interesting to observe that this depth is pretty nearly the same in all seas. Between the tropics, however, the separation of the littoral and deep-sea faunas, on the principle here adopted, seems to be not only ideal, but to a certain degree real. Thus, according to the observations at present extant, it would appear that within the tropics, below a depth of 30 fathoms, there follows an extremely sterile region with few animals, and that a more abundant fauna recurs only in proportion as, with increasing depth, true deep-sea animals begin to make their appearance in great variety at 80 and 90 fathoms. Consequently within the tropics the littoral fauna would be separated from the deep-sea fauna by a comparatively sterile region, extending about from 30 to 90 fathoms.

In the temperate and cold seas such an intermediate zone is unknown. Here, on the contrary, the two faunas intermingle very plentifully at their boundary-line, and thus produce a very great abundance of animals precisely in this critical boundary region.

In this way it is explained why, as Nordenskiöld has again quite recently indicated, there is in temperate latitudes a much greater abundance of animals at a depth of 40, 50, and 60 fathoms than the tropical seas present at the same depth.

If, then, founding upon the preceding statements, we regard the depth of 50 fathoms as the boundary between the littoral and deep-sea faunas, the question next arises, by what physical conditions this boundary-line is determined, and what, consequently, is the true conditioning cause of the appearance of the deep-sea fauna.

When the study of the bathymetric distribution of organ-

* "Verzeichniss der auf der Weltumsegelung der 'Gazelle' gesammelten Anthozoen," Monatsber. Berlin. Akad. 1878, p. 676.

isms commenced, it was so much the custom to regard conditions of temperature as the efficient factor, that, without further consideration, it was employed for the explanation of the bathymetric distribution of marine animals; and as it was found that in the sea the temperature diminished with increasing depth, and as it was further observed that some animals which are found only in the depths in the warmer seas, occur in the littoral region in the boreal and arctic seas, people became so thoroughly convinced of the truth of this opinion, that even at the present day we find the temperature almost universally regarded as the limiting factor, governing not only the horizontal, but also the bathymetrical distribution of marine organisms*.

Now it certainly cannot be denied that every individual species of animals is confined within certain limits of temperature, within which alone it finds the possibility of continued existence; and so far the limiting influence of the conditions of temperature certainly cannot be denied. But, true as this may be, it is equally certain, on the other hand, that the universal contrast that we find over the whole globe between the littoral fauna, on the one hand, and the deep-sea fauna, on the other, is in no way connected with the conditions of temperature, and must be brought about by some quite different conditions.

Dana has already repeatedly and emphatically pointed out that temperature plays only a very subordinate part in the distribution in depth of sea-animals†; and the facts which may be cited in favour of this are of so convincing a nature that one cannot help wondering how such an opinion as the above could so long prevail.

The reef-forming corals require in order to thrive an average temperature of 23°–25° C. (73°–77° F.); and it should never fall below 20° C. (68° F.). But, according to recent investigations, throughout almost the whole of the tropical part of the Pacific Ocean a temperature of 25° C. prevails at a depth of 80 fathoms, and of 21° C. (70° F.) down to 100 fathoms; and consequently, so far as it depends upon temperature alone, the reef-building corals, with the whole wealth of their fauna, might occur nearly to 100 fathoms. Never-

* Thus, even quite recently, in the general introduction to the zoological publications of the 'Challenger' expedition, Thomson treated temperature as the most important factor in the distribution of marine animals in depth.

† See, for example, Dana, "On the question whether Temperature determines the Distribution of Marine Species of Animals in Depth" (Amer. Journ. vol. xv. 1853, p. 204).

theless it is well known that they cannot well go below 8-10 fathoms, and that they are never met with living below 20 fathoms.

In the Red Sea a temperature of 21° C. prevails down to the bottom at a depth of 600 fathoms, and consequently tropical organisms might occur down to a depth of 600 fathoms. But, so far as we are yet acquainted with the characters of the Red Sea, this appears to be by no means the case; and with regard to the coral-reefs and their fauna we know with certainty that in general they do not extend further down here than elsewhere, *i. e.* 8-10 fathoms, and that living reef-corals are never found below 25° C.

There is also another fact which is equally convincing. In the Polar seas there prevails perennially, from the surface down to the greatest depths, a uniform temperature of about 0° C. (32° F.), which only rarely rises 1° or 2° higher, or falls to about the same extent. If, now, the temperature were the limiting factor in the bathymetrical distribution of organisms, we ought properly, in the Arctic and Polar seas, to meet with the deep-sea fauna in the littoral region, and here that contrast between the littoral and deep-sea faunas which prevails in the warmer seas could by no means occur. As is well known, however, none of these suppositions are correct. In the littoral region of the Arctic and Polar seas we find no traces of deep-sea Corals and Brachiopoda, of vitreous sponges, *Echinothurix*, and *Pourtalesia*, no trace of Crinoids, *Brisingæ*, Elasmopodia, or of that swarm of remarkable Crustacea and fishes which characterize the deep-sea fauna. All these forms of animals occur, indeed, in the Arctic seas, but here also always only in the deep water, and not in the littoral region; and here the general contrast between the littoral and deep-sea faunas is just as sharply defined, and in the same manner, as in warmer seas.

It is true, indeed, as already stated, that there are some species of animals which, in warm seas, are found only in deep water, but which occur in shallow water in the Arctic seas; but their number is so inconsiderable, and they are at the same time so uncharacteristic, that they in no respect merit the importance which has hitherto been ascribed to them. It must also be noticed that very many of those so-called "arctic" animals which are found at great depths in southern latitudes only bear the designation "arctic" because they were first known from the Arctic seas; but that even here they by no means occur in the littoral region, but are also confined to the deep water as in warmer seas. Moreover there are also a number of species of animals which are found in warmer

seas in shallow water, and in the Arctic seas only in the depths*.

Further proofs of the small influence that temperature exerts upon the bathymetrical distribution of organisms are obtained if we examine into the occurrence of the deep-sea fauna at different points.

In the Arctic Sea, between Norway, Iceland, and the Farøes, we find at the bottom a temperature of from -1° to -2° C. ($30^{\circ}2$ to $28^{\circ}4$ F.). Notwithstanding this low temperature, the fauna there is extraordinarily rich, and consists of the ordinary characteristic deep-sea forms. We find in great abundance deep-sea corals (*Lophohelia*, *Amphihelia*, *Caryophyllia*, *Flabellum*, *Umbellularia*), Brachiopoda (*Terebratulæ septata*, *Platydia anomioides*, &c.), vitreous sponges, *Echinothuria*, *Pourtalesia*, starfishes, Ophiurans, Crustacea, and the usual Mollusca of the deep sea.

Not far removed from this region, to the north-west of Scotland and Ireland, the bottom shows a temperature of $6^{\circ}5$ to $8^{\circ}5$ C. ($43^{\circ}7$ to $47^{\circ}3$ F.) in exactly the same depth as before. But although the temperature here is only 8° to 10° C. (14° to 18° F.) higher than in the preceding case, the fauna still shows exactly the same character. Here, again, we find the same genera (*Lophohelia*, *Amphihelia*, *Caryophyllia*, *Flabellum*, *Umbellularia*), and we also find Brachiopoda, vitreous sponges, *Echinothuria*, *Pourtalesia*, together with perfectly similar starfishes, Ophiurans, Crustaceans, and Mollusca; nay, to a great extent even the species are the same in both regions.

On the Pourtales Plateau there is a temperature of from 7° to 13° C. ($44^{\circ}6$ to $55^{\circ}4$ F.); and a temperature of at least 13° C., and probably considerably more, must prevail upon the deep-sea bottoms near the island of Barbadoes, upon which, as upon the Pourtales Plateau, the above-mentioned rich deep-sea fauna is found.

The Mediterranean, as is well known, in the same way as the Red Sea, presents abnormal conditions of temperature, the water from a depth of about 200 fathoms to the bottom

* Semper ('Die natürlichen Existenzbedingungen der Thiere,' in English under the title of "The Natural Conditions of Existence as they affect Animal Life," 1881) particularly calls attention to this remarkable phenomenon, and endeavours to explain it by the hypothesis that the animals in question require not so much a definite degree of temperature as a uniform temperature. But a uniform temperature is found in the warm seas at a less depth than in the colder temperate seas. Sars also has quite recently called attention to this phenomenon ('Mollusca regionis arcticæ Norvegiæ:' Christiania, 1878).

possessing a uniform temperature of from 12° to 13° C. (53° ·6 to 55° ·4 F.). Nevertheless it possesses a perfectly well-marked and tolerably rich deep-sea fauna; for besides the multifarious deep-sea corals, Brachiopoda, and various deep-sea Mollusca which were previously known, a whole series of true deep-sea animals not previously known from this sea were discovered in the course of last summer (1881) by the dredging-expedition of the French ship 'Travailleur'*, such as several vitreous sponges (*Tetilla*, *Holtenia*), deep-sea starfishes (*Archaster bifrons*, *Asterias Richardi*), the genus *Brisinga*, and numerous deep-sea Crustacea (*Dorhynchus*, *Geryon*, *Ebalia*, *Ethusa*, *Munida*, *Lophogaster*, *Galathodes*), several of which are blind.

On the *Euplectella*-grounds which occur at a depth of 100 fathoms near the Philippines, the temperature, according to Semper, is 15° C. (59° F.), and off the island of Cebu, according to Moseley, even 21° C. (69° ·8 F.)†. A fauna of precisely similar character and exactly similar composition occurs, however, as already mentioned, in other places at a temperature of 0° C., and still lower.

If we once more glance over what has just been stated, taking it in connexion, it becomes so clear that the occurrence of the deep-sea fauna is in no way connected with the temperature of the water, that it would be superfluous to point this out again expressly. But if it is not the temperature that causes the appearance of the deep-sea fauna, what is the condition governing it?

The chemical characters of the water, the amount of absorbed air contained in it, or the movement of the water have been suggested; but not one of these conditions seems to agree with the existing circumstances. The chemical characters of sea-water show no essential differences from the surface to the bottom. The amount and relative composition of the absorbed air certainly present some alteration with increasing depth; but this alteration is scarcely of any consequence at a depth of 50 fathoms, and could only exert a perceptible influence much lower down.

As regards the movement of the water, if we only take into consideration the wave-movements produced by storms, the circumstances appear at the first glance rather more

* Milne-Edwards, "Compte rendu sommaire d'une exploration zoologique faite dans la Méditerranée à bord du navire de l'état 'Le Travailleur'" (Comptes Rendus, 1881, p. 876); translated in Ann. & Mag. Nat. Hist. ser. 5, vol. ix. p. 37.

† Besides *Euplectella* and other vitreous sponges, the following Echinodermata also occur off Cebu at the above depth:—*Salenia hastigera*, *Aspidodiadema tonsum*, *Micropyga tuberculatum*, *Asthenosoma pellucidum*!

favourable, as, in fact, the wave-movement produced by violent storms makes itself perceptible, according to the prevailing opinion, down to a depth of about 50 fathoms; and even elsewhere the influence of the motion of the water upon the fauna is not to be denied. But on closer examination the thing seems extremely improbable. For instance, if the littoral fauna were connected with the motion of the water, we ought to observe an ascent of the deep-sea fauna in quiet bays, which, however, is by no means the case. But, on the other hand, we must consider that the great currents of the sea descend much deeper than the littoral fauna, and, indeed, the Gulf-stream especially is inhabited by the deep-sea fauna in its depths.

But if it be neither the temperature, nor the chemical conditions, nor the movements of the sea that regulate the bathymetrical distribution of marine animals, there remains in reality only one factor that can be taken into consideration; and this is *light*.

Light is the most powerful factor amongst all the agents which influence life upon the earth; and its importance is generally overlooked only because on the surface of the earth it is everywhere pretty uniformly distributed, and therefore gives but little occasion for the production of differences. But in the sea the conditions are quite different. The light as it penetrates into the water is gradually absorbed by the water; it is thus gradually changed, and finally entirely absorbed, so that, at a certain depth, the sea must be perfectly dark. It is to be remarked, however, that the relation of the sun's light to the water of the sea is not perceptibly modified either by the temperature or by any existing variations in the chemical composition of the water, and that therefore this relation must remain pretty nearly the same over the whole earth. If we now place this condition vividly before us, the enormous mass of the sea, above a thin illuminated zone, below a great dark mass, the conviction must, to a certain extent, *à priori*, force itself upon us, that *this fundamental difference in the external conditions of life must find expression in a corresponding difference of the living world.*

If we now consider that, according to the experiments of Secchi, Pourtales, and Bouguer, the inferior limit of light in the sea lies between 43 and 50 fathoms, and that this is exactly the depth that we fixed upon at starting as the boundary-line between the littoral and deep-sea faunas, there can scarcely any longer be a doubt that *the difference which is produced in the fauna of the sea by its conditions of light is no other than that which we distinguish as littoral fauna and deep-sea fauna—*

in other words, *that the littoral fauna is nothing but the fauna of light, and the deep-sea fauna the fauna of darkness.*

To prove that this is actually the position of matters, several other circumstances may be cited.

Thus it must above all be indicated that the dependence of the organic world upon light not only shows itself at the above fundamental critical point of 50 fathoms, but **that it** can also be demonstrated at the subordinate degrees of intensity. For example, Lorenz, in his investigations in the Gulf of Quarnero, with his imperfect method of research arrived at the depth of 24-30 fathoms as the lower limit of light. This depth of course cannot be accepted as the actual lower limit; but it certainly forms the limit for a certain intensity; and it is not without interest that we remark that this depth exactly agrees with that which is given as the limit of plant-growth in the sea.

On a former occasion I have called attention to the fact that the depth already mentioned of 43-50 fathoms, found by Secchi, Pourtales, and Bouguer, cannot represent the absolute limit of light, but that small quantities of light no doubt penetrate considerably deeper into the sea, and, indeed, from the analogy of Forel's investigations in the Lake of Geneva, as far as 100-200 fathoms. Now it is certainly very remarkable that Carpenter states the limit to which Nullipores occur at 150 fathoms, and that Agassiz cites precisely the same limit for the greater part of those littoral animals which extend beyond their normal boundary for some distance into the region of the deep-sea fauna*.

With their character of animals of darkness numerous peculiarities in the organization and nature of the deep-sea animals agree. Thus it is known that very many deep-sea animals either have uncommonly large eyes, after the fashion of nocturnal animals, or are completely blind; it is also well known that they are for the most part either pale and colourless or unicolorous, and that varied coloration is exceedingly seldom met with among them; and, finally, it is likewise well known that a very large proportion of deep-sea animals, in many groups, indeed the majority, are vividly luminous.

This last peculiarity is of special importance; for it is clear that luminosity can be of consequence only to such animals as are destined to live in darkness, and, in point of fact, scarcely any luminous animals are known to us from the littoral

* From the investigations of Forel in the Lake of Geneva, of Weismann in the Lake of Constance, &c., it seems to me decidedly to follow that in freshwater lakes also the bathymetrical distribution of animals is determined chiefly by light.

region. Travellers in the tropics represent in lively colours the overpowering impression produced upon the spectator by a living coral-reef with its multifarious and varied fauna. But what an impression would such a reef produce if its inhabitants shone at night in the most different colours! But no traveller has described any such phenomenon. The littoral coral-reefs are perfectly dark at night; but if deep-sea corals are brought to the surface, nearly all of them are seen to glow with the most vivid colours.

Various naturalists have already noticed, and the fact has lately been again brought prominently forward by Moseley, that the pelagic fauna shows a very great resemblance to the deep-sea fauna; for example, the Scopelidæ and Sternoptychidæ are among the most strikingly pelagic animals, but at the same time among the most characteristic of deep-sea animals. It is well known that by far the greater part of the pelagic animals are animals of darkness, dwelling during the day in the obscure depths of the sea, and only coming to the surface at night. But if it be the case that the deep-sea animals are in their nature animals of darkness, the numerous relations manifested between the deep-sea fauna and the pelagic fauna can no longer surprise us in the least; for the pelagic animals are then in their nature fundamentally nothing but deep-sea animals. In connexion with this it must further be indicated that luminosity is just as much diffused among the pelagic animals as among those of the deep sea, and that the above-mentioned pelagic Scopelidæ and Sternoptychidæ especially are as well provided with luminous organs as their relatives in the depths.

By the conception of the deep-sea fauna as a fauna of darkness, moreover, it may be quite easily explained why it appears to be so completely independent of temperature in its occurrence, and at the same time why it commences nearly at the same depth over the whole surface of the earth.

There is, however, a means by which we may test the correctness of the view here put forward in a very simple and exact manner. Thus, if it be true that the animals of the deep sea are nothing but animals of darkness, animals must occur in the caverns and grottoes of the sea which show a certain resemblance to deep-sea animals, or even directly agree with them. No direct investigations in this direction are known to me; but nevertheless there is a series of facts which seem to show that such conditions actually exist. Thus, for example, in the great depths of the Lake of Geneva there is a blind Amphipod, *Niphargus stygius*; but precisely the same animal occurs in springs as well as in the caverns of Carniola,

and exactly similar species are known from the American caves. Moreover the case is precisely the same with the blind Isopod genus *Cecidotæa*, which occurs both in the great depths of the Lake of Geneva and in the American and Carniolian caves *. Among the most abundant and characteristic of deep-sea fishes are those near allies of the Gadidæ, the Ophidiidæ; and among them several blind species occur. Now it is certainly very remarkable that two blind Ophidiidæ, showing the closest resemblance to their relations of the deep sea, are found in the caves of Cuba.

According to Moseley the corals of the Bermudas show a remarkable sensitiveness to light. The great brain corals (*Diplosia cerebriformis*) grow by preference in the bright sunshine; *Millepora ramosa* and *Symphyllia dipsacea* prefer the shade; and the extremely delicate white *Mycedium fragile* occurs in great abundance in the beach-region, in the interior of cavities. The genus *Mycedium*, which is here found in the beach-region in the interior of cavities, and therefore apparently in darkness, is, however, properly a deep-sea genus, which otherwise occurs only at great depths.

According to Falkenberg, Algæ occur near Naples in a dark grotto at a very small depth, which elsewhere are found only at greater depths at the lower limit of Algæ †.

I have no doubt that these examples will be greatly multiplied if only more attention be paid to these conditions; and I would warmly recommend the study of this question to all naturalists who are in a position to make pertinent observations ‡.

Here, however, I would notice a second question nearly related to the preceding. It is well known that a number of littoral animals penetrate in depth far beyond the limits of the true littoral region, nay, that there are some species (especially of Echinoderms and Vermes) which are found at all depths, from the beach to 2000 fathoms and more. It would certainly be interesting to examine whether these animals of extraordinary bathymetrical distribution are not perhaps nocturnal animals in the littoral region, hiding themselves during the day in dark places, or shutting themselves up in their

* According to Cope and Packard the so-called *Asellus Borelli* of the Lake of Geneva belongs to the genus *Cecidotæa* ("The Fauna of the Nickajack Cave," Amer. Nat. 1882, p. 877).

† See Dodel-Post, 'Illustriertes Pflanzenleben,' Zurich, 1880 (Marine Algæ).

‡ Fries has already called attention to the resemblance between the deep-sea and cave faunas; see "Die Falkensteiner Höhle, ihre Fauna und Flora" (Württemb. Jahreshfte, xxx. 1874, p. 162).

shells, and going about the business of their lives only at night. Should this be proved, we shall have in strictness to regard such animals not as littoral animals which penetrate to unusual depths, but, from their nature, as deep-sea animals which ascend exceptionally into the lighted regions, but here keep themselves concealed during the day, and display their vital activity only at night.

That the Cephalopoda are chiefly nocturnal animals is well known. The great importance that what has been brought forward in the preceding pages must have for the geologist and the palæontologist especially is at once evident.

On the coast of Brazil, according to Dana, the construction of the coral-reefs is completed in a very peculiar manner. The coral-stocks grow up from a depth of 6-8 fathoms in the form of columns, and then widen out at the top, like an umbrella. In course of time the umbrella-like widened parts of the neighbouring columns unite laterally; and thus there is finally produced an extensive roof of coralline limestone, which rests upon numerous vast columns, and has under it extensive dark catacomb-like spaces. Similar extensive labyrinthically branched systems of caverns are described by Klunzinger also in the coral-reefs of the Red Sea; and, according to Dana, extended branching caves are a perfectly ordinary phenomenon in the coral-reefs of the Pacific Ocean. If, therefore, the preceding hypotheses are correct, a fauna of the character of the deep-sea fauna must occur in these submarine cavities of the coral-reefs; and if we imagine these caverns in course of time filled with the remains of these particular animals, together with material washed into them, and then imagine these coral-reefs subsequently upheaved, a future geologist in investigating such a reef would find nests of deep-sea animals in the midst of the littoral reef-limestone, and be considerably embarrassed thereby.

I may here notice a phenomenon to which Süss has called attention in his well-known work on the Brachiopoda of the Kossen beds. Süss states that the so-called Stahremberg beds, which consist of an accumulation of certain small Brachiopoda, always occur in the form of isolated nests in the Dachstein limestone; and he further adds that these nests are at the same time distinguished by their red colour from the white Dachstein limestone. The white Dachstein limestone with its great Megalodonts, however, is undoubtedly a shallow-water formation, produced after the same fashion as our present coral-reefs, while the fauna of the Stahremberg beds bears the character of a deep-sea formation. If we imagine that the Dachstein limestone was actually a reef, and that this

reef was traversed by cavities, and if we further assume that a Brachiopod fauna of the character of the deep-sea Brachiopoda settled in these cavities, and that finally the cavities were filled up by these shells, together with the washed-in "terra rossa," which, indeed, always occurs upon the free surface of coral-reefs, we have exactly those conditions before us which Süss describes in the case of the Dachstein limestone and the Stahremberg beds.

The interest which the conception of the nature of the deep-sea fauna here advocated possesses for geologists and palæontologists is, however, of a much more general kind. On a previous occasion I have shown that during those epochs through which a warmer climate prevailed at the poles, the temperature-conditions of the sea must have been quite different from those of the present day, and that at that time a higher, perhaps even subtropical, temperature must have prevailed down to the bottom of the sea. If, then, as was previously supposed, the conditions of temperature had been the governing factor in the bathymetrical distribution of organisms, we could not at once apply the observations which we make at the present day upon the distribution of animals in depth in the sea to previous geological epochs, and in general we should lose all reliable foundation for judging of the faunistic conditions of geological epochs. But the circumstances become quite different when we know that the bathymetrical distribution of animals is principally determined not by *temperature*, but by *light*, and especially that the distinction which shows itself between littoral and deep-sea faunas has its ground simply in the fact that the former live in the *light* and the latter in *darkness*; for as the behaviour of the sea-water to light has undoubtedly remained essentially the same through all geological periods, we may also with perfect justice assume that the fundamental features of the bathymetrical distribution of marine organisms have mainly always been the same as now.

As a matter of fact, observation teaches us that the difference between the littoral and deep-sea faunas which we find in existing seas may be traced back in the same way through all formations; and, conversely, this fact may also be made use of in its turn as a further proof of the correctness of the view here advocated.