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STUDIES

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FROM THE

BIOLOGICAL LABORATORY

EDITED BY

PROFESSOR H. N. MARTIN

AND

PROFESSOR WILLIAM K. BROOKS

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SALPA IN ITS RELATION TO THE EVOLUTION  
OF LIFE

By WILLIAM K. BROOKS, PH. D.

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BALTIMORE

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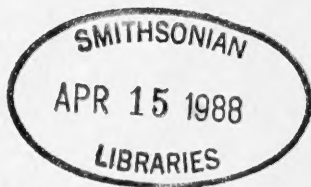
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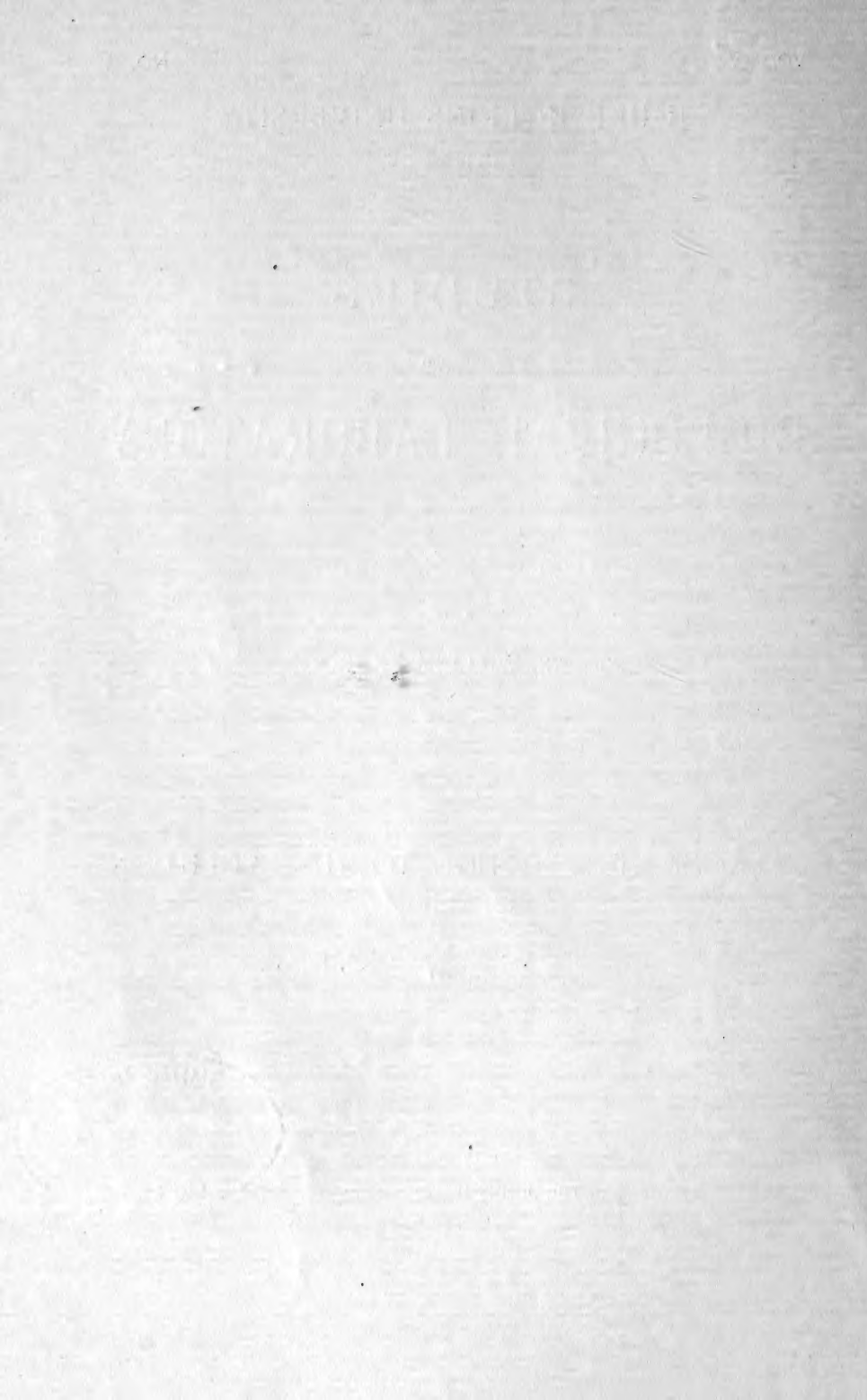
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## INTRODUCTORY NOTE.

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*(This paper consists of two chapters, VII and VIII, printed, in advance, from my memoir on the Genus Salpa, which is now passing through the press.)*

In chapter VI of my memoir on the Genus Salpa I shall give, at length, reasons which, briefly stated, are as follows, for believing that, while salpa is remotely descended from a pelagic, appendicularia-like ancestor, it is more immediately derived from a sessile form, similar in its habit of life, and essentially, in structure also to the ascidians.

In the first place, comparative anatomy forces us to believe that the atrium of salpa is identical with the perithoracic and atrial chamber of ordinary ascidians, and the facts of embryology show beyond question that this is a real homology.

Writers on the embryology of salpa and allied animals have involved the history of the atrial system in unnatural obscurity, for its origin in the salpa embryo and in the aggregated salpa is in perfect accordance with the teaching of comparative anatomy, and quite irreconcilable with any view except the one which regards these structures in salpa as strictly homologous with the median and lateral atria of ordinary ascidians.

As Leuckart pointed out long ago, the atrial aperture of salpa is much nearer the mouth when it first appears than it is later, and in this respect the ontogeny of salpa exhibits evidence of an ascidian-like stage in its ancestry. The compactness of the ganglion of salpa, as contrasted with the elongated central nervous system of primitive chordata, and its position between the two apertures of the body, are also features of resemblance to the ascidians; and while there are now no traces, at any stage of its development, of numerous stigmatic gill-slits, like those of pyrosoma, there is ample

indirect evidence that they at one time existed in the ancestors of salpa, which were in this respect, pyrosoma-like.

The muscle bands of salpa are easily intelligible as modified oral and atrial sphincters, and they are distinctly more irregular in the young than they are in the adult. In the young aggregated *Salpa cylindrica*, the fourth and fifth body muscles are clearly seen to arise as branches from an atrial sphincter, and some of the body muscles arise in the same way in the aggregated *Salpa pinnata*.

The peculiar anatomical relations of the pharynx and atrium of ascidians are generally and justly regarded as modifications which were gradually added on to the primitive tunicate type, as adaptations to a sedentary life. If salpa has been evolved from a swimming ancestor like appendicularia through an uninterrupted series of free pelagic stages, we can give no explanation whatever of its ascidian type of structure, while this is perfectly intelligible on the view that it is a modified ascidian.

W. K. BROOKS.

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## **SALPA IN ITS RELATION TO THE EVOLUTION OF LIFE.** By W. K. BROOKS.

Salpa is distinctively a pelagic animal, adapted by its whole structure for a free existence, and for life at the expense of the micro-organisms in the water of the ocean.

To understand its position and significance in the economy of nature, we must have before us the broad outlines, at least, of a picture of the conditions under which oceanic life has been evolved.

I believe that the history of the evolution of salpa, as told by its embryology, is most suggestive and important, and that it contributes to the solution of some of the most profound and fundamental problems of biology, and brings us into conflict with some of the most favorite dicta of modern morphology. I shall therefore devote considerable space to a review of certain familiar features of ocean life, in order that I may present in this way my view of the significance of the phylogeny of salpa, in its bearing upon the first principles of morphology.

### **CONTRAST BETWEEN TERRESTRIAL LIFE AND MARINE LIFE.**

In a picture of the land, the mind calls up a vast expanse of verdure, broken only by water, and stretching through forest and meadow from high up on the mountains, over hills and valleys and plains, down to the sea.

Our picture of the ocean is an empty waste, stretching on and on with no break in the monotony, except, at long intervals, a floating tuft of sargassum, or a flying fish, or a wandering sea-bird, and we never think of the ocean as the home of vegetable life.

It contains plant-like animals, "zoophytes," in abundance, but while they resemble plants or flowers in form and color, and in their mode of growth, they are true animals and not plants.

At Nassau, in the Bahama Islands, the visitor is taken in a small boat, with windows of plate glass set in the bottom, to visit

the "sea-gardens" at the inner end of a channel, through which the pure water from the open sea flows between two coral islands, into the lagoon. Here the true reef corals grow in quiet water where they may be visited and examined.

The bottom of the boat is below the surface ripples and reflections. When illuminated by the vertical sun of the tropics, and by the light which is reflected back from the white bottom, the pure transparent ocean water is as clear as air, and the smallest object, forty or fifty feet down, is seen distinctly.

As the boat glides over the great mushroom-shaped coral domes which arch up from the depths, the dark grottoes between them, and the caves under their overhanging tops, are lighted up by the sun far down among the flower-animals or anthozoa and the animal plants or zoophytes which are seen through the waving thickets of brown and purple sea fans and sea feathers as they toss before the swell from the ocean.

There are miles of these "sea-gardens" in the lagoons of the Bahamas, and it has been my good fortune to spend many months studying their wonders, but no description can convey any conception of their beauty and luxuriance, and I never spent a day among the reefs without longing, at every turn, for the skill to copy with a brush the new beauties which never ceased to present themselves.

The general effect is very garden-like, and the beautiful fishes of black and golden yellow and iridescent cobalt blue hover like birds among the thickets of yellow and lilac gorgonias. The parrot fishes (*Diodon* and *Ballistes*) seem to be cropping the plants like rabbits, but more careful examination shows that they are biting off the tips of the gorgonias and branching madrepores, or hunting for the small crustacea which hide in the thicket, and that all the apparent plants are really animals. The delicate star-like flowers are the vermilion heads of boring annelids, or the scarlet tentacles of actinias, and the thicket is made up of pale lavender bushes of branching madrepores and green and yellow and olive masses of brain coral, of aleyonarians of all shades of yellow and lilac and purple and red, and of red and brown and black sponges. Even the lichens which incrust the rocks are hydroid corals, and the whole sea-garden is a dense jungle of

animals where plant life is represented only by a few calcareous algæ, so strange in shape and texture that they are much less plant-like than the true animals.

The scarcity of vegetation becomes still more noticeable when we study the ocean as a whole.

On land, herbivorous animals are always much more abundant and prolific than the carnivora, as they must be to keep up the supply of food. Insectivorous birds are very abundant, but they are not numerous enough to keep the plant-eating molluscs and insects in check, and the devastation which is caused every year by the armies of grasshoppers and locusts and herbivorous beetles and by other less conspicuous insects, shows that their natural enemies are not numerous enough to overtax their productive power.

The birds which feed upon grain and seeds and fruit are very abundant indeed, and they sometimes gather at their breeding grounds, or places of assembly, in innumerable multitudes, but the hawks and owls which prey upon them are never numerous.

The small rodents, such as the rats, mice, squirrels, and rabbits, are the most abundant and prolific of animals; but the small carnivora are so rare that their very existence is known to few except naturalists and trappers.

The homes of the wild sheep and goats, deer, antelopes, cattle and horses support these large mammalia in incredible numbers, but their carnivorous enemies are never abundant. It is clear that if the destruction of the plant-eaters exceed their productive power, both herbivora and carnivora would disappear, and terrestrial life would come to an end.

The animal life of the ocean shows a most remarkable difference, for marine animals are almost exclusively carnivorous.

The birds which live upon the ocean, the terns, gulls, petrels, divers, cormorants, tropic birds and albatrosses, are very numerous indeed; so numerous that in many parts of the ocean some are always visible in calm weather around the vessel, wherever it may be. The only parallel to the pigeon-roosts and rookeries of the land is found in the dense clouds of sea-birds around their breeding places, but these sea-birds are all carnivorous; most of them are fishers, and others, such as the petrels, scoop up the copepods and pteropods from the surface. Even the birds of the sea-shore

subsist almost exclusively upon animals such as molluscs, crustacea and annelids.

The seals pursue and destroy fishes ; the sea-elephants and walruses live upon lamellibranchs ; the whales, dolphins and porpoises, and the marine reptiles, all feed upon animals, and most of them are fierce beasts of prey. The manatee is a vegetable feeder, but it is not strictly a marine animal, since its home is in the mouths of great rivers.

There are a few fishes which pasture in the fringe of seaweed which grows in the littoral zone of the ocean, and there are some which browse among the floating tufts of algæ upon its surface, but most of them frequent these places in search of the small animals which live among the plants. All the floating fishes whose home is the floating sargassum ; the file fishes and trigger fishes (*Ballistida*) ; the trunk fishes (*Ostracion*) ; the frog fishes (*Antennarius*) ; and the puffing fishes (*Tetradon* and *Diodon*) are carnivorous, living upon the barnacles and molluscs and hydroids which grow upon the sargassum, or upon the crustacea, young fishes and the floating larvæ which seek its shelter.

In the Chesapeake Bay, the sheephead (*Diplodus probatocephalus*) browses among the algæ upon the submerged rocks and piles like a marine sheep, but its food is exclusively animal, and I have lain upon the edge of a wharf watching it crush the barnacles and young oysters until the juices of their bodies streamed out of the angles of its mouth and gathered a host of small fishes to snatch the fragments as they drifted away with the tide.

Many important fishes, like the cod, pasture on the bottom, but their pasturage consists of molluscs and annelids and crustacea, instead of plants.

The vast majority of marine fishes are fierce hunters, pursuing and destroying smaller fishes, and often exhibiting an insatiable love of slaughter, as in the case of our own blue-fish and the tropical albacore and barracuda. Others, such as the herring, feed upon smaller fishes and the pelagic pteropods and copepods ; and others, like the shad, upon the minute organisms of the ocean, but all, with few exceptions, are carnivorous.

In the other great groups of marine animals we find some scavengers, some which feed upon micro-organisms, and others

which hunt and destroy each other, but there is no group of marine animals which corresponds to the herbivora and rodents and plant-eating birds and insects of the land. The pelagic copepods are, of all the marine Metazoa, the ones whose place in the economy of nature is most like that of the terrestrial plant-eaters. They swarm in innumerable multitudes at the surface of the ocean, and also below it down to a depth of a mile or more, and they furnish the chief food for most young fishes, and for great armies of herrings and pteropods and jelly-fishes and siphonophores, and for most pelagic larvæ.

There are plant-eating molluscs and echinoderms and annelids in the ocean, but not in sufficient numbers to play any conspicuous part in its economy, and the copepods are the only plant-eaters which exist in sufficient numbers to be compared with those of the land, and the food of the copepods is only partially vegetable, for they devour microscopic animals as well as microscopic plants, and probably to an equal amount.

The group crustacea as a whole is a carnivorous one, however, for while a few subsist on algæ, their number is inconsiderable. Others chew the mud of the bottom and extract its organic matter, but this is chiefly animal and consists of foraminifera and rhizopods and infusoria.

The molluscs as a whole are carnivorous, and while there are many exceptions, such as the nudibranchs for example, many nudibranchs feed on hydroids.

The cephalopods and pteropods and heteropods and many of the gasteropods pursue and destroy their prey, and other gasteropods are scavengers, while the lamellibranchs gather up the microscopic organisms which are drawn into their gills with the water.

The majority of the worms and echinoderms are animal-feeders. Some of them, like the common starfish, are actively predaceous; others, like the crinoids, gather up microscopic organisms from the water; others, such as most holothurians, eat the mud of the bottom and digest out of it the foraminifera and small molluscs and annelids and crustacea which it contains, while others, such as the sea-urchins of the coral reefs, grind away and swallow the living coral. The universal presence of a poisoning apparatus in the cœlenterates shows that the food of this great and important

group of marine animals must consist, in the main, of animals which are able to resist or to escape, and observation shows that this is true. Floating jelly-fishes and siphonophores are often found fastened to the half-digested carcasses of sagittas or heteropods or fishes larger than their captors, and they consume enormous numbers of copepods, pteropods, young fish, and pelagic larvæ of all sorts. So far as we know, all the sea-anemones and coral polyps and aleyonarians and hydroids are carnivorous. Some of the discomedusæ, the rhizostomes, feed upon microscopic organisms, but this mode of life is exceptional, and some recent observations, as yet unpublished, by Dr. R. P. Bigelow, show that the food of the rhizostomes consists of copepods.

Except for a few plant-eating fishes and molluscs and worms and echinoderms, all the animals of the ocean fall into two classes, those which subsist on microscopic organisms, and those which prey upon each other and correspond to the rapacious animals of the land.

There is practically nothing in the ocean corresponding to the terrestrial herbivora, and nothing like terrestrial vegetation, except the fringe of seaweeds in the shallow water along the coast, and a few floating islands of algæ like the Sargasso Sea.

While these tracts of vegetation are pretty extensive, they are totally inadequate to support the animal life of the ocean, and as the whole animal world is dependent directly or indirectly upon plants, we must ask what takes the place of terrestrial vegetation.

#### THE FAUNA OF MID-OCEAN.

There is so much room in the vast spaces of the ocean, and the part which is open to our direct observation is such an inconsiderable part of the whole, that it is only when great multitudes of pelagic animals are gathered together at the surface that the abundance of marine life becomes visible and impressive; but some faint conception of the boundless wealth of the ocean may be gained by observing the quickness with which marine animals become crowded at the surface in favorable weather.

On a cruise of more than two weeks from Cape Hatteras to the Bahama Islands I was surrounded continually, night and day, by

a vast army of dark-brown jelly-fishes (*Linerges mercutia*), whose dark color made them very conspicuous in the clear water. They were not densely crowded, although they were so abundant that nearly every bucketful of water we dipped up contained some of them. We could see them at a distance from the vessel, and at noon, when the sun was overhead, we could look down into the water to a great depth through a well in the middle of the vessel where the centreboard hung, and as far down as the eye could penetrate, fifty or sixty feet at least, we could see the brown spots drifting by like motes in the sunbeam. We cruised through them for more than five hundred miles, and we tacked back and forth over a breadth of almost a hundred miles, and they were everywhere in equal abundance.

The recent literature of pelagic exploration, which has been summarized by Haeckel (*Plankton Studien: von Ernst Haeckel, Jena, 1890*), is full of references to great accumulations of pelagic animals, from which I have selected those which follow.

Chiercha says that during a cruise of forty days between Peru and Hawaii the net brought in from the surface and from all depths down to about two miles, a multitude of pelagic animals which would be incredible to those who have not witnessed it.

The naturalists of the *Challenger* found the waters of the equatorial Pacific swarming with life, not at the surface alone, but in its deeper layers, and the ship often sailed through great banks of pelagic animals.

The equatorial Atlantic is like the Pacific, and Chiercha says that its zone of equatorial calms is rich beyond all measure in animal life, and that the water often looks and feels like coagulated jelly.

Of the Indian Ocean, Haeckel says that in his voyage to and from Ceylon he was wonderstruck with the wealth of pelagic life day after day on the mirror-like surface. At night it was an unbroken sheet of sparkling light as far as the eye could reach, and the water which was dipped up at random held such a thick swarm of densely crowded luminous animals (*Ostracods, Salpæ, Pyrosomas, and Medusæ*) that a printed book could be read distinctly in a dark night by this pelagic light.

In temperate and arctic waters there is less diversity, but, as Haeckel shows, there is no evidence of any decrease in individuals,

and banks of pteropods (*Clio* and *Limacina*), so dense that they seem almost solid, are met even beyond the arctic circle.

Haeckel says that in a cruise to the northwest of Scotland he met with such enormous masses of *Limacina* that each bucket of water which was dipped up contained thousands.

The tendency to gather in crowds is not restricted to the smaller pelagic animals, and many species of raptorial fishes are found in densely packed banks.

The fishes in a school of mackerel are as numerous as the birds in a flight of wild pigeons. Goode, in his *History of Aquatic Animals*, tells of one school of mackerel which was estimated to contain a million barrels, and of another which was a windrow of fish half a mile wide and at least twenty miles long; but while the pigeons are plant-eaters, the mackerel are rapacious hunters, pursuing and devouring the herrings, as well as the pteropods and pelagic crustacea.

Herring swarm like locusts, and a herring bank is almost a solid wall. In 1879 three hundred thousand river herring were landed by a single haul of the seine in Albemarle Sound; but the herrings are also carnivorous, each one consuming myriads of copepods every day. In spite of this destruction and the ravages of armies of medusæ and siphonophores and pteropods, the fertility of the copepods is so great that they are abundant in all parts of the ocean, and they are met with in numbers which exceed our powers of comprehension.

On one occasion the *Challenger* steamed for two days through a dense cloud formed of a single species, and they are found in all latitudes from the arctic regions to the equator, in masses which discolor the water for miles. We know, too, that they are not restricted to the surface, and that the banks of copepods are sometimes a mile thick. When we reflect that thousands would find ample room and food in a pint of water, we can form some faint conception of their universal abundance.

#### THE PRIMARY FOOD-SUPPLY.

As the result of our review, we find that the organisms which are visible without a microscope in the water of the ocean and on the sea bottom are almost universally engaged in devouring each



other, and many of them, like the blue-fish and the albacore, are never satisfied with slaughter, but kill from mere sport.

Insatiable rapacity must end in extermination unless there is some unfailling supply, and as we find no visible supply in the water of the ocean we must seek it with a microscope. By its aid we find a wonderfully rich and diversified fauna made up of innumerable larvæ of all sorts of marine animals, together with a few minute and simple metazoa, but these things cannot form the food-supply of the ocean. It is clear that a single carnivorous animal could not exist very long by devouring its own children, and the result must be the same however great the number of individuals or species.

The total amount of these organisms is inconsiderable, however, when compared with the abundance of a few forms of protozoa and protophytes, and both observation and deduction force us to recognize that the most important element in the total amount of marine life consists of some half-a-dozen types of protozoa and unicellular plants, of globigerinæ and radiolarians, and of trichodesmium, pyrocystis, protococcus, and the coccospheres, rhabdospheres and diatomes.

Modern microscopic research has shown that these simple plants, and the globigerinæ and radiolarians which feed upon them, are so abundant and prolific that they meet all the demands made upon them and supply the food for all the animals of the ocean.

This is the fundamental conception of marine biology. The basis of all the life in the modern ocean is to be sought in the micro-organisms of the surface.

This is not all. The simplicity and abundance of the microscopic forms and their importance in the economy of nature show that the organic world has gradually shaped itself around and has been controlled by them.

They are not only the fundamental food-supply, but the primeval supply, which has determined the whole course of the evolution of marine life.

The pelagic plant-life of the ocean has retained its primitive simplicity on account of the very favorable character of its environ-

ment, and the higher rank of the littoral vegetation and that of the land is the result of hardship.

On the land the mineral elements of plant-food are slowly supplied as the rains dissolve them ; limited space brings crowding and competition for this scanty supply ; growth is arrested for a great part of each year by drought or cold ; the diversity of the earth's surface demands diversity of structure and habit, and the great size and complicated structure of terrestrial plants are adaptations to these conditions of hardship.

The conditions of the surface of the ocean ; the abundance and uniform distribution of mineral food in solution ; the area which is available for plants ; the volume of sunlight and the uniformity of the temperature are all favorable to the growth of plants, and as each plant is bathed on all sides by a nutritive fluid, it is advantageous for the new plant-cells which are formed by cell multiplication to separate from each other as soon as possible in order to expose the whole of their surface to the water. Cell aggregation, the first step towards higher evolution, is therefore disadvantageous to the pelagic plants, and as the environment is so homogeneous at the surface of the ocean that there is little opportunity for an aggregation of cells to gain a compensating advantage by seizing upon a more favorable habitat, the pelagic plants have retained their primitive simplicity.

The list of pelagic micro-organisms is a long one, but a few forms are so predominant that the others have little significance at the present day in comparison, and we may regard the great primary food-supply as made up of two simple protozoa, globigerina and the radiolarians, and some five or six unicellular plants.

Of these only two, the radiolarians and the diatoms, show any great diversity of species, and while the radiolarians are so diversified that the Challenger collection alone furnished more than four thousand species, this variety does not obscure the primitive simplicity of the type, and the most distinctive peculiarity of the microscopic food-supply of the ocean is the very small number of the forms which go to make up the enormous mass of individuals.

THE ORIGIN OF PELAGIC ANIMALS.

All the animals of the ocean are dependent upon the microscopic food-supply, and many of them are adapted for preying upon it directly. Among these Salpa is one of the most conspicuous examples. It passes its whole life in the open water, and it has no sessile stage in its ontogeny, as many floating animals have. It abounds in all parts of the ocean, and over some great seas it is always present at the surface. As the result of three years' observation, Schminkewitch says that the salpas are perennial pelagic animals, and Chun has shown that they are also found in abundance at great depths.

As long as it is alive and breathing a steady stream of micro-organisms is slipping along its pharynx and down through its œsophagus into its stomach, and sections of the intestine of salpa afford most beautiful preparations of radiolarians and diatoms.

The pelagic food-supply is very ancient, and we have, in salpa, an animal which has been especially evolved to pass its life swimming through the living broth of the mid-ocean.

If we were to select the typical pelagic animal we should probably choose salpa, and it is therefore most surprising to find that salpa itself has not been produced at the surface of the ocean by gradual evolution from a simple pelagic ancestor.

The structure which fits it so well for its mode of life has come to it by the inheritance of peculiarities which were originally acquired by bottom animals in adaptation to the needs of a sessile life.

This is all the more remarkable since both salpa and its fixed allies show by their embryology that still more remotely they are descended from a pelagic form like appendicularia.

The place in the pelagic world which Salpa fills so well has been ready for it from primeval times.

Why then has not the simple pelagic appendicularia given rise, in the open sea, to series of more and more perfected pelagic descendants culminating in salpa?

Why should the descendants of a pelagic ancestor have passed through a sessile stage before they acquired their improved pelagic structure?

If this were a solitary case it would not deserve notice ; but examination will show that no highly organized animal has ever been evolved at the surface, although all depend on the pelagic food-supply.

The animals which now find their home in the open waters of the ocean are, almost without exception, the descendants of forms which live upon or near the bottom or along the sea-shore or upon the land, and the exceptions are all simple animals of minute size. The metazoa which are primitively pelagic, that is, those which have been pelagic throughout their whole history and do not owe their structure to competition with improved forms from the bottom or the shore, are astonishingly few, and these few are among the smallest and simplest of the metazoa.

It is only necessary to review the chief groups of metazoa in order to perceive that most of their pelagic representatives exhibit the clearest evidence of descent from forms which lived upon or near the bottom or the shore. Many indeed have no pelagic members, but are restricted to the bottom.

The sponges are obviously a bottom group ; most of them are fixed, all are sedentary, and their whole organization is an adaptation for life in the bottom.

The coral polyps, actinias and alcyonarias, are among the most characteristic bottom forms, and the abundance of the fossil remains of polyp skeletons proves that these animals became established on the bottom very early, and that the whole history of their evolution has taken place at the bottom. The acraspedote medusæ are universally and justly regarded as the descendants of fixed polyp-like ancestors, and we may state with confidence that they are not primitively pelagic, but that a fixed period in their history has come between the modern swimming jelly-fish and its remote and unknown primitive pelagic ancestor.

The veiled medusæ are usually held to have had a similar history, but I shall soon give my reasons for holding that some of these at least are primitively pelagic. There can, however, be no doubt that the evolution of hydroid cormi has taken place at the bottom. The siphonophores are descended from ancestors like the anthomedusæ, and the various families and genera and species of siphonophores have most certainly been produced by divergent special-

ization among pelagic forms, and the greater part of their history, if not the whole of it, is therefore pelagic.

The echinoderms are most characteristic inhabitants of the bottom, as they have been from palæozoic times, and while synapta is sometimes found at the surface of the open ocean, this is exceptional, and we may state without hesitation that the evolution of the echinoderms has taken place at the bottom. This is equally true of the brachiopods and of most of the animals classed as vermes, the gephyreans, bryozoa, nemertians, and so forth. The pelagic annelids, such as Tomopteris, are secondary modifications of bottom forms, and while some of the more primitive annelids may possibly be originally pelagic, the group as a whole is as characteristic of the bottom as the echinoderms.

Many groups of crustacea have pelagic representatives, and the pelagic crustacean fauna is rich and varied, but in most cases the pelagic forms show unmistakable evidence of secondary change of habit, and all the higher crustacea have been evolved at the bottom in adaptation to a bottom life.

I shall soon give my reasons for believing that there is one important exception to this rule, however, and I shall try to show that there is good ground for holding that the copepods are primitively pelagic, and that while the greater part of the history of the crustacea is bottom history, the characteristics of the crustacean type were outlined in pelagic animals at a very early period in the history of the metazoa.

The heavy calcareous shells of the molluscs could not have been acquired at the surface, and that most characteristic molluscan organ, the lingual ribbon, is adapted for attacking more solid bodies than the delicate primitive pelagic animals. The classes and orders of molluscs must have been evolved at the bottom, and there is ample evidence that the swimming shellless gasteropods and cephalopods have, like those great pelagic groups the pteropods and heteropods, been secondarily adapted for a pelagic life.

Many of the marine fishes are strictly pelagic, and the structure and habits of fishes are in all respects so well fitted for a wandering life in the open water that the pelagic habit of fishes seems at first sight to be their most distinctive peculiarity, although a little

examination will show that there is ample evidence that it is secondary, and not primitive.

The perfection of their adjustment to a free life in the open sea is no evidence that this life is primitive, for the highest marine animals and those whose adaptation to a pelagic life is most complete, the sea-birds and cetacea and marine reptiles, are air-breathing terrestrial animals which have gone back into the ocean.

The most primitive groups of living fishes are the cyclostomes, elasmobranchs and ganoids. The cyclostomes are too small a group, and the living forms are too aberrant in habit, to contribute much information regarding the nature of the primitive vertebrates, but they exhibit no evidence of adaptation to a pelagic life, and our scanty knowledge of them is quite in harmony with the view that their remote ancestors were bottom animals.

The case is very different as regards the great groups of modern fishes for which the term palæichthyes is often used; the sharks, rays and ganoids.

The living representatives of these great and ancient groups are of peculiar interest to naturalists on account of their close affinity to the oldest vertebrate fossils which have been discovered. These points of resemblance to the more modern, but still ancient, amphibia and teleosts show that the modern palæichthyes have preserved their ancient structure with very slight modification, and that we have in them one of the most remarkable stem forms in the whole animal kingdom. This is shown still more conclusively by the fact that some of the palæozoic families of elasmobranchs have lived through period after period of geological history and have held their ground up to our own times.

The abundance and variety of the remains of elasmobranchs in the palæozoic rocks prove the great development of the group at this remote and early period, and the silurian sharks probably differed but little from those of the present day, although we are forced to see in them the ancestors of the ganoids and of all the divergent groups of extinct and living vertebrates.

Of the three groups of modern elasmobranchs, two, the chimæras and the rays, are bottom-feeders. The whole organization of the ray is as obviously adapted for life upon or near the bottom as that of a bird is for life in the air, and the flat pavement teeth are adapted

for crushing and grinding the hard-shelled molluscs and crustacea and echinoderms of the bottom.

It is true that the sawfish is not confined to the bottom, and the devil-fishes often capture their prey at the surface. In the West Indies they are often found very far from land, but these cases are exceptional, and the true rays rarely leave the bottom, nor are they adapted for rapid movement through the water.

The rays are undoubtedly much more modern than the true sharks, but there is ample evidence that they have retained habits of life which are common to all the primitive elasmobranchs.

Many of the modern sharks live on or near the bottom, where they are found in immense numbers and at considerable depths. In 1888 I was invited by Marshall McDonald, the Superintendent of the U. S. Fish Commission, to make use of the opportunity for surface collecting which was afforded by an expedition which was sent out to fish with hook and line on the bottom and along the edge of the Gulf Stream. The fishing commenced at the 500 fathom line, and every time the line was taken in we found numbers of dogfish (*Scyllium*) on the hooks, even when the water was considerably more than half a mile deep.

Many genera of sharks, such as the houndfish (*Mustelus*) and the dogfish (*Scyllium*), are known to feed upon the molluscs and crustacea and worms of the bottom, and the flat pavement-teeth of other genera whose habits are less known show that their mode of life is the same. Some of the bottom-feeding sharks (*Cestracion* for example) are the oldest of living vertebrates.

The mailed ganoids were undoubtedly derived from a shark-like ancestor, and the structure of the oldest ones, such as *perichthys*, *coccosteus*, and *cephalaspis*, shows that they were not very rapid swimmers. They were, undoubtedly, bottom-feeders like the modern sturgeon, and like many large and important families of modern teleosts, such as the cod, the siluroids and the pleuronectidæ.

So far as we know the palæozoic waters from fossils, there were no active locomotor animals of large size to furnish prey for raptorial fishes and the existence at the present day of so many species and genera and families of bottom-feeders, and the fact that the most archaic forms have this habit, are all grounds for

believing that the fishes are secondarily adapted to a pelagic life, like the sea-birds and the cetacea.

So far as amphioxus furnishes evidence, this bears in the same direction, for its home is in the sand of the bottom. In fact it may almost be called a subterranean animal, for when it is placed in an aquarium it sinks into the sand at the bottom and disappears at once, and it makes its way through the sand with great ease and rapidity.

All the evidence shows that the primitive vertebrates lived upon or near the bottom, and that the early steps in the evolution of the classes of vertebrated animals were made at the bottom.

As the result of this review we see that the evidence from palæontology, from embryology, and from the structure and habits of living animals all bears in the same direction, and shows that there are no large or highly organized animals which have been pelagic through all the stages of their evolution, and that, in this particular, the life-history of *Salpa* is not exceptional, but typical.

In its descent from an inhabitant of the bottom and in its secondary adaptation to a pelagic life, its history resembles that of all the highly organized pelagic animals.

Embryology also gives us good ground for believing that *Salpa* follows the analogy of all the metazoa in its still more remote descent from a small and simple pelagic ancestor, and there is good ground for believing that the earliest metazoa were all pelagic, and that they were represented at a very early period in the history of life by floating or swimming animals of minute size and simple structure. We may see in the free larval forms of many marine metazoa, such as the tornaria of *balanoglossus*, the swimming echinoderm larva, the ascidian tadpole, the floating ciliated larvæ of annelids, brachiopods and molluscs, in the coelenterate planula, and, as I believe, in the crustacean nauplius, traces of this primitive mode of life; often obscured or complicated by more recent adaptation and sometimes almost obliterated by secondary changes.

When this fact is seen in all its bearings and its full significance is grasped, it is certainly one of the most noteworthy and instructive features of the history of evolution.



The food-supply of the ocean consists of a few species of unicellular microscopic plants, and of a few simple protozoa which feed upon them. This supply is inexhaustible, and it is the only source of food for all the inhabitants of the ocean, except a few which live upon floating sargassum and the littoral algæ, and the drainage from the land.

Many marine animals are adapted for direct subsistence upon these organisms, and some of them, like Salpa, are universally distributed and are found in enormous numbers in all parts of the ocean.

The food-supply is not only inexhaustible, it is also primeval, and all the life of the ocean has gradually taken shape in direct dependence upon it during the history of its evolution.

In view of all these facts we cannot but be profoundly impressed by the thought that all the highly organized marine animals are products of the bottom, or of the shore, or of the land, and that while the largest animals on earth are pelagic, the few which are primitively pelagic are very small and very simple.

The reason is obvious. The conditions of pelagic life are so easy that there is no fierce competition, and the inorganic environment is so simple that there is little chance for diversity of habits.

The growth of terrestrial plants is limited by the scarcity of food, but there is no such limit to the growth of pelagic plants or the animals which feed upon them, and while the balance of life is undoubtedly adjusted, competition for food is never very fierce even at the present day, when the ocean swarms with highly organized animals which have become secondarily adapted for a pelagic life. Even now the destruction or escape of a microscopic pelagic organism depends upon the accidental proximity or remoteness of an enemy rather than upon defense or protection, and survival is determined by space relations rather than by a struggle for existence.

The abundance of food is shown by the ease with which wanderers from the land, like birds, find places for themselves in the ocean, and the rapidity with which they spread over its whole extent.

As a marine animal, the insect, halobates, must be very modern as compared with most pelagic forms, yet it has spread over all

tropical and subtropical seas, and it may always be found skimming over the surface of the water as much at home as a gerris in a pond. I never found it absent in the Gulf Stream when conditions were favorable for collecting.

The easy character of pelagic life is also shown by the fact that the larvæ of innumerable animals from the bottom and the shore have retained their pelagic habit, and I shall soon refer to facts which prove that the larva of a shore animal is safer at sea than it is near the shore. The absence of fierce competition in the open ocean is well shown by the simultaneous existence in the modern ocean of graded stages in the evolution of a type, such as the series of Pelagidæ; and also by the persistency of a stem form like the elasmobranch, side by side with, and often in competition with, various improved lines of divergent descendants.

In the primitive pelagic fauna and flora there was little opportunity for an organism to gain superiority by seizing upon an advantageous site or by acquiring peculiar habits, for one place was like another, and peculiar habits could count for little in comparison with accidental space relations.

After the pelagic fauna had been enriched by the addition of all the marine animals which are secondarily pelagic, competition with these improved forms from the bottom brought about improvements in those which were strictly pelagic in their origin, and through this competition, complicated animals of considerable size, like the siphonophores, have been evolved at the surface, but while their whole history has thus been pelagic they are not primitively pelagic; that is, they are not the outcome of purely pelagic influences. The wanderers from the bottom have introduced another factor in the evolution of pelagic life, for their bodies have been utilized for purposes of protection or concealment or on account of other advantages, and we now have fishes which shelter themselves in the poisoned curtain of physalia; crustacea which live in the pharynx of salpa; barnacles and sucking fishes fastened to whales and turtles, besides a host of external and internal parasites. The primitive ocean furnished no such opportunity, and the conditions of pelagic life must, at first, have been extremely simple.

Among the higher metazoa and the higher plants size is, in itself, an important factor in evolution. Variations in the con-

stituent cells of a large organism are continually being seized upon and fixed by natural selection, on account of their value in the functions of relation to other parts. Primitive pelagic organisms are all minute, and it is easy to understand why. To plants which are bathed on all sides by food, like the pelagic protophytes, small size is advantageous, since a small body has a larger surface in proportion to its bulk than a large one; and the pelagic plants are, as I have shown, most favorably placed for rapid growth when new cells separate as soon as they are formed, and thus expose all their surface.

The same ratio between bulk and nutritive surface tends to limit in the same way, if not to the same degree, the growth of the pelagic animals which live in the midst of an abundant supply of vegetable food.

Competition was not entirely absent among the primitive pelagic organisms, for the conditions of life are never absolutely uniform, although the possibilities of evolution must have been extremely limited and the progress of divergent modification very slow, so long as life was restricted to the waters of the ocean.

There can be no doubt that pelagic life was abundant for a long period during which the bottom was uninhabited. The history of the slow process of geological change by which the earth gradually assumed its present character, presents a boundless field for speculation, but there can be no doubt that the surface of the primeval ocean became fit for life long before the deeper waters or the sea-floor.

The early steps in the evolution of plants must have been taken in the transparent surface water under the influence of sunlight, and as both animals and plants are dependent upon oxygen, the primal flora and fauna must have lived in aerated water. The oxygen which is diffused through the ocean from the surface, where it is absorbed from the air, is gradually exhausted by oxidizable substances, both inorganic and organic, and it diminishes with the distance from the source of supply at the surface. The oceanic circulation tends to equalize its distribution, and no part of the ocean now seems to be totally without oxygen. Oxygen has been shown to be reduced to a minimum at the bottom of some of the great depressions of the sea-floor, and it is clear that a slight

change in the conditions which influence it might render the sea-bottom unfit for life.

In early palæozoic times the sea-floor was perhaps more level than it is now, and there may have been no deep hollows like those in which the oxygen is now found to be deficient, but the average depth must have been considerably greater, when all the water which is now locked up in the sedimentary rocks of the bottom and of the shores was still free in the ocean. The circulation may also have been less active when geographical conditions were more simple, and the air was undoubtedly less rich in oxygen in early palæozoic times than it is at present.

It is therefore easy to understand that long after the crust of the earth had acquired essentially its present character, there may have been a period when the supply of oxygen was so scanty that the activities of pelagic organisms and the products of their decomposition used it up in the surface water, so that life on the bottom was impossible at a time when the superficial water supported a luxuriant fauna and flora.

During this period the proper conditions for the production of large and complicated organisms did not exist, and while the total volume of life was probably very great, it consisted of the organisms of minute size and simple structure which I have termed the primitive pelagic fauna and flora.

#### THE PRIMITIVE PELAGIC FAUNA.

In using this term I do not, of course, intend to imply that these organisms are the beginning of life, or to express any opinion as to the way in which life first came into existence. I use it merely as a convenient designation for the total sum of the organisms which have been evolved by purely pelagic influences from a starting-point which is absolutely unknown at present.

The attempt to reconstruct in imagination the primitive pelagic fauna and flora is most fascinating, but all the available evidence is indirect, and as we can have little hope of finding any record of it in the rocks, we must trust to deduction rather than observation.

The modern pelagic protophytes have probably retained nearly their ancient form, but the modern radiolarians and pelagic fora-

minifera exhibit indications of secondary adaptation, and they have undoubtedly been modified by competition with improved organisms from the bottom.

All the metazoa have pelagic larvæ, or else larval or embryonic stages, which must be regarded as the degenerated vestiges of a pelagic habit; but in most cases these larvæ have been so much changed by the accelerated development of adult features, or by the acquisition of habits or structures to fit them for the conditions of modern pelagic life, that we can deduce little more from them than the former existence of pelagic ancestors. When a pelagic larva is still represented by a modern pelagic adult of minute size and simple structure, as the tadpole larva of ascidians is represented by *Appendicularia*, we may be confident that it is a pelagic production, and that it existed in the primitive pelagic fauna, although this view is directly opposed to accepted dogmas regarding the origin of the Chordata. When all the members of a great group have a definite pelagic larval stage which adheres to the same plan of structure in all of them, we may be pretty confident that this larva is the representative of a primitive pelagic adult animal, even if this ancestor has now no unmodified descendants.

To my mind the best example of the retention, by all the members of a great group, of a larval stage which represents an extinct primitively pelagic ancestor is to be found in the crustacean nauplius, and notwithstanding the popular verdict against it, I do not hesitate to regard the nauplius as a pure pelagic product, and to include it in the primitive pelagic fauna, although I shall discuss this question further on. In cases like that of the echinoderms, where the pelagic larvæ of the various classes and orders are very different from each other in the details of their organization, we are hardly safe in assuming more than the primitive existence of an unknown pelagic organism, from which they have been derived. This is true to even a greater degree of the trochic larvæ of annelids, molluscs, etc., but while there is little ground for regarding the forms of these modern larvæ as ancestral, we must regard their pelagic habit as an inheritance from unknown ancestors in the primitive pelagic fauna, in which we must therefore include representatives of such larvæ as the molluscan veliger, the nemertean pilidium, the actinotrocha of phoronis, the brachiopod larva, the cœlenterate planula, and so

forth, although we are quite unable to say how many independent starting-points these various metazoic lines had in the primitive pelagic fauna, or what these starting-points were like. Our inability to describe or picture these ancestral forms is no reason for doubting their reality, for in biology the weight and certainty of a deduction are often independent of its definiteness. We may, for example, feel sure that the cetacea are descended from terrestrial animals and yet find it impossible to picture their ancestor, or even to decide whether their ancestral lines converge into one stem before or after the pelagic habit was acquired.

We may in the same way feel sure, even in the absence of sufficient evidence to trace their direct paths, that all the great groups of metazoa ran back to minute pelagic ancestors, and we must, therefore, include in the primitive pelagic fauna a great, but indefinite, number of distinct and somewhat widely separated ancestral forms, and together with them, no doubt, an equal or greater number of somewhat similar forms which have been exterminated and have left no descendants. In these extinct forms we should, if we could study them, find the connecting links between divergent groups, and we would thus be able to complete the genealogical tree of the metazoa by bringing together the great divergent branches of the metazoic stem whose primary relationships now seem beyond discovery.

In addition to the primitive pelagic animals which are known to us only by the traces of their former existence which they have left in the structure and habits of modern larvæ and embryos, there are a few modern pelagic adult animals which show by their minute size and simple structure and by their systematic affinities that they are primitive pelagic animals, owing their structure to purely pelagic influences.

Appendicularia is a good example of this class, and I believe that the copepods are the most important group of the primitively pelagic metazoa.

#### THE ORIGIN OF THE CRUSTACEA.

The view that the copepods are degenerated descendants from crustacea like the phyllopods, and that the crustacea were evolved on the bottom, and that the pelagic habit of the copepods is

secondary, is so generally accepted that it is hardly worth while to advance a different view in this place where there is no room for its exhaustive treatment.

The consideration which seems to have the greatest weight with morphologists is the supposed necessity of a phylogenetic explanation of metamerism, but a little reflection will show the persistent existence of an influence which tends to metamerism at the present day.

For this influence, which is shown by such phenomena as the inheritance by the child of polydactylous feet from the polydactylous hands of the parent, or the development of wing-feathers on the toes of fantail pigeons; the influence which has carried the feet of the horse family along the same line of evolution with the hands, I have, in another place, proposed the term ontogenetic inheritance. Among the arthropods, examples of this sort of modern metamerization are very common, both as normal features of their structure, in the movable body-rings of the ocular and antennary somites of stomatopods, for example, and as monstrosities, as in the twelve-legged coleoptera.

I believe that a thorough study of this most interesting and instructive class of facts will convince any one that there is no philosophical necessity for assuming that the primitive crustacean had a highly metamerized body like that of a phyllopod, and that all the common features in the structure of arthropods may have been derived from a common ancestor as simple as a nauplius.

The analogy between the parapodia of annelids and the limbs of crustacea has been held to prove that the primitive crustacean limb was not a rowing organ fitted for a pelagic life, like the limbs of the nauplius and the copepod, but flat and leaf-like and adapted for movement over the bottom.

It is hardly possible, however, to believe that the arthropods have been derived from the higher polychætous annelids, and as the simpler and more primitive annelids have no parapodia, the resemblance, which is not actually very noteworthy, can be nothing more than an analogy.

There are plenty of degenerated copepods, and we have in their structure abundant proof of the degeneracy, and an adequate explanation of it in their parasitic habits, but they are degenerated

descendants of ordinary swimming copepods, and not of phyllopods, and there is no reason for holding that the copepodan type itself is degenerate, except the supposed exigencies of morphological philosophy.

The active locomotor habits of the eucopepods of the open ocean would seem to be conducive to advancement rather than to degeneration, and the occurrence of phyllopods in the lower Cambrian is, of course, no more evidence that they are primitive crustacea than the occurrence of pteropods and gasteropods is that they are primitive molluscs.

I am unable to see any valid objection to the view that the copepods are primitively pelagic; that they have been evolved at the surface of the ocean from pelagic nauplii, and that the great group crustacea has been derived from them.

We have already seen that the eucopepods are the chief intermediary between the micro-organisms of the ocean and the larger and higher marine animals; that they prey upon the protophytes and protozoa, and in their turn supply either directly or indirectly most of the food for the large inhabitants of the water; that most pelagic larvæ feed upon them; that they are the food of the great pelagic banks of pteropods and heteropods, of many cœlenterates, of the young of most fishes, and of some of the most abundant and important adult fishes, like the herring, and that the sea-birds, the cetacea, and in fact almost all of the larger pelagic animals, prey upon animals which in their turn prey upon copepods.

The animals which are most important at one period in the earth's history are often replaced by others at another period, and it is, of course, possible that the modern copepods now fill a place which was in former times filled by something else; but as their organization, as compared with that of the other crustacea, exhibits all the characteristics of a primitive pelagic stem-form, and inasmuch as the remains of animals, like the pteropods, which now live almost entirely upon copepods, are found in the oldest fossiliferous rocks, there is every reason to believe that the group formed an important constituent of the primitive pelagic fauna.

No one who advocates at one time the morphological heresies which are involved in the view that appendicularia is a stem-form which is pelagic in its origin; that the nauplius is a persistent



representative of the primitive crustacea, and that the whole history of the copepods has been pelagic; and that the veiled medusæ have been evolved in direct relation to pelagic influences; no one who makes these statements can hope to escape the charge that his view "ist die unwahrscheinlichste von Unwahrscheinlichkeiten."

The books all tell us that the free active appendicularia is the "degenerated" descendant of an ancestor which crept over the bottom; that the nauplius is a secondary larval form; that the active free-swimming copepods are degenerated phyllopods; and that the locomotor hydro-medusa is, in its origin, a specialized member of a sessile, polymorphic, hydroid cormus.

The first of these opinions, that appendicularia is a degenerated form, rests upon a supposed necessity for deriving the body of a vertebrate, which consists of a series of segments homologous with each other, but highly differentiated among themselves, from an ancestral aggregation of similar, but less differentiated, segments. The second opinion, that the copepods are degenerated and that the nauplius is a secondary larval form, is the result of a supposed necessity for explaining the segmentation of the arthropods in the same way, while the third view has its origin in the belief that the polymorphic members of a hydroid cormus must have arisen through specialization and division of labor from an ancestral undifferentiated aggregation.

These are a few, from among many, illustrations of the general acceptance among morphologists of a dogma which, while it is often refined and qualified until its character is almost lost, may be broadly stated as a belief that the homology between different parts of the same organism is always to be explained, like the homology between corresponding parts of different animals, as the result of phylogenetic inheritance; or, to state it in a different way, that the vegetative duplication of parts in animals has a phylogenetic significance, and implies descent from a duplicated ancestor.

The dogma is not the dictum of any one teacher, and it has grown almost imperceptibly from its starting-point in the discovery that the body of a metazoon is an aggregation of cells, each with an individuality of its own, specialized and differentiated by polymorphism and division of labor, and each one homologous with an unicellular organism.

The dogma has been a most useful and suggestive working hypothesis when well controlled, but when uncontrolled it has led to the most fantastic and grotesque unscientific speculation. The climax of inconsistency into which its blind adherents have been led was well shown by the simultaneous appearance, in a recent morphological journal, of two memoirs, one an essay on "The Origin of the Vertebrates from the Arachnids," and the other on "The Origin of Vertebrates from a Crustacean-like Ancestor."

After my first examination of the second of these memoirs I laid it down, much distressed in mind by the thought that this author had unkindly descended from the sphere of experimental research in physiology, to expose the unscientific methods of the morphologists by a severe and well merited, if somewhat ponderous, satire.

In my next chapter on the morphological significance of appendicularia I shall try to show that there is no philosophical necessity for a phylogenetic explanation of duplicated structures in animals, whether they are radical, bilateral, metameric or indefinite, and I must refer the reader to that chapter for my reasons for including appendicularia, the copepods and the veiled medusæ among the primitive pelagic animals.

#### THE PHYLOGENY OF THE METAZOA.

The primitive pelagic fauna, before the influence of the bottom and of the shore had been brought to bear upon it, consisted of small animals of simple structure; but we are forced, by the facts of comparative anatomy and embryology, to believe that a number of distinct types of structure were found among them.

Most of the great metazoic stems show by their embryology that they run back to simple and minute pelagic ancestors, and that their common meeting-point must be projected back to a still more remote time, before the differentiation of their pelagic ancestors had been effected. After we have traced each great line of metazoa as far back as we can from the study of fossils and by the aid of comparative morphology, we still find these lines distinctly laid down. The lower cambrian crustacea, for example, are as distinct from the lower cambrian echinoderms or pteropods or brachiopods

or lamellibranchs, as they are from those of the present day. The efforts of anatomists and embryologists to reconstruct the primary phylogeny of the metazoa have so far yielded few trustworthy results, and the results which are most trustworthy are usually those which are the most indefinite.

We are therefore forced to believe that the early steps in the establishment of the various types of metazoa were taken under conditions which had some essential difference from those which have prevailed, without any fundamental changes, from the time of the oldest fossil to the present day ; and we are also forced to believe that most of the great lines of descent were represented at some time in the remote past by ancestors which, living a different sort of life, differed essentially in structure as well as habits, from the representatives of the same types which are known to us. Furthermore, embryology teaches that each great group still bears internal evidence of descent from pelagic ancestors, and while the characteristics of these ancestors are in most cases unknown, a few, like appendicularia, are still found alive.

Our knowledge of the evolution of the metazoic types has certain general features which are essentially the same for all, but each group has also in its history much that is individual, and any general statement requires so much qualification that the history of an illustrative group is more instructive than a general summary.

In the echinoderms we have a well-defined type represented by abundant fossils, very rich in living forms, very diversified in its modifications, and therefore well fitted for use as an illustration.

This great stem contains many classes and orders, all constructed on the same plan, which is sharply isolated and quite unlike the plan of structure in any other group of animals. All through the series of fossiliferous rocks echinoderms are found, and the plan of structure is always the same. Palæontology gives us most valuable evidence regarding the course of evolution within the limits of a class as in the crinoids and in the echinoids ; but we appeal to it in vain for light upon the organization of the primitive echinoderm, or for connecting links between the classes. To our questions on these subjects and on the relation of the echinoderms to other animals, palæontology is silent, and throws them back upon us as unsolved riddles.

The morphologist unhesitatingly projects his imagination, held in check only by the laws of scientific thought, into the dark period before the times of the oldest fossils, and feels absolutely certain of the past existence of a stem-form, from which the classes of echinoderms have inherited the fundamental plan of their structure, and he affirms with equal confidence that the structural changes which have separated this ancient type from the classes which we know were very much more profound and extensive than all the changes which each class has undergone from the earliest palæozoic times to the present day.

He is also disposed to assume, but, as I shall show, with much less reason, that the amount of change which structure has undergone is an index to the length of time which the change has required, and that the period which is covered by the fossiliferous rocks is only an inconsiderable part of that which has been consumed in the evolution of the echinoderms.

The morphologist does not check the flight of his scientific imagination here, however, for he trusts implicitly to the embryological evidence which teaches him that, still further back in the past, all the echinoderms were represented by a minute pelagic animal which was not an echinoderm at all in any sense except the ancestral one, although it was distinguished by features which natural selection has converted, under the influence of more modern conditions, into the structure of echinoderms. He finds, in the embryology of modern echinoderms, phenomena which can bear no interpretation but this, and he unhesitatingly assumes that they are an inheritance which has been handed down from generation to generation through all the ages from the prehistoric times of zoölogy.

Other groups tell the same story with equal clearness. Who can look at a living *lingula* without being overwhelmed by the effort to grasp its immeasurable antiquity, and by the thought that, while it has passed through all the chances and changes of geological history, the structure which fitted it for life on the earliest palæozoic bottom is still adapted for a life in the sands of the modern sea-floor?

The everlasting hills are the type of venerable antiquity; but *lingula* has seen the continents grow up, and has maintained its integrity unmoved by the convulsions of nature which have given to the crust of the earth its present form.

As measured by the time-standards of the morphologist, lingula itself is modern, for its life-history still holds, locked up within it, the record of a structure and of a habit of life which were lost in the unknown past at the time of the lower cambrian, and it tells us, vaguely but unmistakably, of a life at the surface of the primitive ocean at a time when the brachiopod stem was represented by minute and simple pelagic animals.

Broadly stated, the history of each great line of metazoa has been like that of the echinoderms or brachiopods, for while the brachiopods are certainly much more closely related to the polyzoa or the gephyreans than to the echinoderms, and while these latter are nearer to the chordata than to the brachiopods, yet each great line stands sharply by itself.

The oldest pteropod or lamellibranch or crustacean or echinoderm or vertebrate which we know from fossils exhibits its own type of structure with perfect distinctness, and later influences have done no more than to expand and diversify the type, while anatomy fails to guide us back to the point where these various lines met each other in a common source, although it forces us to believe that this common source once had an individual existence.

Embryology teaches that each line once had its own pelagic representatives, and that the early stages in the evolution of each type have passed away and left no record.

The palæontological side of the subject has recently been ably summed up by Walcott in an interesting memoir on the oldest fauna which is known to us from fossils (*The Fauna of the Lower Cambrian or Olenellus Zone*, by Charles Doolittle Walcott, U. S. Geological Survey, 10th Annual Report, Washington, 1890).

The fossils of the lower cambrian are not absolutely the oldest known, but it is the oldest fauna which is represented with sufficient completeness for a general view, and is, therefore, interesting to biologists.

Walcott says that no plants are known in the rocks of the lower cambrian, and that he has satisfied himself, after a study of all the reputed species of algæ, that they are not plants, but the trails of worms or molluscs.

The number of species is small, but their diversity is most noteworthy and remarkable.

Walcott's collection of 141 American species from the lower cambrian is distributed over most of the marine groups of the animal kingdom, and, except for the absence of the remains of vertebrates, the whole province of animal life is almost as completely covered by these 141 species as it could be by a collection from the bottom of the modern ocean.

Four of the American species are sponges, two are hydrozoa, nine are actinozoa, one an echinoderm, twenty-nine are brachiopods, three are lamellibranchs, thirteen are gasteropods, fifteen are pteropods, eight are crustacea, fifty-one are trilobites, and the trails and burrows show the existence of at least six species of bottom forms, probably worms or crustacea.

The most noteworthy characteristic is the completeness with which these new species outline the whole fauna of the modern sea-floor.

Nothing brings home more vividly to the zoologist a picture of the diversity of the lower cambrian fauna and of its intimate relation to the bottom fauna of to-day than the thought that he would have found, on the old cambrian shore, about the same opportunity to study the embryology and anatomy of pteropods, gasteropods and lamellibranchs and crustacea and medusæ that he now has at a marine laboratory, and that his studies in phylogeny would have had about the same form then that they have now.

Biological evidence based on embryology and anatomy and on the habits and affinities of animals is justly regarded, by zoologists at least, as a more perfect record of the early history of life than palæontology, and we accept, without question, proofs of phylogeny which refer to a time very much more remote than the age of the oldest fossils.

We must not forget, however, that our generalizations in primitive phylogeny rest for the most part on the study of swimming or floating larvæ of minute size and simple structure, which we can have little hope of finding as fossils.

In the formations which follow the lower cambrian, species gradually become more numerous, but this is due to divergent specialization, and Walcott says that if a comparison be made between the olenellus zone (lower cambrian) and the silurian fauna, the superiority of the latter in number of species, genera and families is at once apparent.

“If the comparison be extended to class characters, the disparity between the two is very much reduced, and it is made evident that the evolution of life between the epoch of the *Olenellus* fauna and the epoch of the Ordvician fauna has been, with one or two exceptions, in the direction of differentiating the class types that existed in the ‘earlier fauna.’”

The ground which we have covered in our review of these various broad aspects of the animal kingdom brings us, then, to the following point of view :

There are no highly organized animals which have been pelagic through all the stages of their evolution. The metazoa, which have been pelagic through their whole history, are either small and simply organized, as compared with the higher representatives of the group to which they belong, like appendicularia, or else, like the siphonophores, they have been perfected through competition with higher types.

Marine life is older than terrestrial life, and as all marine life has shaped itself in relation to the pelagic food-supply, this itself is the only form of life which is independent, and it must therefore be the oldest. There must have been a long period in primeval times during which there was a pelagic flora and fauna, rich beyond limit in individuals, but made up of only a few small simple types. During this time the pelagic ancestors of all the great groups of metazoa were slowly evolved, as well as others which have no living descendants. So long as life was restricted to the surface, no great or rapid advancement through the influences which now modify species was possible, and we know of no other influence which might have replaced these. We are, therefore, forced to believe that the differentiation and improvement of the primitive flora and fauna was slow, and that for a vast period of time life consisted of an innumerable multitude of pelagic organisms made up of a few forms. During the time which it took to form the thick beds of older sedimentary rocks the physical conditions of the ocean gradually took their present form, and during a part, at least, of this period, the total amount of life in the ocean may have been about as great as it is now without leaving any permanent record of its existence, for no rapid advancement took place until the advantages of a life on the bottom were discovered.

THE DISCOVERY OF THE BOTTOM, AND ITS  
EFFECT ON EVOLUTION.

We must not think of the populating of the bottom as a physical problem, but as colonization, very much like the colonization of oceanic islands. Physical conditions for a long time made it impossible, but its initiation was the result of biological influences, and there is no reason why the starting-point should be the point where the physical obstacles were first removed. It is useless to speculate upon the character of the physical obstacles; there is reason to believe that one of them, probably a very important one, was the deficiency of oxygen in deep water.

Whatever their character may have been they were all, no doubt, of such a nature that they first disappeared in the most shallow water around the coast, but it is not probable that bottom life was first established in shallow water, or before the physical conditions had become favorable at considerable depths.

The sediment near the shore is destructive to most pelagic animals, and recent explorations have shown that a stratum of water of very great thickness is necessary for the complete development of the pelagic flora and fauna. It is a mistake to picture pelagic life as confined to a thin surface stratum. Pelagic plants probably flourish as far down as the light penetrates, and pelagic animals are abundant at very great depths. As the earliest bottom animals must have depended directly upon the floating organisms for food, it is not probable that they first established themselves in shallow water, where the food-supply is not only scanty in amount but also mixed with sediment; nor is it probably that their establishment on the bottom was delayed until the great depths had become favorable to life.

The belts around elevated areas which are far enough from shore to be free from sediment and to have above them a sufficient depth of water to permit the pelagic fauna to reach its full development, are the most favorable spots, and I shall soon show that there is palaeontological evidence which indicates that they were seized upon very early in the history of bottom life. It is very probable that colony after colony was established on the bottom, and after-



wards swept away, like clouds before the wind, by geological changes, and that the bottom fauna which we know was not the first.

Colonies which started in shallow water were exposed to accidents from which those in great depths were free, and in view of our present knowledge of the permanency of the sea-floor and of the broad outlines of the continents, it is not impossible that the first fauna which settled in the deep zone around the continents may have persisted and given rise to our modern life. However this may be, we must regard this deep zone as the birthplace of the fauna which has survived; as the ancestral home of all the improved metazoa.

The effect of life upon the bottom is more interesting than the place where it began, and we have now to consider its influence in the evolution of animals.

The effect of the secondary acquisition of a sedentary life by modern animals has been fully discussed by many writers, but no one, so far as I am aware, has ever considered the effect of the first settlement of the bottom by pelagic animals, all whose competitors and enemies had previously been pelagic.

It is doubtful whether the animals which first settled on the bottom secured any more food than the floating ones, but they undoubtedly obtained it with less effort, and were able to devote their superfluous energy to growth and to multiplication, and thus to become larger and to increase in numbers faster than pelagic animals.

Their sedentary life must have been favorable to both sexual and asexual multiplication, and the tendency to multiply by budding must have been quickly rendered more active. It is sometimes stated that the capacity for budding has been acquired among the metazoa as the result of a sedentary life, but this view hardly seems to be the true one. Capacity for asexual multiplication is very old, older in all probability than sexual reproduction, and there is no reason to believe that it has ever been lost even by the highest animals, for it must be regarded as nothing more, in ultimate analysis, than discontinuous growth. The tissues of all animals have vegetative power, and external influences determine whether this shall result in continuous or discontinuous growth, and a trace of the power to multiply asexually is retained even among the embryos of mammals. It is therefore wrong to speak of the *acquisition*

of a capacity for budding, and it is not at all improbable that the primitive pelagic metazoa multiplied by buds; although the tendency to form connected cormi, and to retain the connection between the parent and the bud until the latter was able to obtain its own food and to care for itself, was a result, and probably one of the first results, of life on the bottom.

The animals which first acquired the habit of resting upon the bottom therefore soon began to multiply faster, both sexually and asexually, than their swimming allies; and their asexual progeny remaining for a longer time attached to and nourished by the parent stock, were much more favorably placed for rapid growth. As bottom animals live on a surface, or at least a thin stratum, while swimming animals are distributed through solid space, the rapid multiplication of bottom animals must soon have led to crowding and to competition, and it soon became harder and harder for new forms from the open water to force themselves in among the old ones, and colonization soon came to an end.

The great antiquity of all the types of structure which are represented among the modern metazoa is therefore what we should expect, for after the foundation for the fauna of the bottom was laid it became, and ever afterwards remained, difficult for new forms to establish themselves.

Our knowledge of the sea-bottom is for the most part from three sources: from dredgings and other methods of exploration; from rocks which were originally laid down beyond the immediate influence of the continents, and from the patches of the bottom fauna which have been gradually brought near its surface by the growth of coral reefs; and from all these sources we find testimony to the density of the crowd of animals on favorable spots.

Deep-sea exploration can give only the most scanty and fragmentary basis for a picture of the sea-bottom, but it shows that its animal life may thrive with the dense luxuriance of tropical vegetation, and Sir William Thomson says that he once brought up at one time on a "tangle," which was fastened to a dredge, over 20,000 specimens of a single species of sea-urchin.

While cruising on the U. S. Fish Commission schooner *Grampus*, I was interested to find that when a ground-line with baited fish-hooks had been sunk to the bottom in nearly a mile of water, several

of the hooks dropped into the mouths of large sea anemones, so that they were brought up uninjured, and were carried more than three hundred miles to the laboratory, where they lived for some time in an aquarium.

The number of remains of palæozoic crinoids and brachiopods and trilobites which are crowded into a slab of fine-grained limestone is most astounding, and it testifies most vividly and forcibly to the wealth of life on the old sea-floor.

No description can convey an adequate conception of the boundless luxuriance of a coral island, but nothing else affords such a vivid picture of the capacity of the sea-floor for supporting life.

The marine plants are not abundant on coral islands, and the animals depend either directly or indirectly upon the pelagic food-supply, so that in this respect their life is like that of animals in the deep sea far from land.

The abundant life is not restricted to the growing edge of the reef, and the inner lagoons are often like crowded aquaria. At Nassau, my party of eight persons found so much to study in a little reef in a lagoon, close to our laboratory, that for four months and more we found new things every day, and our explorations seldom carried us beyond this little tract of bottom. Every inch of the surface was carpeted with living animals, while others were darting about among the corals and gorgonias in all directions; but this was not all, for the solid coral was honeycombed everywhere by tubes and burrows; and, when broken to pieces with a hammer, each mass of coral gave us specimens of nearly every great group in the animal kingdom. Fishes, crustacea, annelids, molluscs, echinoderms, hydroids and sponges could be picked out of every fragment, and the abundance of life inside the solid rock was most wonderful.

The absence of pelagic life in the landlocked waters of coral islands is as impressive and noteworthy as the luxuriance of life upon and near the bottom.

On my first visit to the Bahama Islands I was sadly disappointed by the absence of pelagic animals where all the conditions seemed to be peculiarly favorable.

The deep ocean is so near that, as one cruises through the inner sounds past the openings between the islets which form the outer

barrier, the deep-blue water of mid-ocean is seen to meet the white sand of the beach, and soundings show that the outer edge is a precipice as high as the side of Chimborazo and much steeper. Nowhere else in the world is the pure water of the deep sea found nearer land or more free from sediment, and on the days when the weather was favorable for towing outside, we found siphonophores and pteropods and pelagic molluscs, crustacea, salpæ, and all sorts of pelagic larvæ in great abundance in the open sea just outside the inlets.

Inside the barrier the water was always calm, and day after day it was as smooth as the surface of an inland lake. When I first entered one of these beautiful sounds where the calm, transparent water stretches as far as the eye can reach, and new beauties of islets and winding channels open before one, as those which are passed fade away on the horizon, I felt sure that I had at last found a place where the pelagic fauna of mid-ocean could be taken home alive and studied on shore.

The water proved to be not only as pure as air, but also as empty. At high water we sometimes captured a few pelagic animals near the inlets, but we dragged our surface-nets through the sounds day after day only to find them as clean as if they had been hung out in the wind to dry. The water in which we washed them usually remained as pure and empty as if it had been filtered, and we often returned from our towing expeditions in the sounds without even a copepod or a zoea or a pluteus.

The absence of floating larvæ is most remarkable, for the sounds swarm with bottom animals which give birth every day to millions of swimming larvæ. The mangrove swamps and the rocky shores are fairly alive with crabs carrying eggs at all stages of development, and the boat passes over great black patches of sea-urchins crowded together by thousands, and the number of animals which are engaged in laying their eggs or in hatching their young is infinite, yet we rarely captured any larvæ in the tow-net, and most of those which we did find were old and nearly through their larval life.

It is often said that the water of the coral sounds is too full of lime to be inhabited by the animals of the open ocean, but this is a mistake, for the water is perfectly fitted for supporting the most

delicate and sensitive animals, and we had no difficulty in keeping alive, in water taken from the sounds, the surface animals which we caught outside. Even trachomedusæ and doliolums, which are extremely sensitive to impurities in the water, could be kept alive in the house very much better than in any other place where I have ever tried to keep them, and instead of being injurious, the pure water of the sounds is peculiarly favorable for use in aquaria for surface animals.

The scarcity of floating organisms can have only one explanation. They are eaten up, and competition for food is so fierce that nearly every organism which is swept in by the tide, and nearly every larva which is born in the sounds, is snatched by the tentacles around some hungry mouth.

Nothing could illustrate the fierceness of the struggle for food among the animals on a crowded sea-bottom more vividly than the emptiness of the water in coral sounds. The only larvæ which have much chance of establishing themselves for life are those which are so fortunate as to be swept out into the open ocean, where they can complete their larval life under the milder competition of the pelagic fauna, and while it is usually stated that the pelagic habit has been retained by the larvæ of bottom animals for the purpose of distributing the species, it is more probable that it has been retained on account of its comparative safety.

There can be no doubt, in view of these facts, that competition came swiftly after the establishment of the first bottom fauna, and that it soon became very rigorous and led to rapid evolution; and we must also remember that life on the bottom introduced many new opportunities for divergent modification and for the perfecting of animals.

The increase in size, which came with the economy of energy, increased the possibilities of variation, and led to the natural selection of those peculiarities which improved the efficiency of various parts of the body in their functions of relations to each other, and this has certainly been an important factor in the evolution of complicated organisms.

The new mode of life also permitted the acquisition of protective shells, hard supporting skeletons, and other imperishable structures, and it is therefore probable that the history of evolu-

tion in later times gives us no index as to the time which was required to evolve, from pelagic ancestors, the oldest animals which were likely to be preserved as fossils.

Life on the bottom also introduced another most important influence in evolution—competition between blood relations. In the animals which we know most intimately, divergent modification, with the extinction of connecting forms, results from the fact that the fiercest competitors of each animal are its closest allies, which, having the same habits, living upon the same food, and avoiding enemies in the same way, are constantly striving to hold exclusive possession of all the essentials to their life. When a stock gives rise to two divergent branches, each of them escapes competition with the other, so far as they differ in structure and habits, while the parent stock, competing with both at a disadvantage, is exterminated.

Among the animals which we know best, evolution leads to a branching tree-like phylogeny with the topmost twigs represented by living animals, while the rest of the tree is buried in the dead past. The connecting form between two species must, therefore, be constructed in imagination or sought in the records of the past.

Even at the present day things are somewhat different in the open ocean, and they must have been very different in the primitive ocean, for a pelagic animal has no fixed home, one locality is like another, and the competitors and enemies of each individual are determined, in great part, by accidents. We accordingly find, even now, that the evolution of pelagic animals is often linear instead of divergent, and the early steps in the series often live on side by side with the later and more evolved forms. The radiolarians and the medusæ and the siphonophores furnish many well-known illustrations of this feature of pelagic life.

No one is much surprised to find in the South Pacific or in the Indian Ocean a salpa, or a pelagic crustacean, or a surface fish which has previously been known only in the North Atlantic, and the list of species of marine animals which are found in all seas is a very long one. The fact that pelagic animals are so independent of those laws of geographical distribution which limit land animals is additional evidence of the easy character of the conditions of pelagic life. We have seen that one of the first results of life

upon the bottom was to increase asexual multiplication and to lengthen the time during which buds remained united to and nourished by their parents. One result of this is the crowding together of individuals of the same species, and competition between relations. We have in this and in other obvious peculiarities of life on the bottom a sufficient explanation of the fact that, since the first establishment of the bottom fauna, evolution has resulted in the elaboration and divergent specialization of the types of structure which were already established, rather than in the production of new types.

Another result of the struggle for existence on the bottom was the escape of varieties from competition with their allies by flight from the crowded spots and a return to the open water above; just as in later times the cetacea and sea-birds have gone back from the land to the ocean. These emigrants, like the civilized men who invade the homes of peaceful islanders, brought with them the improvements which had come from fierce competition, and they carried everything before them and produced a great and rapid change in the character of the pelagic fauna.

The rapid intellectual improvement which has taken place among the mammalia since the middle tertiaries, and the rapid structural development which took place in animals and plants when the land fauna and flora were first established, are well known; but the fact that the discovery of the bottom initiated a much earlier, and probably much more important era of rapid development in the forms of animal life has never received the attention which it so well merits.

If the views which I have advanced are correct, the primitive bottom fauna must have had the following characteristics:

1. It was entirely animal, without plants, and it at first depended directly upon the pelagic food-supply.

2. It was established around elevated areas in water deep enough to be beyond the influence of the shore.

3. The great groups of metazoa were rapidly established from pelagic ancestors.

4. There was a rapid increase in the size of the bottom animals and hard parts were quickly acquired.

5. The bottom fauna soon produced progressive development among pelagic animals.

6. After the establishment of the bottom fauna, elaboration and differentiation among the representatives of each primitive type soon set in and led to the extinction of the connecting forms.

There is no reason to suppose that the first animals which were adapted for preservation as fossils have been discovered, and many of the oldest fossils, like the pteropods, are most certainly the modified descendants of simpler ancestors with hard parts, but it is interesting to note that the oldest fossil fauna which is known to us is an unmistakable approximation to the primitive bottom fauna as I have outlined it.

Walcott has given the following sketch of the broad general characteristics of the lower cambrian fauna :

The lower cambrian fossils are distributed through strata which in Washington and Rensselaer counties in New York, are nearly two miles thick, and some of them, at least, were deposited in water of considerable depth. This is shown by the fineness of the sediment and by the perfect preservation of tracks and burrows in soft mud and of soft animals like jelly-fishes. These show that the sediment was laid down slowly and gently, in water so deep as to be free from disturbance, and under conditions so favorable that it contains the remains of some animals which are not found again until we reach a very much more modern period. The fossil medusæ of the lower cambrian are so perfect that their identity is unquestionable, yet it is not until the Solenhofen lithographic slate of the Jura is reached in ascending the geological scale, that medusæ are again met with ; and corals and lamellibranchs are found in the lower cambrian, although as they are not found again until the silurian rocks are reached, we have no record of their existence through the long period covered by the middle and upper cambrian.

The fauna of the lower cambrian, while it undoubtedly lived in water of very considerable depth, was not oceanic but continental, and Walcott says that "one of the most important conclusions is, that the fauna of the lower Cambrian lived on the eastern and western shores of a continent that in its general configuration outlines the American continent of to-day. Strictly speaking, the



fauna did not live upon the outer shore, facing the ocean, but on the shores of interior seas, straits, or lagoons that occupied the intervals between the several ridges that ran from the central platform east and west of the main continental land-surface of the time."

The lower cambrian fauna was rich and varied, but it was not self-supporting, for no fossil plants are found, and the primary food-supply was pelagic. Animals adapted for a rapacious life at the surface, such as the pteropods, were abundant, and they prove the existence of a rich supply of pelagic animals. All the forms are either carnivorous animals, such as medusæ, corals, crustacea and trilobites, or they are adapted, like the sponges, brachiopods and lamellibranchs, for straining minute organisms out of the water, or for gathering up those which rained down from above, and the conditions under which they lived were obviously very similar to those on the bottom at the present day.

Walcott's studies show that the earliest known fauna had the following characteristics :

1. So far as the record goes it consisted of animals alone, and these animals were dependent upon the pelagic food-supply for support.

2. While small in comparison with many modern animals, they were gigantic in size as compared with primitive pelagic animals.

3. The species were few, but they represented a very wide range of types.

4. All the types have modern representatives, and most of the modern types are represented in the lower cambrian.

5. The habitat was not the bottom of the deep ocean, but the submerged surface of a sinking continent, under water of considerable depth.

Remains of bottom animals are found in rocks below the cambrian, and Walcott believes that while the olenellan fauna adds a little more to our knowledge of the rate of convergence backwards in geological time of the lines representing the evolution of animal life, it also proves, at the same time, that an immense interval has elapsed between the beginning of life and the epoch represented by the olenellan fauna. He says: "That the life in the pre-olenellus seas was large and varied, there can be little, it

any, doubt. The few traces known of it prove little of its character, but they prove that life existed in a period far preceding lower Cambrian times, and they foster the hope that it is only a question of search and favorable conditions to discover it."

No one can question the validity of the basis for Walcott's hope, for pelagic animals have undoubtedly established themselves on the shores of elevated tracts again and again, during the oscillations of the sea-bottom, and we have every reason to expect and look for their remains.

If, however, it is true that the primitive stem-forms were pelagic and minute, there is little hope of finding their delicate microscopic remains in the sedimentary rocks of the shore.

The cambrian fauna is usually regarded as a half-way station in a series of organisms which reaches back into the past for an immeasurable period, and it is even stated that the history of life before the cambrian is longer, by many fold, than its history since.

So far as this opinion rests on the diversity of types in cambrian and silurian times it has no good basis, for if the view which I have advocated is correct, the evolution of the ancestral stem-forms took place at the surface, and all the necessary conditions for the rapid production of types were present when the bottom fauna first became established.

As we pass backwards towards the lower cambrian we find closer and closer agreement with the biological conception of the primitive life at the bottom.

We cannot regard the olenellan fauna as the first bottom fauna, for it contains forms which have been secondarily adapted for a pelagic life, such as the pteropods.

We may, however, feel confident that the first bottom fauna resembled that of the lower cambrian in its physical conditions, and in its most distinctive peculiarity, the abundance of types and the slight amount of differentiation among the representatives of these types.

Far from seeing in the lower cambrian fauna a half-way station in a long series of bottom animals, the biologist must regard it as an unmistakable and decided approximation to the primitive fauna of the bottom, beyond which life was represented only by simple and minute pelagic organisms.

THE ORIGIN OF THE CHORDATA, CONSIDERED IN ITS RELATION  
TO PELAGIC INFLUENCES.*Section 1.—The Ancestral Chordata.*

I shall now attempt to study the origin and significance of the structure of appendicularia in accordance with those conditions which must, as Dohrn has pointed out (*Studien, etc., VIII, p. 79*), direct all inquiry into the genealogy of animals.

All biologists will agree with Dohrn that no amount of morphological information, or of exhaustive microscopical study of the structure and development of animals, can suffice, in the absence of comprehensive knowledge of their mode of life and of the conditions of their existence, for the institution of inquiries into their phylogenetic relationship.

Unquestionably the first condition for genealogical inquiry is, as Dohrn says, the establishment of a direct connection between our morphological studies and the facts of physiology and biology.

“The homologies which are established by comparative anatomy, and the primitive identities which are established by comparative embryology, are only the means for this end. They are in themselves valuable in phylogenetic inquiry only so far as they furnish us the opportunity to pass from the consideration of the structure of organs as they now exist, and of the functions of these organs at the present time, to the consideration of conditions which have passed away; to the study of the history of the modifications which have come between these structures and functions and those which we must attribute to the same organs at an earlier genealogical stage.”

Keeping these conditions of genealogical inquiry in view, let us try to study the structure of appendicularia in relation to the conditions of its life, so far as these are known to us, and let us see what functions we must, according to the principle of change of function, attribute to the organs of the remote ancestors of the tunicates, and what are the paths these organs have traversed in reaching their modern structure.

If the reader of the following pages should think that I wander too far from the beaten paths of observation, I must plead as my

excuse that the study of phylogeny is impossible without the use of the imagination, and that the field is already occupied by a phylogeny of the tunicata which cannot be set aside until a more satisfactory one has been found.

Appendicularia is a very simple organism, and while much ingenuity has been expended in the negative task of accounting for the absence of all the structures which it lacks, I hope that the more positive attempt to account for its actual structure will not lead us into any great difficulties.

In the belief that the sequel will justify the assumption, I shall, as my starting-point, picture the ancestor of appendicularia as a simple, minute, unsegmented, chordate animal, leading a free, locomotor, pelagic life and subsisting upon the micro-organisms of the ocean. I shall also assume that this ancestor had an elongated, unsegmented body stiffened by an axial, unpaired, unsegmented notochord, like that of amphioxus, appendicularia, and the ascidian larva; that it had a simple, elongated, dorsal, nervous system, and an elongated, ventral, digestive tube, without pharyngeal clefts; that this tube was nearly straight; that it had a capacious lumen, and that, as in amphioxus and the tunicates, this was permanently distended and ciliated, and that the water, with the micro-organisms that float in it, was swept through it by endodermal cilia and not by muscular contractions.

In order to entangle the floating particles of food and to hold them while the water swept on through the intestine and out of the anus, gland-cells for the excretion of slime were scattered among the ordinary ciliated endoderm cells of the digestive tract. In origin, these slime-cells may have been modified or specialized digestive gland-cells.

As particles which are entangled and held captive near the oral end of the gut are more perfectly exposed to its digestive action than those which continue to float with the stream, the most anterior slime-cells are most efficient and valuable, and as each variation in this direction gave its possessor an advantage, the slime-cells gradually, through the action of natural selection, became localized in the pharyngeal region, and this region gradually became enlarged and was thus set apart, at a very early period, as a specialized tract of the gut.

It is also probable that, at a very early stage in the phylogeny of these primitive chordata, a blind pouch was developed, behind the pharynx, to catch the food-particles as they were hurried past with the stream of water and to retain them long enough for perfect digestion, and that the rudiment of the organ which has in the higher vertebrates become the liver was thus established.

In these primitive animals the current of water through the digestive organs was most useful as the vehicle for floating food, but while necessary, it was a necessary evil, for the large distended lumen which furnished it a channel also permitted undigested food to be swept away and lost.

The immovable, permanently distended, ciliated digestive tract of a modern lamelibranch is very similar to that of these primitive chordata, but the lamelibranchs have acquired an apparatus for straining off the water from the captured food, so that the digestive tract is relieved from this disadvantageous current.

If, after the pharynx had been established, a secondary opening from it to the exterior were to be formed, this opening would permit the water to escape without passing through the intestine, and as the advantage of this new arrangement is obvious, there can be no doubt that after an opening of this sort was once formed, it would be preserved and perfected by natural selection, as a channel for the escape of the water after the food has been strained out and entangled by the excretion of the pharyngeal slime-glands.

I shall show, further on, that if an useful opening of this sort were to be fixed and preserved by natural selection on one side of the body, the laws of growth would soon cause it to be duplicated on the other side. These two openings are the so-called gill-slits of appendicularia, although they are beyond question much older than the modern appendicularia, dating back to a time before this animal had acquired the features which distinguish it from its more primitive chordata ancestors.

I am not able to suggest what led to the first establishment of a secondary opening into the pharynx; but, once formed, its preservation and gradual improvement, by natural selection, as a channel for the escape of superfluous water, and its duplication on opposite sides of the body, are easily intelligible.

If we accept the view that the chordata type was evolved under purely pelagic influences, we are forced to believe that the first chordata were minute, and that their small bodies were soft, and unprotected by a hard covering. If we also admit that their digestive tract was a channel for a current of water, we can hardly believe that they needed respiratory organs, or, for that matter, excretory organs, for all the tissues of a minute soft animal, bathed within and without by pure water, must have been sufficiently aerated and purified without any organs for this purpose.

It is not at all probable, then, that the pharyngeal clefts were originally either gills or renal organs, and we have seen that the conditions of pelagic life furnish a much more simple explanation of their advantage, and I believe that the view that they were originally concerned in nutrition rather than in respiration will commend itself to all who approach the subject without any philosophical preconception.

After they were once established they gradually effected a rearrangement of the slime-cells and ciliated cells of the pharynx, for as it now became important that all the food particles should be entangled by the product of the slime-cells before it reached the pharyngeal clefts, the slime-cells were gradually restricted to the anterior part of the pharynx, while the ciliated cells gradually became specialized to carry the entangled food past the openings and to convey it safely into the œsophagus.

All the parts of the pharynx of appendicularia are beautifully constructed for this purpose. The pharyngeal clefts are situated far back in the pharynx, and are separated by nearly its whole width from the œsophagus. They are fringed by large cilia to expel the water, and they are separated from each other by a vertical shelf or velum on the ventral floor of the pharynx, so placed as to prevent cross-currents.

In front of this shelf the slime-cells are brought together in two rows, near the middle line, just inside the mouth, to form the hypopharyngeal band or endostyle. Between these two rows of slime-cells there is a median row of large ciliated cells, so placed that they drive the slime forwards to the point where a ciliated peripharyngeal band receives it and carries it up each side of the pharynx just behind the mouth, into the most favorable place for entangling the food, as this enters with the current of fresh water.

On the dorsal middle line the threads of slime are gathered up and guided along the epipharyngeal band or dorsal lamella, beyond the influence of the current of water which sets backwards, on each side of the ventral velum, to the pharyngeal clefts, and the food is thus safely conducted into the œsophagus while the water escapes.

Up to this point I believe that the ancestral history of the tunicates was identical with that of the vertebrates, for the hepatic cæcum, the dilated pharynx, the pharyngeal clefts, the hypopharyngeal gland and the peripharyngeal bands have been inherited by all the chordata, and have impressed themselves so firmly in their organization that even the highest vertebrates still retain them, either as vestiges, or as organs which have been fitted to new functions.

I believe, however, that while they were acquired before the tunicates diverged from the chordata stem, they were acquired by an organism whose environment and habits of life were essentially like those of the modern appendicularia.

All the parts of the pharynx of appendicularia are so beautifully co-ordinated for effecting a purpose so useful and so well adapted to the conditions of its simple pelagic life, that we find it difficult to resist the belief that its ancestors had essentially the same habits, and that they lived under essentially the same conditions, and that this simple organization was directly acquired in adaptation to these conditions.

If this view involved any great or unusual difficulties we might well distrust it, notwithstanding its simplicity ; but I shall try to show that it does not. In the preceding chapter I have shown that it accords with our knowledge of the fundamental principles of the general biology of the ocean, and further on I shall try to show that it is equally in accord with the principles of morphology.

At present we must devote our attention to the history of the evolution of the tunicates from this primitive chordata stem.

### *Section 2.—The Origin of the Tunicates.*

Like most recent students of the tunicates, I believe that we have in appendicularia a persistent representative of the primitive tunicata ; but, unlike many of them, I fail to find in its structure

any evidence of degeneracy, or in its habits any basis for the assumption that it is degenerated. In most respects its structure is like that of the hypothetical ancestor whose evolution we have traced. It has an unsegmented notochord, and a capacious lumen throughout the whole course of the digestive tract from mouth to anus. This lumen is permanently distended and food is carried through it by cilia. It has a blind diverticulum from the stomach, and the greatly expanded pharynx opens laterally through two ciliated pharyngeal clefts, through which the water escapes while the food passes into the œsophagus. There is a ventral slime-gland just inside the mouth, and its excretion is conveyed upwards around the pharynx by the cilia of the peripharyngeal bands, and is then swept into the œsophagus with the entangled food.

This increasing complexity and perfection of the pharynx is accompanied by an increase in its size, so that in the primitive tunicates it soon comes to be the most important and dominant organ of the body, and brings about adaptive changes in other parts. One of these is the differentiation of a stomach for the retention and digestion of the food, in the direct course of the gut. As long as the food was mixed with great quantities of water, digestion and assimilation probably went on simultaneously in all parts of the post-pharyngeal gut, but as the water found another exit and the food thus became more compact and solid, the stomach of appendicularia became established and thus divided the gut into an œsophageal, a gastric, and an intestinal region.

Our knowledge of the primitive vertebrates seems to me to be too scanty to show whether this differentiation occurred before or after the tunicates diverged from the ancestors of the vertebrates. We are now concerned with the history of the tunicata line alone, and the fact that the differentiation now exists in all tunicates shows that it was brought about very early in their history.

Another most important change in the relations of the gut also took place very early in their history. The intestinal portion became bent upon the enlarged pharynx so as to form a  $\sqsubset$  with the intestinal bar of the  $\sqsubset$  ventral to the pharyngeal portion, and with the anus on the ventral middle line under the pharynx. Herdman represents the primitive condition of the digestive tract of tunicates as a  $\sqsubset$ , with the intestine and anus dorsal instead of ventral (page



128); but I shall show further on that the relations exhibited by appendicularia are the primitive ones, from which we must derive those which are exhibited by other tunicates.

By this change the tail was freed from the gut and was made much more efficient as an organ of locomotion, while the fæces were discharged from the anus into the current of water which set out through the pharyngeal clefts. This latter feature may not have been of any value so long as habits of active locomotion were retained, but, as we shall see, it became very important at a later stage.

The embryology of the ascidians shows that this arrangement of the digestive tract was secondary; that at one time it was straight, extending into that region of the body which is now specialized in appendicularia as a tail. The advantage to an active pelagic animal of this change is obvious, since it permits the tail to become purely locomotor. As each slight variation in this direction must have given a slight increase in the freedom of movement, the shape of the body of appendicularia is easily intelligible as the result of natural selection, and while the change is complete in this, the most primitive tunicate which we know, so that we can only conjecture the transitional stages, the change itself is not a complicated one. It presents little difficulty, although the resulting differentiation of appendicularia into two regions or "segments," a body and a tail, has been made the basis of much speculation.

The great development of the pharynx and the reduction of the tail to an organ of locomotion soon resulted in a pronounced change, of the sort for which Dana long ago proposed the term *cephalization*.

As the functions of the pharynx, and of its oral end in particular, became more and more complicated and more and more exactly co-ordinated, while those of the tail became simplified, the elongated nervous system became differentiated in a corresponding way, and its caudal portion became reduced to a caudal nerve, while its oral extremity became evolved into a cerebral vesicle with sense-organs and nerves in relation with the co-ordinated structures of the pharynx.

All the characteristics of appendicularia, except the structure of the heart and the structure and position of the reproductive organ, are thus seen to be intelligible as direct adaptations to a pelagic life; for its distinctive features, as compared with other primitive

chordata, are the U-shaped folds of the digestive cavity, the sharp separation of the tail from the body, and the differentiation of the nervous system into a caudal nerve and anterior vesicle.

We have little basis for speculation as to the path by which the reproductive organ acquired its present position, and it is by no means certain whether the tunicate heart is homologous with that of the other chordata.

The conditions of pelagic life are so permanent that we may safely make use of the structure and habits of the modern pelagic forms to reconstruct this part of the ancestral history of the tunicates, for time writes no wrinkles on the azure brow of the ocean.

As regards the later history the case is different. Between appendicularia and the ascidians there is a great gap which we can bridge only in imagination. The transitional animals are totally unknown, and the conditions of life on the bottom of the modern ocean may, possibly, be very different from those which prevailed when the fixed ascidians were first evolved.

It is easy to imagine changes which might have gradually converted an ancestor like appendicularia into a descendant like the fixed ascidians, through successive adaptations to a sedentary life, but in the absence of all evidence we cannot feel implicit confidence that the imaginary picture bears any minute and detailed resemblance to the actual history.

It seems probable that after the bottom of the ocean became fit for life, some of the descendants of the primitive pelagic tunicates gradually acquired the habit of sometimes swimming upon or near it in an inclined position with the mouth downwards to suck up the organic sediment, and that they also acquired the habit of resting upon the bottom in this position.

We may well doubt whether these animals obtained any more food than their pelagic ancestors, but it is well known that it is not the amount of food, but the ratio between the supply and the amount of expended energy which affects size. As this new habit economized energy both during rest and during activity, it permitted an increase in size, and it is interesting in this connection to note that Chun has found at great depths appendicularias which may well be called gigantic as compared with all which are known to exist at the surface.

With each increase in size, the habit of visiting the bottom must itself have become more and more fixed, until the life upon the bottom, which may have been at first only intermittent and more or less accidental, at last became established in the ancestors of the ascidians as a constant characteristic peculiarity.

As this new mode of life was gradually acquired, some method of aerating the fluids of the body must also have been gradually evolved; for without it, a minute animal adapted for a free active life in the highly aerated surface-water, could not, at the same time that it grew larger, acquire a less active habit of life in the bottom strata where the water is less perfectly aerated, the products of decomposition of organisms more concentrated, and the capacity for passing from exhausted and impure water to a fresh environment, restricted both by the more stationary habit and by the fact that life in space has been exchanged for a home which is limited by a surface.

Undoubtedly the change of habit was accompanied by the gradual perfection of the system of blood-spaces around the pharynx, which, at first indefinite and irregular, became constant on the margins of the pharyngeal clefts, which thus gradually acquired a new function and became gill-slits, and also became duplicated as the animals grew larger and the need for more perfect respiration increased with their change of habits.

I hope that no one will interpret the last sentence as an expression of the belief that the need for respiration caused the gill-slits to multiply. I believe, and shall try to show further on, that the tendency to duplicate a structure, either radially, bilaterally or serially, is a result of the method of growth by cell multiplication, and that in the case in question the serial reduplication has been fixed and preserved by natural selection on account of its value in respiration.

The context shows that I also regard the gill-slits of vertebrates and those of tunicates as homologous structures inherited from a common source, the primary pharyngeal clefts; but that I regard the increase in their number as a secondary change which has occurred in both lines after their genealogical paths had diverged.

It does not seem necessary to defend the thesis that the number of gill-slits in the ascidians is the result of secondary multiplication,

since, as I shall show further on, it is accepted by Dohrn (*Studien*, etc., IX, 417), who has proved himself a most rigorous critic of the logic of morphology.

There is reason to believe that the multiplication of gill-slits in the tunicates has not only taken place independently, but that it has taken place in a peculiar way. Anatomy and embryology give evidence that while the perforations of the tunicate pharynx multiplied, the perforations of the outer wall of the body did not; and that the external portions of the two primary clefts became distended into a pair of spacious perithoracic chambers, each with numerous ciliated openings into the pharynx, and a single opening to the exterior which perhaps became enlarged as the gill-slits multiplied.

So long as the primary function of the first pair of pharyngeal clefts, the discharge of the superfluous water, was the only one, they probably remained circular like those of appendicularia; but as they became concerned in respiration and increased in number, and were furnished with definite blood-vessels, they became elongated vertically and, forming a series side by side over a considerable area on each side of the pharynx, they thus became much more efficient organs for the aeration of the blood.

In this simple way metamerism, that fetish of the morphologists, was established among the tunicates, and there is no evidence that it has ever involved any of their organs except the gill-slits and the pharyngeal blood-vessels.

A vertical series of slits, elongated longitudinally, would undoubtedly have permitted the water to escape just as well as a longitudinal series elongated vertically, but it is possible that, during the gradual establishment of the respiratory circulation, those of the irregular and variable blood-spaces which were most nearly transverse to the current of water from the mouth to the primary clefts, were the ones which were first made definite by natural selection, and that the arrangement of the gill-slits was thus determined.

We can only conjecture how this unknown ancestral swimming organism first became fixed, but the discovery of its descendants on the modern sea-floor is among the possibilities of future explanation.

The sedentary habit undoubtedly came gradually, and at first it may have been temporary, confined perhaps to the breeding season,

when, loaded down with eggs, the animal may have learned to rest upon the fragments of crinoids, or the shells of trilobites or brachiopods or molluscs, to avoid clogging its delicate ciliated and vascular pharynx with sediment. At the point where the heavy anterior end of the tadpole-shaped body rested, the ectoderm cells, just below the mouth, probably became modified for the excretion of an adhesive cement.

The sedentary habit, which must have resulted in a still greater economy of energy and a corresponding increase of size, undoubtedly became more and more firmly established, and the changes which followed and resulted in the evolution of the ascidian type are easily intelligible as adaptations to a fixed home, although we have little to show the sequence of their acquisition.

So long as the animal led a free life the fate of the deoxidized water after it left the gill-slits had no meaning, but with the fixed habit came the need for driving it away as far as possible, and the external apertures of the perithoracic chambers became small, moved towards each other, and finally united to give to the exhaled current the strength of concentration. The attitude of the animal upon the bottom undoubtedly determined the dorsal instead of ventral location of the common aperture and of the median atrium or cloaca. As each step in this process of concentration must have been advantageous, its evolution by natural selection is easily intelligible. The accumulation of fæces from the intestine, around a fixed animal, is so unsanitary that the anus has disappeared in many sedentary metazoa, while in others, such as the crinoids and the lamellibranchs for example, secondary adaptations for sweeping away the refuse matter have been acquired.

The folding of the originally straight digestive tract of the primitive chordata into a U with the anus and intestine ventral to the pharynx, took place in the ancestral tunicates as an adaptation to locomotion, but, as appendicularia shows, it incidentally brought the anus into the region of the pharyngeal clefts. As the sedentary habit became slowly established the anus became shifted from the middle line into the exhaled current from the left perithoracic chamber, and finally into the margin of its aperture, so that, during the migration of the exhalent openings, the U of the digestive tract

became twisted into an 8 in such a way that, as Plate VIII, Fig. 2 shows, the intestine  $p$  passed on the left side of the œsophagus,  $g$ , to open dorsally into the atrium, near the middle line, but a little to the left.

This arrangement of the digestive organs is very characteristic of the tunicates, and the few exceptions are clearly due to later changes. Thus in *doliolum* the atrium has moved backwards as an adaptation to locomotion, and the anus has followed it until the gut has become nearly straight. The intestine and anus of the adult aggregated *Salpa pinnata*, Plate I, Fig. 1, are ventral; but I have shown that in the young the intestine crosses to the left of the œsophagus to open dorsally, as it does in the adults of all ordinary salpæ. In the *Polyclinidæ* the loop of the intestine has been elongated, with the elongation of the body, until the bend of the 8 has been obliterated, and the presence of the characteristic 8 in more primitive ascidians such as *clavelina* shows that the *Polyclinidæ* have been more recently modified.

All sedentary animals which take their food by means of cilia have their apertures raised in some way above the reach of sediment. In the crinoids this end is reached by a stalk; in the lamellibranchs it is attained either by siphons, or by the vertical elongation of the shell as in the oyster; and the shifting of the area of attachment of the ascidians from the oral end to the aboral end, the elongation and approximation of the mouth and the atrial aperture, the acquisition of oral and atrial sphincter muscles, the degeneration and disappearance of the locomotor tail, and the simplification of the nervous system, are such obvious adaptations to a sedentary life that it is not necessary to discuss them.

### *Section 3.—The Annelidian Hypothesis.*

I believe that the structure of the tunicates has been acquired as an adaptation to the biological conditions which prevailed at the surface of the primitive ocean, and that it has been evolved by the gradual addition of successive complications on to the body of a still more primitive and simple ancestor. This involves the total rejection of the dogma that the vertebrates are modified annelids, and that the tunicates are degenerated vertebrates.

While it is not my purpose to discuss the ancestral history of the vertebrates, the remote phylogeny of the tunicates is unquestionably identical with that of the other chordata, and I cannot ignore the general acceptance of an opinion which is absolutely irreconcilable with the one which I have presented.

This prevailing opinion has interwoven itself with the literature in such a complicated way that one may well shrink from the interminable labor which the critical revision of the whole of it would involve. I myself decline to undertake what I regard as an unprofitable and useless task; unprofitable, as the literature rests on an untenable and false basis, and useless, since I do not hope to induce those who have stored their minds with the endless details of morphology docketed and pigeon-holed according to a false system, to unload all this rubbish and to build again on a new foundation.

I shall therefore restrict myself to a discussion of the origin of the two most characteristic systems of tunicata organs, the gill-slits, and the pharyngeal ciliated cells and gland cells; and I shall here confine myself to the observations and reflections of a single writer, Dr. Dohrn.

I make this selection the more willingly, as Dohrn's name is most intimately associated with the annelidian hypothesis, and because his writings are not only the ones which have been most influential, but also the ones which are most comprehensive and most attractive to the reader.

The "*Ursprung der Wirbelthiere*" is a most fascinating book. Soon after it appeared I placed it in the list of works which my students are advised to read, and for many years an acquaintance with it has been expected of all who have been examined for the degree of Ph. D. in the Johns Hopkins University.

My students have even prepared for their own use an English translation of it, and I have read it with them several times with interest and pleasure. At the first reading my pleasure was almost that of conviction, but as the ingenious details became familiar, and the essay was more sharply focused in its completeness, and was held, as it were, at arm's length, so that the whole picture could be seen at one view, I have read it, as I have read Gulliver's Travels, with admiration for the skill which has elaborated it in

such logical minuteness from a fundamental assumption which is purely imaginary.

The story, as told by Dohrn in the "Ursprung," is so consistent and logical that I see no reason why animals like the tunicates might not have been evolved in the way which he pictures so vividly, although I believe that the actual tunicates have been produced in a very different way.

I shall therefore examine the account of the origin of the gill-slits which Dohrn gives in the "Ursprung," and the view of the ciliated and glandular structures of the pharynx which is developed in his "Studien," especially in Parts VII, VIII and IX, in order to determine how far the origin of these structures is accounted for by the annelidian hypothesis, and what superiority, if any, this has over the much simpler hypothesis which is here advanced.

Dohrn says (Ursprung, p. 10) that the branchial apparatus of the tunicates and that of balanoglossus *are so much more complicated* than that of the selachians, and their origin is so much more difficult to understand, that they are of no help to us in our attempt to trace the origin of gill-slits.

I am quite at a loss for the meaning of this passage, for no secondary perforation of the pharynx could possibly be less complicated than the gill-slits of appendicularia, nor could it be developed in a simpler way than by the involution of a pit on the side of the body.

It is quite true that we do not know how the gill-slits of appendicularia first came into existence, or what influence led to their formation, but their usefulness as channels for the escape of the water which, before they were formed, must have passed through the intestine, is clear, and we can understand why they have been preserved, by natural selection, on account of this advantage.

We are forced to believe that the pharynx did, in some way, acquire a secondary communication with the exterior, although we are not able to say how it was acquired.

Dohrn's view of the origin of gill-slits is based upon the need for an explanation of the original formation of the perforation. He says (Ursprung, p. 10): "What is a gill-slit? Perforations of the body-wall do not take place directly, and still less do they form connections with corresponding perforations of the digestive tract,"



and he therefore undertakes to study the origin and primitive function of gill-slits by the aid of the law of the change of function, and to find in a more primitive function an explanation of their present function as channels for water.

As his point of departure is the need for an explanation of the origin of the perforation, we feel a natural hope that we are to be led to this explanation, but this hope ends in disappointment.

He regards the gill-slits as modified segmental organs, but he tells us explicitly, on page 10, that "we are not able to assign any reason why segmental organs should unite with the gut," and his explanation of the origin of the perforations is no explanation at all, since it simply assumes, but does not account for, the very phenomenon which it is supposed to make clear.

His inability to understand the direct origin of the secondary perforations of the gut has one most remarkable result, for the view that the gill-slits are segmental organs involves the view (Ursprung, p. 57) that the anus of the tunicates is not a primary anus nor a secondary one, but a tertiary one, and that the ancestors of the tunicates have not only acquired two new secondary anal apertures, but that they have lost one mouth and acquired a second, and that they have lost this and acquired a third. As these mouths are supposed to be modified segmental organs, we are, according to the acknowledgment on page 10, "unable to assign any reason why they should have united with the gut."

The original mouth of the ancestors of the chordata was, according to Dohrn (page 3), on what is now the dorsal surface, and the primitive œsophagus passed through what is now known as the fossa rhomboidea of the brain.

This ancestral mouth degenerated and disappeared as it was gradually superseded in the remote progenitors of the vertebrates by a second mouth (page 5), which is the mouth of the vertebrates of the present day, and of the ancestors of the tunicates (page 57) as well, although it was gradually converted first into a sucker, and finally into an organ for fastening the tunicata to foreign bodies, while these animals gradually acquired a tertiary mouth (page 58) by the formation of a secondary communication between the nasal chamber and the gut.

Dohrn says (page 60) that these assumptions "set the relation between the fishes and the ascidians in the right light," although the perforation of the gut, which the hypothesis is to explain, is not only left unaccounted for, but is multiplied so many times that, like the man with an unclean spirit, its last state is worse than the first.

Dohrn says that the secondary nature of the mouth of the vertebrates is proved by its very late appearance in the young vertebrate after its embryonic body and its great systems of organs are fully formed, and by the fact that, when it does make its appearance, it does not lie at the anterior end of the body, in the place which it finally occupies in the great majority of vertebrates, but at a spot some distance behind this place.

It is not possible to attach much weight to either of these arguments, for slight changes in the position of organs are not unusual, and it is well known that the ontogenetic acceleration or retardation in the relative time of appearance of structures is by no means exceptional, and it would be as safe to assume that the change in the pitch of the voice of man is phylogenetically older than the sexual maturity of the ancestors of man, as it is to assume, from the same sort of evidence, that the aortic system of vertebrates is older than the mouth.

The vertebrate mouth unquestionably bears a great morphological resemblance to a pair of gill-slits. As Dohrn points out, it is bordered, like the gill-slits, by a pair of visceral arches, it lies in front of the first pair of true gill-slits, it arises at the same time with them in the embryo, and like them it opens into a section of the gut.

A ventral view of a shark shows the resemblance between the mouth and the true gill-slits in the most impressive way, and if any pair of them were to be united with each other at their ventral ends, they would become perfectly equivalent to the mouth. The armature of the mouth is repeated on the gills, and there is reason to believe that the jaw-arches have at one time carried gills like the gill-arches.

This resemblance is not imaginary. Beyond all question it is real, and it is certainly most remarkable and suggestive, but does it prove that the vertebrate mouth is phylogenetically a pair of gill-slits?

When, in my student days, my instructor held before me the skull of a turtle and called upon me to observe the centrum, the transverse processes and the neural arch of the occipital vertebra, I was, for the time, convinced that the occipital bone had arisen by the differentiation and specialization of a bony vertebra, like those in the neck of a turtle, and that its history had been identical with that of the thoracic vertebrae, which have been differentiated and specialized in the same way into constituent parts of the bony box which covers the body of the turtle, as the skull covers the brain.

In all these cases the morphological resemblance is undeniable, but our opinion of its phylogenetic significance depends upon our view of the nature and origin of the metamerism of vertebrates, a question which will soon be discussed.

At present we must confine ourselves to a narrower point of view, and learn where we are led by Dohrn's opinion that the vertebrate mouth is actually a pair of gill-slits.

If the present mouth of the vertebrates was once a pair of gill-slits, the ancestors of the vertebrates must have had at that time another mouth, and during the long series of stages of development, while the gill-slits were gradually assuming the function of a mouth, food must have been taken in through both openings; for the new function of the gill-slits must have been acquired slowly alongside their old function, until the new mouth finally became so perfectly adapted for its new function that it supplanted and replaced the old one.

According to Dohrn, these considerations force us to believe that the primitive mouth of the ancestors of the vertebrates and of the tunicates was situated in the fossa rhomboidea, where an œsophagus pushed inwards to join the mid-gut, in the same way that it is joined in insect embryos by the fore-gut. This primitive mouth and its œsophagus were homologous with the corresponding organs of modern arthropods and annelids. The mouth of the modern vertebrates is then to be regarded as a secondary mouth, which has gradually supplanted and replaced the old one on account of its greater efficiency.

It follows from this, according to Dohrn (p. 56), that the "so-called larva" of the ascidians is a degenerated fish, and that all the features which show the derivation of the cyclostomes from

the fishes show also that the process of degeneration has reached its extreme in the tunicates. The cyclostomes are held to owe their degeneracy to parasitism, and the most important element in the more advanced process of degeneration is that the ascidians no longer fasten themselves to fishes nor make use of their bodies as food, but that they fasten themselves to stones, to ships, or to the bodies of other animals which do not serve as food, such as the shells of crabs or the tubes of annelids.

The mouth (p. 57) which in the cyclostomes serves both as an organ for attachment to the skin of fishes, and also as a sucker for extracting their blood, has become converted in the ascidians into an organ for attachment; and these animals have thus lost their old mouth, which was homologous with that of the true vertebrates, and have acquired a new one which is homologous with the vertebrate nasal chamber.

The process, Dohrn says, must be represented as follows: The fishes take in the water for respiration through the mouth, but as this is used by the parasitic cyclostomes as a sucker, they have acquired another arrangement, and the water is not only discharged through the gill-slits, but is also inhaled through them, and, in the myxenoids, through the nasal passage also, which has in the tunicates become the functional mouth. The vertebrate mouth has lost its old function in the cyclostome-like ancestors of the tunicates, as these have gradually lost their parasitic habit, and have established themselves on lifeless bodies; but the original lips have remained, and they are to be recognized in the so-called sucking knobs of the ascidian larva, while the teeth of the cyclostomes are supposed to be represented by "bristle-carrying end knobs" upon the suckers.

The "so-called larva" of the ascidians is represented in almost every feature of its organization by the adult, sexually mature, appendicularia. No better example of the correspondence between an adult animal and an ontogenetic stage in the history of another can be desired, and we may feel confident that, whatever the phylogenetic history of appendicularia has been, that of the ascidian larva has been the same.

Nearly all of the students who have devoted themselves to the study of the tunicates agree in regarding appendicularia as a per-

sistent representative of their primitive condition ; but appendicularia is an active swimming organism, and I have shown that its simple structure is so well adapted to the needs of its pelagic life, that there can be no inherent improbability in the view that it owes its origin to simple pelagic influences.

Nothing whatever in its habit of life or in its structure lends the least support to the view that it is a degenerated animal, and if we accept it as evidence, we are forced to believe that, far from being the fixed and degenerated descendants of parasitic vertebrates, the tunicates are descended from free, active, pelagic animals of very simple structure and minute size.

Even Dohrn seems to admit that the ancestors of the tunicates were swimming animals, for he tells us in support of his view of the homology of the endostyle (Studien, etc., VIII, p. 62) that the ancestors of the tunicates were "obviously" free swimming animals, and therefore in the position to seize their food by hunting. "Offenbar waren sie frei schwimmende Geschöpfe und damit in der Lage, ihre Nahrung durch Jagd selbst zu packen."

If the tunicates are, as their embryology and comparative anatomy indicate, the descendants of an ancestor which was *obviously* a free swimming animal, it is surely simpler, in view of all the facts, to regard the gill-slits as perforations which were originally retained and fixed by natural selection as channels for the exit of the water which was taken into the mouth with the food, than to refer them back to imaginary segmental organs which have left no other trace of their existence in the body of any known tunicata.

Minute pelagic animals, with soft bodies bathed on all sides by pure water, do not need special organs of excretions or respiration, and it is not at all probable that the pharyngeal clefts were originally respiratory ; but it is easy to understand how the channels through which the water flowed became converted into gill-slits, in accordance with the law of change of function, as the descendants of the primitive tunicates grew larger and became sedentary, and thus came to need respiratory organs.

It may be argued that the thing to be explained is not the existence of gill-slits, but their serial reduplication or metamerism. It may be held that the metameric repetition of the gill-slits of ascidians forces us to regard the ascidian pharynx as the primitive

form, from which that of appendicularia has been produced by "degeneration." As we are told, however, by no less an authority than Dohrn (*Studien*, IX, p. 417, and VIII, p. 61) that the great number of gill-slits in the ascidians is due to secondary multiplication, "nachträgliche Vermehrung," this consideration need not detain us.

If the logical conditions of sound morphological philosophy admit the possibility of "nachträgliche Vermehrung," and permit us to believe that the twenty or thirty pairs of gill-slits which are found in ascidians are to be traced back to the eight pairs which the primitive fishes are said to have possessed, the same logic will surely permit us to believe, on sufficient evidence, that they have arisen not from eight but from a single pair like those of appendicularia.

All the vertebrates have a peculiar organ known as the thyroid gland, and while it holds no prominent place in our general conception of a vertebrate, this gland is actually one of their most constant and characteristic organs.

In all the jawed vertebrates, from the sharks up to man, its typical structure is adhered to so closely as to prove that the gland as it exists in man is an <sup>2</sup>organ of vast antiquity. In all these animals it is a ductless gland, situated far back in the throat, behind the hyoid skeleton; but at an early stage in its ontogeny it is a part of the endodermal epithelium of the pharynx, and it arises on the middle line just within the mouth.

Its function in the jawed vertebrates is problematical, but these two features in its ontogeny seem to show that far back in the remote past, before it had assumed its characteristic form, it had another function which stood in some direct relation to the mouth.

The tunicate endostyle is a conspicuous organ which attracts the eye of all observers, but its true structure was first demonstrated by Fol, who proved that it is a pharyngeal gland with excretory cells to produce slime, and with ciliated cells to drive the slime out through the long, narrow, slit-like duct into the pharynx. Fol also showed its true relation to the ciliated peripharyngeal bands and dorsal lamella, and proved by simple but conclusive experiments that these organs are co-ordinated parts of a single system, which has for its function the capture of the microscopic floating food which enters the mouth with the water.

W. Müller was the first to point out the homology of the tunicate endostyle with the vertebrate thyroid gland, and this homology has been established beyond the possibility of doubt by Schneider's discovery that the thyroid body of ammocetes is a slime gland with an opening into the pharynx near the mouth, and that on each side of this opening a ciliated furrow or peripharyngeal band runs upwards on the inner wall of the pharynx, just in front of the first gill-slit, to its dorsal middle line, where the two unite to form an epipharyngeal band or dorsal lamella which runs backwards to the œsophagus. Even more conclusive proof of this homology is afforded by Dohrn's account (*Studien*, VIII) of the histological structure of the pharyngeal gland of ammocetes, for his studies show on the one hand a most complete fundamental identity with the very peculiar and characteristic histological structure of the tunicate endostyle, and they also, on the other hand, prove its identity with the vertebrate thyroid gland, by showing that, as development progresses, it is cut up by ingrowths of connective tissue into the isolated follicles which are so characteristic of the thyroid gland. Still further confirmation is furnished by Dohrn's discovery in the torpedo embryo (*Studien*, VIII, p. 60) of two endodermal grooves which run from the ventral margins of the spiracles to the ventral middle line of the pharynx, to end at the median unpaired thyroid invagination in such a way as to prove that they are rudimentary peripharyngeal grooves.

This most remarkable homology can no longer be questioned. The simplest explanation, and the one which first presents itself, is the one which Müller advances, that the common ancestor of the tunicates and of the other chordata, possessed this system of organs in the form in which we now find it in the tunicates, and that while all the jawed vertebrates have inherited the ventral pharyngeal gland, it has been turned in them to some new use, as yet undiscovered by the physiologists, and has lost its primitive connection with the pharynx and its functional relation to the mouth, and has become a ductless aggregation of follicles far back in the throat.

I have tried to show that the structure and anatomical relations of this system of organs in the tunicates are quite consistent with the view that it was originally acquired for the purpose which it now serves, the capture of food.

The simplest explanation of its origin is that which attributes it to the preservation by natural selection of a long series of slight changes, each of which improved the adaptation to the simple conditions of primitive pelagic life.

Dohrn disputes this position, and says that "many persons would have great difficulty in believing that this simple mechanism is primitive" (Studien, VIII, p. 62). The future must show how many of these persons there are, but I shall now lay before them Dohrn's own explanation, that they make comparisons for themselves.

"We ask," he says (p. 62), "how the ancestors of the tunicates obtained their food before the endostyle was formed. Obviously they were free swimming animals, and therefore in the position to seize their food by hunting. It is as certain that they needed other contrivances than the ciliated furrows and the slime-gland, as it is that the ancestors of the cirripeds sought food in some other way than by the formation of little vortices to sweep into their mouths everything within their influence. The limbs of the swimming forefathers of the cirripeds were certainly different from the cirri of modern barnacles; even so were the ancestors of the tunicates differently constructed from the modern ones, and before the slime-gland and the ciliated grooves became the exclusive means of nutrition, they must have been the accessory aids to some more primitive mode of capturing food" . . .

"*Ammocoetes* lives in the sand, into which even the youngest larvæ bore. Although direct observations fail, it must be assumed that the excretion of slime and the ciliation have some advantage in the nutritive or respiratory functions of organisms which live in the mud. May we not believe that, in spite of all the sifting through the oral tentacles and the velum, the hard particles of sand would be injurious to the delicate epithelium of the gut, if this were not protected by a thick coating of slime; that the ciliated furrows are adapted for conveying this slime to the most exposed parts, and that, in this function, they have their starting-point? Once brought into existence, it is not remarkable to see these useful structures further evolved until the whole mass of food is invested with a slimy admixture to facilitate its passage through the gut. It is not impossible that besides acting mechanically as an invest-



ment, the slime also acts chemically as an aid to digestion. If this is the case, it is easy to understand how a peculiarity so useful to sedentary animals like the ascidians, or to floating ones like the salpæ, gradually assumed the whole function of nutrition. Thus the problem of the change of function is solved."

Although it seems as if the delicate walls of the gut of a burrowing animal would be more effectively protected if slime were directly excreted "upon the most exposed spots," than by this highly specialized system of organs, we might yet believe that the system "has its starting-point" in the habits of ammocetes, if we did not find in the structure and embryology of every chordata animal which is known to exist evidence of descent from an ancestor in which it had attained, not a starting-point merely, but its full development.

The ontogenetic evidence that the vertebrate thyroid body was at one time a pharyngeal gland opening just within the mouth, and the discovery by Dohrn of rudimentary peripharyngeal grooves in the torpedo embryo (Studien, etc., VIII, Plate H, Figs. 7f, 7g, 7h and 7i), seem to me to be convincing proofs that the organs did not have their starting-point in the habits of ammocetes nor in any degenerated fish, but that they arose in a lineal ancestor of the selachians and of the higher vertebrates, which was also an ancestor of the tunicates and cyclostomes.

Passing now from the biological relations of the system of the endostyle to its homologies, we are told by Dohrn that it is equivalent to two pairs of gill-slits; that these gill-slits were present and functional in the fish-like ancestors of the cyclostomes and tunicates, and that two of them, the mandibular clefts, moved downwards and met on the ventral middle line to form the thyroid gland or endostyle, while the endodermal portions of the others, the spiracular clefts, lost their connection with the exterior and became converted into the peripharyngeal grooves (Studien, etc., VII and VIII).

Homologies are expressions of genetic relationship, and Dohrn tells us (p. 79) that they are valuable in phylogeny only as they furnish us with the opportunity to pass from the consideration of the structure of organs as they now exist, and of the functions of these organs at the present time, to the consideration of conditions

which have passed away ; to the study of the history of the modifications which have come between these structures and functions, and those which we must attribute to the same organs at an earlier genealogical stage.

I regard the structures which we find in the tunicates and in ammocetes as primitive, and as homologous with those which we find in the jawed vertebrates ; and I have tried to trace the history of the modifications which have come between these structures of modern vertebrates and those which we must attribute to the same organs at an earlier genealogical stage in the primitive history of the ancestral pelagic chordata. The reader must judge of my success.

Let us now see what light Dohrn's homology throws on the history of these primitive modifications. He tells us (*Studien*, etc., VII, p. 47) that he will point out, further on, the significance of the changes which have led to the fusion, on the middle line, of structures which were originally paired ; but I have been able to find nothing more upon this point except the acknowledgment, on page 63, that "I frankly admit that I have at present no available argument to bring the peculiar organization (of the ciliated grooves) of ammocetes from a pair of imperforated (spiracular) gill-slits, into accordance with the concept of change of function ; and that the origin of the slime-gland of ammocetes from two ventrally fused (mandibular) gill-slits must for the present remain an unsolved problem."

Whatever may be thought of my own view, it must be admitted that Dohrn's homology of the endostylic system with two pairs of gill-slits has very little phylogenetic value, even when measured by his own test : the opportunity it furnishes for passing from the structure and functions of modern organs to the history of earlier genealogical stages.

Dohrn's memoirs upon the thyroid body are full of interesting anatomical details, such as the similarity between the thyroid body of the shark embryo and the true gill-slits, in their relations to the cartilages, to the muscles and to the blood-supply (VII, p. 44) ; and the resemblance between the peripharyngeal grooves of ammocetes and the spiracular gills of selachians (VIII, p. 55) ; but as he admits that the annelidian hypothesis leaves the origin of the endostylic structures of tunicates an unsolved problem, our subject,

the history of the tunicates, does not require us to enter into the discussion of these complicated details of vertebrate morphology.

The considerations which I have presented will undoubtedly be met by the assertion that while the simple and direct origin of the tunicates seems plausible so long as we confine ourselves to these animals alone, such a restricted view is unscientific. I shall no doubt be told that we are forced by more fundamental evidence to believe that the body cavity of the chordata is, in ultimate analysis, a segmented enterocœl formed from a series of pairs of gut-pouches, and that the simplicity of appendicularia cannot be primitive, inasmuch as the ancestors of the tunicates once possessed these complicated structures.

The first step to take in discussing this objection is to learn whether there are any traces of gut-pouches in the tunicates.

Seeliger (p. 9) has given us a very minute and detailed account of the history of the mesoderm in the clavelina embryo, and has shown that it arises from two rows of endoderm cells which give origin, in the tail, to the caudal muscles and, in the body, to free mesoderm cells which multiply with great rapidity and wander everywhere through the body cavity, which is bounded on one side by the endodermal wall of the gut, and on the other by the ectoderm.

He says emphatically (p. 128) that the mesoderm arises as two *totally unsegmented* rows of cells, each forming a single layer; that the body cavity is not an enterocœl, but a *primary body cavity*; and that the ontogeny of the tunicate mesoderm gives no evidence of derivation from paired pouches comparable to the cœlomic pouches of amphioxus.

It is a rare thing for students of tunicate morphology to agree, but in this case the phenomena are simple, and Davidoff (p. 16) completely confirms Seeliger's observations, so far as they bear upon the question, by his own studies of clavelina and distaplia.

His account of the origin of the mesoderm differs from Seeliger's in only one minor point, which has no bearing upon the question under consideration. Like Seeliger, he derives the mesoderm from two rows of endoderm cells, but he says that these cells remain as endoderm cells after they have given rise to the mesoderm, while Seeliger states that they become converted into the mesoderm.

In all other respects Davidoff's observations are a complete confirmation of Seeliger's, for he says (600) that in distaplia the mesoderm of the caudal region persists as a solid rudiment and becomes the muscular layer of the tail, while elsewhere it breaks up into wandering mesenchyma cells. "It is to be particularly emphasized that in no part of the mesoderm is *any trace of segmentation* to be discovered, and that there is not the least indication of any cavity comparable to a myocœl. The embryonic history of the mesoderm of distaplia cannot be referred back in any way whatever to anything comparable to Hertwig's conception of the enterocœlomata."

Of clavelina he says (607): "There is not even a transitory division of the mesoderm into a somatopleur and a splanchnopleur. Even where the mesoderm is two-layered, so that a parietal and a visceral layer may be distinguished, there is no homology between these layers and the bounding walls of the cœlom of the enterocœlomata."

After reviewing all the literature on the subject, he gives as the general result of his studies the statement (p. 622) that "the body cavity of the ascidians lies between the two primary germ layers and must be regarded as a blastocœl, which would be identical with the segmentation cavity if this were not temporarily obliterated during gastrulation by the contact of the ectoderm cells and endoderm cells."

While the salpa-embryo is very complicated and unfavorable for studying this question, my own observations, which have already been described, seem to show that the body cavity of salpa is, like that of clavelina and distaplia, a primary one, fundamentally identical with the segmentation cavity, and that the mesoderm arises as free mesenchyma cells derived from the endodermal blastomeres.

The body cavity of the salpa-embryo is identical with the space between the somatic and visceral layers of follicle cells, and while there is a stage in which these two layers are in contact, the follicular cavity is undoubtedly the same as the cavity shown at 15 in Plate XI, Fig. 3, of my memoir on salpa, and this is the same as the space which is shown in Plate X, Fig. 3, between the segmenting egg and the follicle.

In the chapter on the significance of the salpa-embryo I have given my reasons for believing that this space is homologous with the segmentation cavity of more normal tunicate embryos, and if this view be correct the body cavity of salpa is not an enterocœl but a primary body cavity or blastocœl. The mesoderm of salpa consists of free migrating cells, and the chamber of the heart is part of the body cavity, so that these cells pass through it; and while salpa is a peculiarly unfavorable subject, my observations are in complete accord with those which Seeliger and Davidoff have made under simpler and more favorable conditions.

No student of the embryology of tunicates has ever described any trace of a *series* of body cavities, and Kowalevsky, the discoverer of the cœlomic pouches of amphioxus, failed to find anything comparable to them in the tunicates, although the existence of a single pair of enterocœls has been claimed by certain observers. Van Beneden and Julin (*Zool. Anzeiger*, 4, 1881; *Bull. Acad. Belg.* (3) 7, 1884; *Arch. Biol.* 6, 1884) believe that the anterior portion of the body cavity of ascidians arises as a pair of gut-pouches, and that its mesoderm consists of a somatopleur and a splanchnopleur, but Davidoff has shown by careful serial sections that this statement is probably based upon erroneous observations.

Salensky holds (17, 460) that the mesoderm of the blastoderm of pyrosoma consists of two symmetrically placed cœlomic pouches, and that pyrosoma is, therefore, to be placed among the true enterocœlomata. The space between the vertebrate blastoderm and the yolk is undoubtedly homologous with the enteron, but it is by no means certain that this is the case in pyrosoma, where the food-yolk is an independent acquisition; nor do Salensky's figures show, as clearly as we might wish, that the two cœlomic vesicles open into this space, and even if this is the case, we must remember that the pyrosoma-embryo is very aberrant, and that the structure of its body cavity may be a secondary adaptation to the presence of the yolk. Taken alone it certainly is not enough to prove, without corroboration from other sources, that the body cavity of the tunicate is an enterocœl.

The ontogeny and homology of the tunicate mesoderm have been recently discussed at very great length by Seeliger (11, pp. 85-104 and pp. 126-131), by Davidoff (16, pp. 592-628), and by Salensky

(17, pp. 456-462 and pp. 468-470 and 36-46), and as those who wish can find in these papers an extended presentation of the complicated and perplexing theory (?) of the mesoderm, I have attempted to treat it very briefly.

The literature shows that there is no direct evidence whatever of the existence, at any time in the history of the tunicates, of a metameric series of cœlomic pouches, and the supposed necessity for believing that such a series existed in the primitive chordata is only another aspect of the dogma that the metamerism of the vertebrates must have been inherited from a primitive metameric ancestor.

If, as I believe, the metamerism of vertebrates is secondary, the metamerism of the mesoderm and body cavity may have resulted from the duplication of a single pair of cœlomic pouches similar to those of echinoderm larvæ, and it is quite conceivable that these may have been acquired by the ancestors of the vertebrates after the divergence of the tunicates.

If, however, future research should show that there is a pair of gut-pouches in the embryo of appendicularia, or should prove in some other way that the structures which Salensky describes are true enterocœls inherited from an ancestral tunicate, such a discovery, which is certainly among the possibilities, would be no evidence that the primitive tunicate was the degenerated descendant of an ancestor with metameric gut-pouches.

At present, however, the evidence all tends to show that the ancestors of the tunicates had no such structure, and that the presence of cœlomic vesicles in pyrosoma is an adaptation to its peculiar mode of development.

As these chapters from my memoir on Salpa are passing through the press for the second time, I take this opportunity to refer briefly to a paper which has appeared in the meantime by Willey (Studies on the Protochordata, Q. J. Mic. Sc., Jan. 1893, pp. 317-360).

While the author seems to agree with me in rejecting Dohrn's view that the tunicates are degenerated fishes, he holds that the ascidians exhibit, during their development, certain features of resemblance to other primitive chordata which are not exhibited by appendicularia; and he believes that these characteristics prove that the ascidians are more closely related than appendicularia to these protochordata.

The features upon which he lays most emphasis are these: I. The endostyle is at first vertical and pre-oral; II. The organ of fixation is a pre-oral lobe, and its cavity is the pre-oral or anterior body cavity; and III. The first four primary stigmata of *Ciona intestinalis* are developed from one primitive gill-slit; the first and fourth representing the two halves of one slit separated by the precocious development of a tongue-bar, while the third and fourth are formed by constriction from the first and fourth. The six primary stigmata are actually equivalent to three gill-slits, and the innumerable branchial stigmata of the adult are formed by subdivision of the primary stigmata and not by new perforations.

I cannot believe that students of the tunicata will regard the first and second of these arguments as entitled to the least consideration. It has long been known that the endostyle of ascidian larvae is at first vertical or at right angles to the long axis and it is so figured and described by Seeliger, but the relative position of organs is so much influenced by changes in other organs that we cannot attribute a phylogenetic significance to the position of the endostyle. The mouth is formed very late in ascidian larvae, and as the oral region of the pharynx is rudimentary when the endostyle is formed, this latter organ does not occupy its true position until the floor of the pharynx is pushed downwards by the development of the oral region. That this is the true explanation of its change of position is shown by the fact that when the mouth continues to enlarge, as it does in the nutritive zooids of *doliolum*, the endostyle is pushed past its horizontal position until it finally becomes turned upside down with its long axis again at right angles to the long axis of the

body, but with its oral end below, instead of above as it is in ascidian larvæ. See, for example, *Doliolum und sein Generationswechsel*, by Grobbin. Plate IV., Fig. 19.

Seeliger's carefully drawn figures of the organ of attachment of the young clavelina (*Jenaische Zeitschr.*, XVIII, 1885, Plate 4, Figs. 40, 41, 42 and 44) show that it is at first represented by three distinct and separate tracts of cylindrical ectodermal gland cells, p. 36, ventral to the place of the future mouth, and it is only necessary to read his minute account of its ontogeny, p. 36 and p. 52, to see that its embryonic history is exactly what we should expect it to be if it has been directly acquired as an organ of fixation. If the phylogenetic history of the fixed ascidians has been as I have pictured it, each successive stage in Seeliger's account of the ontogeny of the organ of fixation is a recapitulation of a useful stage in its ancestral history, and to my mind, furnishes conclusive evidence that the ascidians are the descendants of swimming tunicates.

Willey's observations add nothing to Seeliger's excellent account of the organ of fixation, and he gives no reason for holding that it is a pre-oral lobe, except that "it contains loose mesenchyma cells derived from the two lateral mesodermic bands." This is equally true of other parts of the body cavity, and there is no more evidence that the organ of fixation is a pre-oral lobe, than there is that it is homologous with the jaws and teeth of sharks.

If it is a pre-oral lobe it is a ventral one, and it cannot be compared with the dorsal one of such protochordata as *balanoglossus* and *amphioxus*.

Willey's observation on the origin of the gill-slits of *ciona* are most novel and interesting and they show that we may look for most valuable results from the study of the subject in other tunicates, but they are not sufficient in themselves to prove that what he has found in one species is typical for all.

It seems to me that the author exaggerates our ignorance of the subject, for while Seeliger's descriptive account of their origin in *pyrosoma* is very short (*Jenaische Zeitschr.*, XXII, 1888, p. 623), his figures show that he has traced their history most minutely, step by step, both in surface views and by sections, and that, in the buds of *pyrosoma*, each gill-slit is an independent perforation, and



that they are formed in succession from in front backwards, as transverse slits without any trace of a U-shaped fold. Salensky has more recently (*Zool. Jahrbücher*, IV, 1891) studied their origin in the primary assidiozooids of pyrosoma, by sections, and has confirmed Seeliger's statement that each slit is an independent perforation. We have pretty satisfactory evidence that this is true of *doliolum* also, and Barrois' observations indicate that it is true of *anchinia*.

The supposed resemblance between the first pair of gill-slits of *Ciona* and a single horseshoe-shaped slit with a tongue bar, comparable to the gill-slits of *amphioxus* is not based upon direct observation, however, for while Willey tells us in his summary, p. 353, that "The four primary stigmata of *Ciona intestinalis* are developed from one primitive gill-slit," we find, on page 322, that "in the actual ontogeny" the two primary gill-slits "arise by independent perforations."

#### THE ORIGIN OF THE CRASPEDOTA.

*This section was intended, when written, to be part of my memoir on the genus Salpa, but lack of room prevented its publication.*

Another group of animals, which, notwithstanding the text-books, I regard as a product of pelagic influences, is the *craspedota*, or so called hydro-medusæ.

The opinion that the hydroid jelly-fish is one of the polymorphic members of a hydroid-cormus, is, like the prevailing views on the origin of the chordata and arthropods, a result from the dogma that the aggregation of units into a compound whole must necessarily be earlier in time than the high evolution of the units.

The blastostyles and macropolyps of hydroids are, unquestionably, modified hydranths, which have arisen, in a cormus, by division of labor, and our first impulse is to believe that the origin of the sexual medusæ must have been the same.

The persistency of this opinion is natural. There seem to be many proofs that the remote ancestors of the hydro-medusæ were sessile, but I shall try to show that none of them are valid.

It may be that the pelagic habit of the acraspeda is secondary, and while the polyps, the craspedota and the acraspeda have unquestionably had a common starting point in a free pelagic ancestor, it is quite possible that the more immediate ancestors of the acraspeda were fixed polyp-like inhabitants of the bottom.

As our opinion of the origin of the medusæ has been evolved under the erroneous notion that the craspedota and acraspeda are very closely related and have travelled the same path in company, it has been assumed that, so far as remote ancestry is concerned, what is true of some medusæ must be true of all.

If the remote ancestors of the acraspeda were inhabitants of the bottom, and if their pelagic habit is a secondary acquisition, it is natural to assume that this must be true of the craspedota as well, although all authorities now agree that the swimming habit has been independently acquired in the two groups, and that the acraspeda teach us nothing of the phylogeny of the craspedota.

Of the four grand divisions of the craspedota, two, the narcomedusæ and trachomedusæ are inhabitants of the open sea, seldom found by the shore collector, and they are so active and irritable and so easily destroyed that general collections of pelagic animals contain few traces of their existence.

While the geryonids are not uncommon near the shore, it is only by oceanic collecting and by research at sea that we can form a just conception of the abundance and diversity and scientific importance of the trachomedusæ and narcomedusæ; and thus the impression has arisen that they are aberrant and exceptional, and that the more familiar leptomedusæ and anthomedusæ and hydroids are the characteristic and typical members of the group.

The hydroid-cormus is a most conspicuous and impressive feature in the life of all our common hydro-medusæ, and in many of them, as in eudendrium, it is everything, and the medusoid structure is so degenerated that its existence is a matter of philosophy, rather than an observed fact.

All these factors have combined, during the historical growth of zoölogy, to give to the hydroid cormus a fictitious value, and this result has been promoted by the fact that many specialists have devoted themselves to the systematic study of the hydra-stage alone, to the neglect of the medusa-stage.

Still more impressive and significant is the fact that all craspedota have a hydra-stage in their life history. Conclusive evidence shows that they are all descended from a hydra-like ancestor.

This undoubted truth has been assumed to involve the belief that this common ancestor was a fixed hydroid-cormus, although this implication is by no means inevitable.

Every one now believes that the hydro-medusa is an expanded and perfected expression of the hydroid type, and that it has been evolved from a simple, hydra-like, starting point, but the writers who have most clearly seen this homology, and who have demonstrated it most conclusively have gone a step further, and have assumed that the locomotor medusa-stage has been added on to the life of hydroids *for the purpose of distributing the species*, and that it has been evolved, according to the law of the division of labor, by the gradual specialization of certain ones among the members of a polymorphic hydroid community.

This view, which seems to have commended itself to all students, and which seems to derive support from the well-known fact that the blastostyles are, actually, nutritive hydranths which have been secondarily differentiated and specialized, by division of labor, in adaptation to the physiological needs of the cormus as a whole, this view has become so firmly established that it is now regarded as a settled and closed question.

I have no hope of effecting any change in views which are so firmly rooted, but I shall now try to show that this established opinion will not stand the test of searching examination.

From the earliest times the very ancient ciliated planula stage has provided for the distribution of coelenterates, and there is no need of other means of dispersal, nor is there any reason to think that the distribution of the species is any less important now than it has been in the past; yet one of the most remarkable and noteworthy peculiarities of hydroids, is the pronounced tendency of the medusa to degenerate and to lose its locomotor habit, and to become a sessil and degraded gonophore. The view that the sessil medusa-buds of hydroids, like hydractinia, are nascent medusæ has, very properly been abandoned, and all morphologists admit that they are degenerated and that their sessil condition is secondary.

I for one cannot believe that hydroid cormi acquired locomotor medusæ to *distribute the species*, and that then these medusæ lost their locomotor habit, and the medusoid structure which they had slowly acquired, and that they sank into sessil, degenerated, bud-like gonophores.

If this degeneration were rare and exceptional, or if it had taken place only once or twice, or if it were an adaptation to any modern change in the ocean it would not be so remarkable, but in reality it is one of the most noteworthy peculiarities of hydroids, and it has taken place over and over again. In every group of hydroids, in the tubularians, in the campanularians, in the hydrocorals and in the siphonophores, there are species or genera or larger groups with degenerated gonophores, and there is ample evidence that this has not been inherited from a common source, but that it has been acquired again and again. Hydractinia, with its sessil degenerated gonophores is clearly related to podocoryne with its free medusa (dysmorphosa). Tubularia with medusa buds is closely related to corymorpha with its free medusa (steenstrupia). Laomedæa stands in the same relation to obelia; bougainvillia to heterocordyla and so on, and by far the best example in the whole animal kingdom of independent modification along parallel lines, is to be found in the degeneration of the sexual locomotor medusæ of compound hydroids. Among the most widely distributed genera and species are some of those in which this degeneracy is most complete, such as the species of eudendrium, hydractinia, laomedæa, cordylophora, and hydra, and I think we may dismiss the idea that the medusa was originally acquired for the purpose of distributing the species, and with it the idea that it has been produced by division of labor, which is disproved by the following facts.

The four great groups of craspedota, the narcomedusæ, the trachomedusæ, the anthomedusæ and the leptomedusæ agree with each other in the possession of a gelatinous bell, a muscular sub-umbrella, and velum, and in the presence of tentacles and sense-organs on the bell margin, and we are therefore justified in assuming that these common structural characteristics were acquired before these groups diverged from each other; that they are older than the modern genera and families, and older than the differentiation of the hydroids into tubularians and campanularians.

Among these are some, the narcomedusæ and trachomedusæ, in which the hydra larva completes its individual development and grows up into a sexual medusa, and others, the anthomedusæ and leptomedusæ, in which there is polymorphic differentiation into hydranths, and sexual medusæ or gonophores. The presumption in morphology, whenever there is nothing which demands the contrary, is that the simple is older than the complex, and we should therefore be justified in holding that the craspedota without polymorphism, where each hydra grows up into a medusa, are more primitive than those with polymorphism, even if there were no positive evidence, and I shall now show that this view is supported by positive proof. Omitting hydra, which is too aberrant and too much isolated to be available for comparison, the hydroids are, almost without exception, larval or sexually immature, and the reproductive persons are all medusæ, or else gonophores which show by their structure that they are degenerated medusæ; even hydra itself is probably a hydroid with gonophores in an extreme stage of degradation. The affinities of hydra are doubtful, however, but in most cases we may state definitely that the hydroid is larval in its sexual nature; and all the hydroids which we know must be traced back to an ancestor with a larval hydra stage and an adult sexual medusa stage; for we must attribute to inheritance from a common ancestor all they have in common except what can be shown to be due to secondary modification.

The question of the origin of the craspedota then narrows itself down to this; was the sessil mode of life, and the habit of forming cormi which has resulted from it, acquired before or after the evolution of the medusa; was the hydra-like ancestor of the hydromedusæ, a solitary pelagic animal as a sessil cormus.

In discussing this question we must keep in mind the following considerations; first, that the history of the polyps and acraspeda has no bearing on the subject, since these animals belong to another line of descent; secondly, we have the very remarkable fact that the sex of all the progeny of a hydroid egg is usually fixed from the start, and is either exclusively male or exclusively female. The egg of a hydractinia may give rise to hundreds of hydranths and machopolyps before it produces blastostyles, and these grow up before they produce medusa buds; the number of medusa buds

which ultimately spring from the progeny of a single egg is very great indeed and practically unlimited, and yet when these buds produce reproductive elements they are of the same sex in all the members of the colony.

This fact is very remarkable when we bear in mind the length of the path from the egg to the sexual bud, and the complicated character of the alternation of generations in hydroids.

One of the most constant results of a sedentary or fixed habit of life is hermaphroditism; and its influence in this direction is so potent that it has, in the barnacles, broken down one of the most ancient and persistent of all the characteristics of animals, the separation of the sexes of arthropods.

If the sessil habit of hydroids were primitive we should certainly expect them to be hermaphrodites and the potential unisexuality of each hydroid cormus would be unintelligible; although it is easily understood if the cormi have arisen by the asexual multiplication of the larvæ of unisexual locomotor adults, for in this case each larva, before it began to form cormi, must have been potentially either a male or a female, and all its progeny, produced by budding, would naturally inherit the same sex, so long as sex remained potential and was not called into activity, for there is no reason why the sedentary habit of larvæ should be followed by hermaphroditism in locomotor adults, nor is there any reason why the sex of larvæ should be modified by a sessil life so long as sex remains latent or undeveloped in the bodies of these larvæ during the sessil stage. It is remarkable that those species in which the gonophores are most degenerated should adhere to the same law, but this fact shows the firm hold which the separation of the sexes has taken upon the organization of hydroids, and is to my mind one of the most conclusive proofs that the sessil cormus is secondary.

In the third place we must remember that the craspedota with a sessil hydroid cormus form only a part of the group; that the trachomedusæ in which, so far as we know, the hydra larva is always a free, floating solitary animal, are numerous and diversified, and that, while the life history of the various narcomedusæ has been greatly modified by parasitism, they may all be reduced to a type in which each egg gives rise to a simple floating hydra-like larva which grows up into an adult like the larva of a trachomedusa.

The structure of an ordinary nutritive hydranth from a cormus, with its funnel-shaped crown of numerous tentacles placed in a circle around the mouth at the oral end of an elongated body, is undoubtedly an adaptation to a life on the bottom, but there is ample evidence that this hydroid type, while the most familiar one, is not the most primitive, nor the one from which the veiled medusæ have been evolved.

Every one who has reared from the egg many species and individuals knows that the hydra which is formed from the planula, shows a marked tendency to pass through a stage with first four and then eight symmetrical, stiff tentacles, so placed that they do not form a crown, since four point forwards and the other four backwards in such a way that they radiate from the body like the pseudopodia of a pelagic rhizopod.

In the simplest and most primitive of the hydroids, the *Codonidæ* or *tubularias*, this larva often has at first, a floating habit, and a distinctive name, *actinula*, has been given to it on account of its star-like shape.

The number of tentacles, like the number of arms in a star-fish, varies somewhat, but they are radially arranged in two alternating sets, and in the majority of the individuals there are four primary radii.

The quadrate structure of young hydroids has been noted by Haeckel, and he points out (*Ueber die Individualität des Thierkörpers*, Jena. Zeitschr., XII, 1878, p. 16) that while the number of tentacles may, at first, have been indeterminate and variable, the early establishment of the number four in the organization of the ancestors of the *acalephs* is shown by the fact that in the young hydra, as well as in many other hydro-polyps, and in the young *actinia* and in many other *acalephs* there are only four primary tentacles.

Haeckel also says that he regards the four-fold condition as primitive for the medusæ, and that all the six rayed and eight rayed medusæ are to be derived from a form with four rays, and that the oral lobes, the primary radial canals and the primary marginal tentacles all lie in the four primary radia. He also gives his reasons for believing that the corals and ctenophores retain traces of this primitive quadrate organization.

Now what does this quadrate structure mean? No one who has watched a pelagic hydro-medusa, as it first swims to the surface, with contracted tentacles, by rapid vigorous pulsations of its bell, and then sinks slowly down, permitting its tentacles to be drawn out by the friction of the water, into long slender threads until they form a living poisoned net, stretched like a spider's web, to entangle the floating organisms of the ocean; no one who has witnessed this can doubt the perfect adaptation of its structure to the conditions of its pelagic life. It does not, like a bilateral organism, pursue its prey in horizontal lines, but it captures it while sinking, and then rises to the surface to repeat the process, and its most important relations to space, are radial to the earth and to gravity while those of bilateral animals are concentric with the earth's surface.

We do not know enough about the biological relations of the medusæ to say what physiological superiority definite radiation has over indefinite radiation, but I think we may feel confident that the quadrate radiation of the hydro-medusæ is an adaptation to a more varied environment than that of a sessil hydra, and that it has been acquired by free animals. In fact the quadrate structure of sessil gonophores is generally accepted as evidence of their descent from free medusæ, and the advocates of the hypothesis of polymorphism attribute the acquisition of the quadrate structure to the free locomotor life of the reproductive persons of the cormus.

If we admit this what shall we say of the quadrate structure of young hydroids? We might see in the four primary tentacles the accelerated acquisition of medusoid characters if the larval hydroid were not in most cases separated from the medusa by the intervention of numerous generations of hydranths with a great and variable number of tentacles.

In the actinula of tubularia and in the cunina larva the proboscis or manubrium is long and the body is short, so that the zone where the tentacles are inserted is more nearly equatorial than it is in ordinary hydranths; and the larva, which is ciliated, is thus more perfectly adapted for a pelagic life.

I shall now show that the quadrate floating hydra and not an ordinary hydranth with an oral crown, is the ancestral type from which hydro-medusæ have arisen.



The *craspedota* of modern times fall into two divergent groups, which must have separated from their common stem very early. In the one group are the *trachomedusæ*, the *anthomedusæ* and the *leptomedusæ*; agreeing in the possession of circular and radial chymiferous tubes, differentiated out of the simple larval digestive cavity by the formation of areas of adhesion between its oral and aboral walls; and in the other we have the *narcomedusæ*, in which chymiferous tubes are absent and the digestive cavity is formed out of that of the hydra-like larva in a much more simple and direct way, as Wilson's account (*The structure of Cunocantha in the adult and larval stages*, by H. V. Wilson, *Studies from the Biol. Lab., Johns Hopkins Univ.*) which has recently been corroborated by the researches of Maas (*Ueber Bau und Entwicklung der Cunicinenknospen. Zoologischen Jahrbüchern, V, 272*) shows.

While the lines of descent represented by these two types are quite distinct we cannot doubt their origin in a common ancestor from which both the hydra-like larva, and the bell, sub-umbrella velum, and marginal tentacles, sense organs and nervous system of all the *craspedota* have been inherited, neither can we doubt that this primitive veiled medusa was still more primitively derived from a hydra-like form.

Now the fact that the sessil funnel-shaped hydra is restricted to a part of the members of one of these primary subdivisions of the *craspedota*, while the solitary star-shaped floating hydra-like larva is found in both of them; in the larva of *cunina*, as well as in that of the *geryonids*, and in the *actinula* of *tubularia*, shows that the ancestral form which the hydra-larva represents was of the latter type, and that the more familiar *hydranth* is a secondary modification of the more simple and ancient form.

In a more extensive discussion of this subject (*The Life History of the Hydromedusæ*, *Mem. Boston Soc. Nat. Hist., 1886*) I have referred to the history of parasitism and its effects, in the *narcomedusæ*, in order to show how easily this primitive larval type may become converted into a polymorphic *cormus* with alternation of generations. Nothing could have been further from my mind than a belief that the *cormi* of ordinary hydroids have been phylogenetically derived from the parasitic *cormus* of *cunina* larvæ.

The knowledge of the true structure and mode of origin of the adult cunina which we owe to Wilson's researches, already referred to, proves that the narcomedusæ represent an independent and very primitive branch of the craspedota and while I was ignorant of this at the time my memoir was written, and while I then, with all other naturalists, believed the narcomedusæ to be much nearer to the hydroids than they really are, I recognized, and thought that I had clearly stated my opinion, that the cormus and the alternation of generations in parasitic cuninas is a secondary and independent acquisition, although I still think, as I did then, that the analogy is most suggestive and instructive, inasmuch as it shows how easily secondary complications, essentially similar to those of hydroid cormi, may be grafted on to the structure of a simple hydra.

I regret that I am not able to refer to my memoir as I write, for critics of my views have spoken as if I regarded the parasitic cunina-cormus, as the ancestor of modern hydroids. Thus, for example, Maas says, p. 295, that Metschnikoff and Brooks hold that the narcomedusæ are primitive forms, *and that the alternation of generations of the hydroid polyps is derived from that of cunina.*

As far as I myself am concerned, I certainly regard the unmodified cunina metamorphosis as primitive, but I regard the complications which have been introduced by parasitism, as analogous to, but quite independent of, the peculiarities of hydroids.

A general view of a subject so full of complicated details as the life history of the craspedota is difficult, as illustrations and minute accounts of specific instances are so necessary. I hope, however, that, notwithstanding Lang's verdict (*Ueber die Einfluss der fest-sitzenden Lebensweise*, p. 159) that it is "the most improbable of improbabilities" the view that the craspedota owe their origin to pelagic influences will commend itself to those who are most familiar with these animals.

It is hardly probable, however, that our modern craspedota are primitively pelagic, for their size, the complication of their organization, and especially their great diversity of structure and habits, would seem to show that while they have been evolved in the open ocean, they are not the product of primitive and simple conditions, but that they show the influence of the more intense and complicated struggle for existence which has come from competition with

animals which, having been evolved at the bottom, have then become secondarily pelagic and have taken their improved structure back into the open ocean.

Haeckel has shown that the highest representatives of the craspedote stem, the Disconnectæ (velella, porpita, etc.) and the siphonophores, are pelagic productions, and that the Disconnectæ can be traced back to an ancestor similar to the Trachomedusæ, while the Siphonanthæ or true siphonophores have arisen from simple Anthomedusæ. (Report on the Siphonophora collected by H. M. S. Challenger; and System der Siphonophoren, Jenaische Zeitschrift, Vol. XXII, p. 1. 1888).

Both these groups are therefore pelagic in their history, and they go back, not to ancestral hydroid cormi, but to ancestral medusæ, but they can hardly be primitively pelagic, and we must regard them as the product of the more modern conditions of pelagic life.

The craspedota were undoubtedly represented in the primitive pelagic fauna, by floating hydras with stiff radiating poisoned pseudopodia-like tentacles, and also by small and simple veiled medusæ, but the higher forms of the group are probably more modern, although there is palæontological evidence that they are as old as the lower cambrian.

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