BIOLOGICAL LECTURES

DELIVERED AT

THE MARINE BIOLOGICAL LABORATORY

OF WOOD'S HOLL

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PREFACE.

THE addresses and lectures contained in this volume, with two exceptions, were delivered at the Marine Biological Laboratory during the summer session of 1890. They are a continuation of the Evening Lectures begun in the previous session.

The educational value which such lectures may be presumed to have, and the consideration that through them the aims, the needs, and the possibilities of biological work might, in some measure, be made better known to the public, especially to those whose liberal benefactions have enabled the Laboratory to carry forward its work, suggested the propriety of publication. This step, however, was not decided upon until late in the session of this year, after most of the lectures here presented had been delivered. The preparation of the Mss. for this purpose has been an extra tax upon the time of the contributors ; and, as this was done at my solicitation, I desire to acknowledge here my great obligation to them for this part of their invaluable co-operation in the work of the Laboratory.

There are one or two points in the *raison d'être* of this course of lectures, which do not lie wholly on the surface, but which deserve to be made clear. It was hoped, through such a course, to bring specialists into mutually helpful and stimulating relations with one another, and at the same time to make their work and thought intelligible and useful to beginners.

It was not intended to take the place of systematic lectures, such as are given in the regular courses of instruction ; it stands rather for the higher and the more general needs of the science. Its leading purpose, if I may be permitted to define it more with reference to the possibilities of its future development than to its present attainment, was to meet the rapidly growing need of co-operative union among specialists. Specialization has now reached a point where such union appears to be an essential means of progress. Specialization is not science, but merely the method of science. For the sake of greater concentration of effort, we divide the labor ; but this division of the labor leads to interdependence among the laborers, and makes social co-ordination more and more essential. This is the law of progress throughout the social as well as the organic world. An organism travels towards its most perfect state in proportion as its component cell-individuals reach the limit of specialization, and form a whole of mutually dependent parts. Scientific organization obeys the same law. As methods of investigation improve, specialization advances, and at the same time the mutual dependence of specialists increases. Isolation in work becomes more and more unendurable. Comparison of results, interchange of views and ideas, and a thousand other advantages of social contact, become of paramount importance to the highest development.

In such considerations may be found the leading motive for this course of lectures. While directed in the main to the higher needs of investigators, they deal, as a rule, with subjects of present, and quite general interest to beginners; and considerable pains has been taken to put them in a form that would be readily understood by such readers. In general, it may be said that the authors undertake to set forth what has been accomplished in their special fields of research, to give the conclusions of the best work and thought, to point out general bearings, and to state the problems that await solution.

Obviously, such a course of lectures admits of unlimited development. Those here offered may serve to emphasize our need, and perhaps may contribute something towards the eventual realization of that more perfect organization which we look for in the establishment of a permanent station with an endowment equal to our great opportunities for marine biological research.

C. O. WHITMAN.

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FIRST LECTURE.

SPECIALIZATION AND ORGANIZATION,

COMPANION PRINCIPLES OF ALL PROGRESS. — THE MOST IMPORTANT NEED OF AMERICAN BIOLOGY.

By C. O. WHITMAN.

A HEALTHY faith in the progress of biology presupposes a correct understanding of the tendency to specialize. It is important to know not only that specialization is a necessity, but a necessity that need not be feared. It may sound a little paradoxical to assert, that this tendency means union as well as separation; but it is only a truth illustrated in the most familiar facts of science and of every-day life. Let us look at some of the broader aspects of this tendency, in order to learn whither it is carrying us and what its implications are.

Naturalists are long accustomed to the idea that the living body represents a commonwealth of cells. The metaphor is based, not upon superficial or fanciful resemblances, but upon analogies that lie at the very foundation of organic and social existence. On the same grounds that the sociologist affirms that a society is an organism, the biologist declares that an organism is a society.

A society is an organized whole, the unity of which consists in, and is measured by, the mutual dependence of its members. The living body is an organization of individual cells with the same bond of unity. The principle of organization in both cases is the division of labor or function. The primitive social aggregate — the undifferentiated germ of society — is composed of practically like units, with like simple needs. Every one is a factotum, fulfilling all needs in and for himself. I [illegible] all self-dependence and no mutual dependence. The coherence of the whole is so slight that it can break up into as many parts as there are individuals, without the sacrifice of a single tie or condition essential to existence.

In course of time, division of labor comes into play, and with it social organization has its beginning. The different members, instead of doing all sorts of work, and aiming only to supply their own individual wants, begin to limit themselves to such work as their tastes, capacities, surroundings, etc., commend to them. This concentration of effort, which Coleridge, in his theory of life, has defined as "the tendency to individuation," both strengthens and improves the productive power, thus enabling a few to do the work of many. Each class of specializers produce in excess of their own needs, and through the exchange of these surplus products the needs of all are supplied.

The social integration that accompanies such division of labor may best be seen under conditions conceived as simple as possible. Let it be assumed that we have an aggregate of a hundred individuals, equal in competency and capacity for work, and all living under like conditions. Let us assume that the necessities of existence for each member require ten kinds of labor in equal quantities.

Now as long as each individual fulfils all ten needs, there will be no division of labor, but rather a divison of energy and correspondingly inferior products. The aggregate will represent a mere chance collection of independent individuals, not a whole of mutually dependent parts. But introduce the division of labor, and see how social integration follows. To take a simple form of division, we will suppose the aggregate divided into ten equal groups, one for each kind of work.

We still have the same workers, the same energy expended, the same work accomplished, and the same needs fulfilled; all we have done is simply to divide the labor instead of the time, and distribute it in such a way that each person gives his entire time to one work instead of dividing it among ten. The change, in itself considered, looks extremely simple and insignificant; but, when measured by the consequences entailed, its importance becomes at once apparent. Each work is now accomplished by ten men instead of a hundred, with the result that each individual fulfils only one-tenth of his own needs, and depends upon his fellows for the rest. Instead of jacks-at-all-trades, we now have specialists working under a social compact, which makes each individual the indispensable servant of every other. The co-ordination of individuals is such as to maintain a complete consensus of functions; which is the fundamental trait of a perfectly organized community, and its chief distinction from a purely gregarious aggregate.

If the members of such a community, in adaptation to the conditions it imposes, should become so far differentiated as to lose the power of providing for more than one or two of the ten necessities of existence, the social unity would become as inviolable as the physiological unity of the higher organisms. Break it, and every member would soon perish, just as certainly as every cell would die if the body were irreparably injured. The social organism might endure the loss of a limited number of its members, as the animal organism survives the death of individual cells and even the loss of certain organs. These losses may be repaired, in the one case by substitution, in the other by regeneration.

If reparation fails, all the remaining parts suffer in proportion to their dependence on the parts lost. In either case, the more complete the division of labor, broadly speaking, the more perfect becomes the unity of parts, the more complete the coincidence of the individual with the general welfare.

The parallel is more complete than our assumed case is suited to illustrate. We have considered only the two extremes of a series, and have not allowed for any connection through intermediate stages of development. But division of labor is not an artificial affair arbitrarily fashioned to our convenience ; it is not a thing of human device, for it antedates both the written and the unwritten history of our race. In the organic world, its development has been as slow and as long as the rise of the beings now inhabiting the earth ; in the human race, its period of growth coincides with that of civilization itself.

We cannot know the circumstances of its first introduction. We assume that opportunities for the first steps in the division of labor presented themselves fortuitously, and that, the opportunities being given, the inherent advantages of the principle in the struggle for existence would be quite enough to secure it the aid of natural selection.

The principle carries with it two grand advantages — two primary conditions of progress. First, the concentration of energy; and secondly, the economical combination of energies. The one holds the possibilities of intensifying and improving; the others, the possibilities of utilizing and augmenting. These conditions and their contained possibilities, given with the division of labor, are *the* possibility, not only of all social, but also of all organic evolution.

We may now go still further and assert that the evolution of the cell, the relatively simple structural unit of the organic world, would have been an impossibility without the division of labor. Imperfect as our knowledge of the cell still is, it is now certain that it has an organization based upon a division of function.

There is already an overwhelming amount of concurrent evidence to show that the nucleus is the real seat of the hereditary tendencies; and the deeper we penetrate into the complexities of its structure, and the more we study its internal transformations and movements, the more evident it becomes that the nucleus has had its evolution, which carries the subdivision of labor still farther back.

Our knowledge, so far as it goes, points to the conclusion that division of labor is not only co-extensive with life, but also coeval with it. Indeed, we should be on the side of all the probabilities, in assuming that the simplest possible form of living matter presupposes this principle. We are not, of course, to confound the principle with life itself, nor with the cause of life ; it is only a condition or means to an end. The universal correlate of division of labor is union of the laborers. It always means specialization, and always implies organization.

Thus the paradox resolves itself. As Herbert Spencer long ago pointed out in his Social Statics, "progress is toward complete separateness and complete union," and "the highest individuation is joined with the greatest mutual dependence."

As you see, the principle is one which may re-inaugurate itself, as often as a new order of units is evolved with needs that can be most economically and efficiently served by a co-operative union. We do not know how many times this may have happened before the cell order of beings arose ; but the general course of development following this stage, we are now very confident about.

Some of these cells, finding independent nomadic life congenial, have persistently declined every temptation to part with individual freedom. They have kept their freedom, but with it the low estate of unaided individual effort. Precious freedom that, which excludes all those larger possibilities of life which we see unfolded in the organic world.

Others preferred company to isolation, and herded together in roving colonies. Some of these were dominated by a gregarious instinct only, and have clung tenaciously to self-freedom, refusing to make any sacrifice of personal independence for the sake of a physiological union. A few such aggregates, whose freedom has been the forfeit of all advancement, still survive, as exemplified in some members of the Volvox family. In Gonium, for example, the colony consists of a few (4–16) flagellate cells, adhering together in plate-like form, each self-moving, self-feeding, and self-propagating.

Among these colonial aggregates, there were some, however, which found out how to take one or two simple steps in labor partnership, and thus advanced to a rudimentary kind of composite individuality. An interesting example is seen in the famous Volvox of Leeuwenhoek, in which the evolutionists of last century found a confirmation of their idea, that the germs of plants and animals are preformations in miniature, incased one within the other. The division of labor is here of such an elementary order, that, as Bütschli has suggested, we may look upon a Volvox colony as a near ally of those simple forms from which all the higher plants as well as the Metazoa arose.

The Volvox colonies, composed of numerous individuals, often more than a thousand, are attached to the inner surface of a colonial envelope, at equal distances. In each colony we find two kinds of cells ; one with two flagella for locomotion, the other without such appendages, fulfilling the work of reproduction. This single division of labor makes one class of individuals the propagators of the species, the other the preservers of the colony. Neither class can dispense with the services of the other; and this dependence of part upon part gives the colony a certain physiological unity. But the integration of the colony is of such a simple order, that we might conceive it splitting up into as many independent colonies as it contains times the least number of cells of both sorts necessary to maintain the physiological connexus. Although in practice, we could not carry the division so far, still we know that artificial, if not spontaneous, division would be possible without destroying the physiological unity necessary to the continued existence of the severed parts.

One feature of labor-division in Volvox deserves mention here, chiefly as foreshadowing more complex conditions seen in higher forms. It is the alternation of agamic with gamic generation. The agamic reproductive cells are all alike, and correspond to parthenogenetic ova; while the gamic generation is represented by two distinct kinds of cells answering to ova and spermatozoa, and conjugation is necessary to development.

This alternation of parthenogenesis with hermaphroditic gamogenesis — is not, we may be sure, an acquisition of the colony; it is rather to be regarded as a combination of features that originated separately and successively among the unicellular ancestors of the colony. Parthenogenesis must have been the primitive mode of reproduction; gamogenesis undoubtedly originated secondarily in adaptation to infusorial conditions of life.

This sequence of generations is common enough among the unicellar Protozoa; and the colonial forms exhibit it as an inheritance of their component cells.

The parthenogenetic colony presents itself, then, as an aggregate of individuals with differentiated, but undivided, reproductive work; the hermaphroditic colony explains itself as an aggregate of individuals with differentiated and sexually-divided reproductive work. The association of both sexes in the same colony is an accident of aggregation; for obviously we might have, in fact do have, dioecious as well as monoecious colonies.

The protozoan colony of the Volvox type, represents the old infusorial system of labor-division and, superadded thereto, the colonial stage of what we may call the intercellular system — which runs through all the higher organisms.

With the intercellular system is given a higher order of units, capable of combining and recombining to form successively higher orders, each carrying all previous systems of labor distribution with its own superimposed thereon. The ascending series ranges through all diversities of form and all complexities of structure between the simplest cell-colony and man. Cells combine into tissues, tissues into organs, organs into organisms, organisms into organic as well as social aggregates, and these in turn into higher units. While the higher units are entering into new combinations, their components of the next order below, of the next below that, and so on to the lowest, may be undergoing simultaneously special modifications, each struggling to keep up its own internal and external adjustments, but always in subordination to the welfare of the entire organism. When we contemplate the finished mechanism, the product of all these consentaneously and yet unconsciously directed energies, these millions of individual minim workers, uniting in such intimate fellowship as to constitute an indissoluble whole — a real conscious intelligent unity — with powers so far transcending those of its units that we can form no conception of the special combinations from which they result, — when we contemplate this miracle of co-adjustments among myriads of units, among these systems of units, and these systems of systems, we are not disposed to ridicule the judgment that once refused to believe that natural forces could produce such wonders, and took refuge from the difficulties that beset every mechanical theory in the doctrine of preformation.

If our microscopical aids have enabled us to know that organisms are not simple unfoldings of pre-existing structures, and have revealed the fact that every developing germ actually re-enacts the wonders of a new creation, still it is no less an unscrutable mystery than before. Indeed one must credit the preformationists with having perceived and emphasized the real difficulty in the way of any rational theory of generation. We endeavor to meet it, by assuming, not pre-existing rudiments, but pre-existing hereditary units; not predelineations, but potentialities, of structure. Predeterminations of some kind or other are a logical necessity, and so there is some analogy between our position and that of Bonnet, Haller, and Cuvier, and other evolutionists of the old school, although we are compelled to regard the process of development as one of epigenesis, as conceived by Aristotle, Harvey, John Hunter, and Casper Friedrich Wolff. The difference between the two schools reduces itself to the difference between potentialities and actualities; and although the difference as understood by the contending parties is utterly irreconcilable, still we can understand how, by modifying our potentialities in one direction and our actualities in another, the difference might be brought near a vanishing point.

Whether we look at the successive stages connecting the relatively homogeneous germ with the completed organism, or at the paleontological succession of forms, we see that progress in the organic world is always from the less to the more heterogeneous. As division of labor advances, complexity of structure increases, and the ties of mutual dependence multiply and strengthen. In a word, the most characteristic trait of evolution is, that increasing *division* of labor conditions increasing *union* of the laborers. Division and union, differentiation and integration, specialization and organization, march hand in hand.

The same truth comes perhaps more clearly into view, when, taking the protozoan colony for our starting-point, we run up the scale of animal organizations. Passing on from the Volvox colony, we soon come to an instructive stage represented in the common fresh-water Hydra. Although we now know that the organization of this animal is far from being as simple as was supposed by its discoverer, Trembley, and by other naturalists of his time, who regarded it as a connecting link between plants and animals, still it affords a striking illustration of the fact, that *physiological unity is a thing of degrees, incomplete according as the division of labor is low.*

A single division of labor, in advance of what we saw in Volvox, makes Hydra an unmistakable Metazoön, placing it fairly on the main line of animal evolution. It is the separation of the digestive from the other functions which characterizes the Hydra stage. In correlation with this important step, we have one grand and several minor structural features introduced. The digestive cells arrange themselves together in the form of a tubular sack open at one end, thus taking the first step towards a rudimentary alimentary canal. Around this sack, the remaining cells station themselves, forming another sack inclosing the first. The sacks are in close contact, and the walls of the outer one are continuous with those of the inner one at its open end, so that the inner sack may be regarded as an infolding, such as we might rudely represent by pushing in the end of a glove-finger. If the material were elastic, so that we could draw out the double wall around the open end into a number of arm-like extensions, we should have a fair model of the Hydra body with its tentacles.

The cells constituting the inner sack, called the entoderm, are in the most favorable situation for attending to the food-supply of the entire cell community; and natural selection has constrained them to specialize in this direction until they have become inoperative in other ways, and even incapable of doing anything else. Trembley succeeded in turning these creatures inside out; and as they lived on after such treatment, he inferred that the functional differentiation of the two layers was so slight that ectoderm and entoderm could exchange places and works. The mistake has only recently been corrected by a Japanese naturalist. Dr. Ischikawa of Tokyo has shown conclusively that Hydra cannot live long turned inside out, and that, if left to itself after the operation, it soon turns itself back into its normal condition. This act of recovery escaped the observation of Trembley, and of others who repeated his experiments; and hence the unity or individuality of the Hydra community of cells has generally been estimated too low.

That the two layers carry functions fundamentally distinct and non-interchangeable, and that the co-operative combination of the two sets of functions is necessary to existence, — is, in fact, the very essence of the Hydra personality, — is shown by still another fact brought out by Mr. Ischikawa. It is generally taught that Hydra may be divided *ad libitum*, and that each fragment will have the power to regenerate the whole individual. But it turns out that there is a very definite limit to such possibilities, which cannot be overstepped without annihilating individuality and extinguishing even the germ of it. An isolated piece of either layer is incapable of regenerating the individual. The mutual dependence of these two layers is such that they must go together or perish. Carry artificial division in any direction that does not sunder these complementary parts, and repeat the operation as often as you like, the smallest fragments in which this vital connection is preserved will represent, potentially at least, the personality of Hydra. This personality comprises a certain number of functional powers; and hence the minimum number of cells combining these powers in vital relations represents all the essential elements of individuality. The fertilized ovum unites all these powers as potentialties, and it is therefore the individuality in germ. If the ectoderm cells, like the entoderm, were all alike, the essentials of a Hydra might be said to exist in a single pair of cells, one from each layer; but of course we could not hope to isolate such a pair of cells in vital union.

The remarkable thing about such an individuality is, that a hundred of them may be added together and the sum total will be but one; and yet you may divide this *one* into a hundred *ones*.

Mr. Ischikawa succeeded in forcing two individuals into complete and permanent coalescence; and for aught we can see, the experiment might be repeated indefinitely. One Hydra was turned inside out, and then pushed into the mouth of another until the digestive sacks of both were brought together one within the other. A bristle was then thrust transversely through both bodies to prevent separation. In the course of a few days, the two bodies were completely merged in one, and the resulting individual was a perfect personal unity, bearing two sets of tentacles as the only mark of its double origin.

Having seen in what the essential unity of Hydra consists, we can readily understand why such an individuality may not be weakened by division or strengthened by doubling. A society of a hundred individuals with ten labors, distributed as we supposed, would represent a unity with ten essential points of union. Now we could double the number of members without increasing the points of union; and we could divide the whole community into ten communities, each with as complete a functional unity as that of all combined.

In the case of Hydra, we could divide more freely, because the points of union are fewer. Now what I wish to emphasize here is this: *The more the points of union multiply in a social or an organic body, the more complex and extended becomes the integration of its parts, and the less susceptible it is to such divisions and fusions* *as we have described.* Bear in mind as we go on, that every point of union is a point of division, or specialization in labor.

Our supposed social aggregate, as I have said, admits of division into ten independent communities. If, however, we multiply the points of union by ten, *i.e.*, if we suppose each labor sub-divided into ten specialties, each member of the aggregate will fulfil only one-hundredth of his own needs, and will depend upon his ninety-nine associates for the rest. The mutual dependence is not only ten times as great, it is also ten times as extensive, for each individual is now a necessity to ninety-nine instead of nine others, and the entire aggregate becomes an indivisible whole.

The same processes are followed by like results among the cell-constituents of an organism, only here we rarely find such simple, and never such complete, uniformity in numerical relations. We find no organism in which the division of function exactly coincides with the number of its component units. Both the division of labor and its distribution here tend to adjust themselves, first of all, in harmony with the primary necessities of existence; and secondly, in correspondence with that complex of relations, conditions, and needs, both internal and external, which hold all the possibilities of improving existence, and rising above it to conscious life and intelligence.

In the organic association of cells, nutrition and reproduction take precedence in determining the direction of development. The needs which centre in them are, as a rule, best served, not by giving the whole of a given kind of work to a single cell, but by dividing it more or less equally among many cells, scattered or grouped according to the nature of the work. Nature is provident as well as bounteous, and so she determines the number of workers not only with reference to ordinary needs, but also with a view to emergencies. The cell cannot work on indefinitely. Exhaustion follows exertion ; rest and recuperation are as necessary to the cell as to an individual ; hence the need of relays. The cell has its own term of existence, which is usually much shorter than that of the organism ; hence the need of substitutes. So each class of specialized cells may greatly exceed in number the actual needs of the moment. One of the best illustrations of this fact is seen in the reproductive cells, which are often so enormously in excess of use, that they are scattered in the water or the wind, with not one chance in a thousand of ever fulfilling the purpose of their existence. All such profuseness, however, has its meaning, even though it only neutralize accident, and so insure a few the realization of their proper destiny.

But these hosts of cells suffice for only one of the many varieties of reproductive work. They are called reproductive cells, not to indicate monopoly of the entire work, but pre-eminence merely in one important branch of it. Propagation of the species is their task ; but this becomes a monopoly only among the higher forms of life. The same work may be accomplished by budding and fission, processes which prevail very largely among plants and many of the lower animals, usually supplemented, however, by the more general process of reproduction by means of specialized cells.

But the generation of the species, which follows such different courses, each of which goes on into almost endless sub-division, is not the whole of reproduction. Reproduction of the species of course includes all other kinds of reproduction; nevertheless it is as distinct from them as the individual is from its component cells. The individual may be the product of a single cell, but, once formed, the heterogeneous components must severally have their own methods of reproduction, otherwise the organism could not keep up its reserves, nor supply the places of exhausted, disabled, or worn out laborers. These specialized modes of reproduction, as varied and as distinct as the histological elements of the organism, although derived from the process which continues the species, yet differ from it in this important respect, that their products are isogeneous rather than heterogeneous.

This distinction is already well marked in Hydra, where we find the entoderm cells so specialized that they can reproduce only cells of their own kind. How different it is with the ova, which reproduce all kinds of cells represented in the Hydra community.

Certain kinds of work exclude the power of reproduction, and such cases call for special provisions of still another class. The loss of such power by any class of cells is generally made good by a closely allied class, or by the younger cells of the same class. Such reserves may play a relatively passive part, until the time arrives for them to take the place of their predecessors; and they may be capable of assuming any one of several different roles. Again Hydra furnishes us with a simple illustration. The superficial ectoderm cells of Hydra, consisting of nettle-cells, nerve-muscle cells, etc., are replaced by deeper and younger cells, called "intermedial." The reproductive cells have the same origin.

The work of reproduction then is not confined to any one or two classes of cells; it is divided and subdivided in endless detail, carried all through the organism, and distributed independently of most other labors. Its elaboration in this or that direction may be correlated with a system of morphological differentiations, so extensive and involved that a whole course of lectures would be required to elucidate the subject. Take the genital system of the vertebrates, or that of forms no higher than the annelids, and you will find no end of problems yet to be settled. What complicated cycles of generation have been followed by many parasitic forms, especially among the worms, and what wholesale modifications of structure in answer thereto. How devious have been the paths of generation in insects, and how wonderful the metamorphoses attending them. How diverse the ways of multiplication among the Tunicates and Cœlenterates, and what puzzling successions and combinations of forms have here tried the sagacity of naturalists.

What peculiar corporation aggregates are represented in Siphonophore colonies, of which we have a most beautiful example in the Portuguese-man-of-war. How long it has taken to decide between the "poly-organ theory" of Eschscholtz, Huxley, Müller, and Metschnikoff, and the "poly-person theory" of Vogt, Leuckart, Kölliker, Gegenbaur, and Haeckel. The complex of reproductive processes in one such colony would still bear a life-time of research, and not be exhausted then. Who is able to trace out the reproductive alternations and metamorphoses of such simple yet strange forms as the Dicyemids and Orthonectids, supposed by some, though probably erroneously, to stand as an intermediate group between the Protozoa and the Metazoa ?

And when we descend to the Protozoa themselves, we find the reproductive cycles specialized in ways as varied as the forms of life. Then behind and underlying the whole of this reproductive work, from Protophyte to Phanerogam, from Protozoa to man, are those intensely interesting phenomena of caryokinesis, which are at once the most varied and the most uniform expression of reproductive energy that modern research has yet revealed.

I need not dwell longer on this subject. We have not found the beginning of reproductive work, nor can we see an end either to its divisions or to the structural unities and divergencies correlated therewith.

We might now turn to nutrition and sketch the general features of its specializations and coördinations ; but we should only find the same principles illustrated in new directions, and might get weary without getting wiser.

I will therefore at once try to bring the leading thought to a focus, and then very briefly point out its application.

Division of labor is the principle underlying all organic as well as all social progress. The development of the principle brings with it mutual dependence of the working units ; and hence, every step in advance leads necessarily to that closer integration of the units which merges their individualities into an individuality of a higher order. The tendency towards unity, as specialization advances is nowhere more strikingly illustrated than in the progress from the lower to the higher segmented animals. In the lower annulose types, the individual represents a chain of segments or somites, which we may regard as so many individuals which have arisen as buds, one after the other, from before backwards, but have remained connected in the order of origin. These somites retain their individuality to such an extent that they are not killed by artificial separation, and indeed often undergo spontaneous fission.

As we glance along the line of forms terminating in the Myriopods, the Crustaceans, the Insects, and the Arachnids, we find the individualities of the somites more and more subordinated to that of the chain they compose. There is a progressive consolidation, which, in its extreme phases, more or less completely obliterates the traces of articulation. The illustration might be extended to the vertebrates, but that would be needless. Let me add only, as one of the broadest conclusions to be drawn from such facts as we have been considering, that *the grade of specialization attained in any group of organisms determines its rank in the scale of life and intelligence.*

In each order of units, specialization seems to have its limit in the highest possible integration of its component elements. When this limit is reached, progress is arrested. The only way then open for advance lies in combining these units into units of a higher order. In this combination is given the possibility of a new system of specializations and integrations, with correspondingly high grades of life. The final stage of each order of units represents a complete individuality, which cannot be divided without destruction. So we advance from certain "physiological units" to the indivisible cell, from the cell to the indivisible organism composed of cells, from the highest units here to those of the social order.

It is unnecessary to enlarge further upon these facts. It remains only to point out their bearing in relation to the biological sciences.

The days when naturalists could presume to take all nature for a subject of study and meditation are a long way behind us. The cosmogonists of olden times engaged single-handed with all the mysteries of the universe. We honor them for their heroic efforts, ineffective as they were from misdirection. At the expense of centuries of baffled efforts, the lesson began at last to be learned, that division of the problem facilitates progress. That a knowledge of the whole presupposes a knowledge of the parts, was a simple enough fact; but it took a long time to turn it into practice.

Division of labor in the sciences, as elsewhere, has been a thing of slow growth, self-originating, self-perpetuating, and self-regulating. It has taken possession of the biological sciences, and presides over their onward march, just as it determines and directs social and industrial progress. It is simply an economical principle, the growth of which began with, advances with, and will always have its limitations in, an actual need — the need of concentrated attention. This need in turn has its limits in our power to improve the methods of investigation. The tendency, then, is regulated by the necessities and advantages of the investigator; and although we may not be able to fix definite limits to its growth, we are not the less certain that it has such limits, and that there is no danger either of a wholesale reaction or of our ever specializing to pieces. As in the organic and social worlds, so in the scientific, there are centripetal forces that keep pace with the centrifugal ones; and the danger of any science flying into disconnected atoms is about as dreamy and remote as the dissolution of the earth itself.

The movement in the direction of separation is general and, as it *now* seems to us, rapid. Cuvier thought that division of labor characterized the natural science of his day; but the movement was then in its earliest infancy. If you wish to know how extensive it has now become, you should look at the ponderous volumes of the "Zoological Record" or the "Naples Jahresbericht." When you reflect that it requires such massive volumes to record the bare titles and a brief abstract of the work of a single year, you realize how impossible it is for any one naturalist to cover the whole ground, or even to read the hundredth part of what his collaborators have to report.

Naturalists then are no longer cosmogonists, but specialists. This being the fact, what is to be done in view of it? Where lies the remedy for every danger of narrowness that may lurk in the tendency to specialize? How is the range of vision to be kept free and broad while focussing attention on some one point of the field? If one specialty absorbs our whole time and energy, how are we to keep its general bearings and relations in full view? Will organization of any kind within our reach effect this? If our specialties are parts of a whole, then this whole must be representable by one or more modes of combination. That kind of organic association which permits each unit to work for itself while making it the servant of all the rest, must be a possibility.

It must be evident to every one who is capable of understanding the situation, that *union* is just as essential a part of the law of progress as division. If specialization is a necessity, so is organization. But there is this difference between the tendencies, — that the one precedes the other and comes into recognition first. Specialization has already forced its way to the front, and is nearly everywhere recognized as a necessity; organization follows, but lags lamentably behind the needs of the times.

The general principle of coöperation has long been at work. The naturalists of all countries are brought into coöperative relations through journals and other scientific publications. Every year multiplies these points of union, and draws the scattered workers into closer mutual dependence. Cut off these indispensable media of communication, and that unity of action on which progress now depends would at once come to an end. Of course the unity of action in so extended a body cannot be complete. Duplication of work will now and then occur, but the waste in this direction is fast becoming reduced to a minimum.

The tendency to specialization is rapidly developing among our journals. This is seen especially in such journals as the *Zoölogischer Anzeiger*, the *Biologisches Centralblatt*, the *Anatomischer Anzeiger*, the *Journal* of the *Royal Mic. Soc.*, the *Zeitschrift f. wis. Mikroskopie, &c.* Manifestly all such specialization is led by the coöperative spirit.

But it is not to the general tendency so much as to our own special need that I would now direct attention. We have now reached a point where our advance, both individually and collectively, depends, far more than ever before, upon the privileges, the opportunities, and the many peculiar advantages inherent in the principle of coöperative work.

Among the ways of bringing together our scattered forces into something like organic union, the most important, and the most urgent at this moment, is that of a national marine biological station. Such an establishment, with a strong endowment, is unquestionably *the* great desideratum of American biology. There is no other means that would bring together so large a number of the leading naturalists of the country, and at the same time place them in such intimate helpful relations to one another. The larger the number of specialists working together, the more completely is the organized whole represented, and the greater and the more numerous the mutual advantages.

Just consider what such an organization implies. It means, first of all, a permanent staff of investigators, with laboratories equipped for special research, and with facilities for extending observation to different points of our varied coast. It means boats, and all needful appliances for collecting, dredging, etc. It means a corps of trained collectors at the service of the investigators.

It means a comprehensive working library; ample funds for serial and monographical publications; funds for travelling research; and resources for coöperative work with similar stations in other parts of the world. It means, further, all those important aids and accessories of investigation, such as conservators of material, assistants in microtomical and other mechanical work, skilled draughtsmen, photographers, lithographers, and so on to the end of all the needs of such an organization.

Create such conditions of work, and how biology would flourish. Specialization would characterize the individual members; but organization would dominate the aggregate. In place of the weakness of isolation, we should have all the power of union. There would be economy of time, money, service, physical and intellectual strength. The productive power of each individual would be intensified and augmented beyond calculation by that of every co-laborer; for while the units ministered to the whole, the power and influence of the whole would redound to the benefit of each. The difference between isolation and a union of this kind, is like that which separates the solitary cell from a highly developed organism, or the nomadic aggregate from civilized society. We need *viva voce* contact for incentive, for stimulation, for inspiration, and especially for maintaining that "*moving equilibrium*" of our specialized forces which constitutes progressive scientific life; and organization in the direction I have roughly indicated will accomplish all these ends.

In conclusion, let me say that the establishment of such a station as I have sketched will probably never be effected through the unaided effort of any one person. But individual effort, though weak alone, has in the growing aggregate a cumulative power that often surprises expectation. Let every one feel, therefore, that his or her personal interest in the matter may be just what is required to make the combined effort of all effective in converting possibilities into actual realizations, and in giving to specialization its consummation in organization.

SECOND LECTURE.

THE NATURALIST'S OCCUPATION.[1]

By C. O. WHITMAN.

I. *General Survey.*

I SCARCELY need remind you that the domain of Biology is a broad one, and that it has long since become impossible for one person to master the different provinces of knowledge embraced in it. The most that I can hope to do, is to take you into one small section of the great realm of life, and try to give you an inside view of some of the problems now occupying attention.

As this many-sided occupation may be approached with almost equal advantage along any one of many intersecting paths, a hasty general survey may be the best means of getting the points of the compass.

Let us take systematic biology as our starting point, and from this as a centre find our way into the other provinces of biology, with a view to understanding their general features and relative positions.

What is the chief end to be reached in the classification of plants and animals? The general drift of bio-

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[1] Delivered at the opening of the Evening Lectures, July 9, 1889.

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logical research is in the direction of a *genealogical* system of classification — a system based upon, and expressing, the kinship which underlies the whole organic world. From this standpoint, the myriad forms of organisms that have arisen since the dawn of life, genealogically arranged and viewed as a whole, would present the branching figure of a tree. The trunk and branches of this great tree, representing ancestral forms, have been buried in the sand and mud of geologic ages, and preserved only as an imperfect fossil frame-work, so that we see only the terminal buds of its topmost twigs in the plants and animals of to-day. To trace out and reconstruct such a tree is a work of magnitude, scarcely dreamed of in the philosophy of cabinet naturalists. The best classification within the range of present possibilities can only have a tentative value. It can have not a single hour's security against the invasion of newly discovered facts — an invasion that is advancing along a thousand lines with plenary authority to spare nothing fictitious. The goal of systematic botany and zoology is not then the terminus of any one line of research, but rather a focal point of all the biological sciences.

Having noted the principal aim of classification, we have now to glance at its position, scope, and functions. The low standards followed by many systematic writers have brought reproach upon this department of knowledge; but the reproach is certainly misplaced, and we must accord to systematic biology the high position to which its true aims and functions entitle it. Its first business, obviously, is to ascertain what forms of life now exist, and to describe, name, and catalogue them for the purposes of easy and certain identification. Although much of this work can have only a provisional value, it is, nevertheless, quite indispensable; for there is not a single department of biology that does not continually profit by its acquisitions, nor indeed is there one that can make any great progress without its aid.

The process of coining names and labelling new species must continue for a long time to come; but, it does not of course follow, because systematic names are indispensable, that we can profitably spend our time in committing them to memory. That is the delusion of inexperience and the conceit of charlatanism. Time was when the knowledge of a thousand names secured one the title of botanist or zoologist, and when the capacity for ten times that number was esteemed the measure of a great naturalist; but if we may believe a celebrated German botanist, Schleiden, such qualifications fell below par more than half a century ago.

In the beginner, and in the general observer, we frequently meet with a superstitious regard for names that blinds them to the real character and aims of natural history. With them, an ideal naturalist is supposed to have an encyclopedic knowledge of names, and to be ready for any worm, beetle, or butterfly, that may be laid before him. If he has the courage to say he does not know the name of the form presented, the inquirer is amazed at the confession of ignorance; if a vernacular name is offered, the information is received with evident disappointment; but if some unintelligible, polysyllabic, cacophonous Greek or Latin compound is glibly enunciated, the awe-stricken recipient retires, feeling profoundly edified, and credits his informer with having fulfilled the function of a great naturalist. This mischievous delusion is too often encouraged by those who are able and willing to impose upon it, or who have not the courage to follow the injunction so often given by Professor Agassiz at Penikese, — "Learn to say you do not know."

Pitiable as is this fear of appearing ignorant, and despicable as is the impostor's pretence of knowledge, there is no ground in either for prejudice against systematic names.

Whoever reflects on what the binary nomenclature, introduced by Linné, has done for zoology and botany, will scarcely need to be told that no misuses, excesses, or abuses to which systematic work is liable, can detract from its importance. Indeed, it may be said that time will increase rather than diminish the value of such work. Thirty years ago our systematic names stood for differences and resemblances, the deeper significance of which had only been caught by Darwin and Wallace. The idea of the genetic unity of the organic world set the whole field of systematic work in a blaze of light, imparting to it an interest and a dignity of the highest order.

The second important function of systematic biology is to arrange its forms in a genealogical system. But for the fulfilment of this function, systematic biology requires the aid of all the sister branches of knowledge, and in return renders the important service of recording their verdicts along with its own. The record, representing as nearly as possible the consensus of all the morphological and physiological sciences, shows how far the reconstruction of the tree of life has been carried, and thus furnishes a chart which is invaluable as a guide in the selection of subjects for investigation.

When the classifier, or taxonomist as he is sometimes called, has taken account of morphological features, modes of reproduction, habits, instincts, and distribution, he has exhausted the resources of his special province. The conclusions reached and the questions raised are then to be submitted to other departments for revision and further investigation.

Let us suppose that the preliminary work of naming and describing has been completed, and that the taxonomist undertakes with purely descriptive data to map out the genealogical tree. With superficial characters alone, it is evident that he could not advance very far, although, according to the supposition, he would have the immense advantage of knowing precisely what the task is. What such an advantage means, becomes clear when we remember that, with all the light of all the sciences, we waited until the last half of the nineteenth century for the formulation of the problem. With this key to the situation, a quarter of a century has outdone the blind plodding of all previous centuries, and the old landmarks have been left with a speed that threatens to make Rip Van Winkles of us all. Armed with such an advantage, the investigator would certainly be able to find in external characters important clews to genetic relationships. But if limited to those methods and means which naturally belong to surface observation, he would remain in absolute ignorance of a great part of the animate world, and would be utterly powerless to discover in what the bond of unity actually lies. He would have no conception of what Huxley has called "the physical basis of life," and the structural unit of all organisms would lie wholly beyond the range of his perception. That isthmus of small life between the animal and vegetable kingdoms, his unaided vision would never discover. In searching for intermediate forms, he would inevitably be led astray by those deceptive appearances under which adaptive development and degeneration have concealed so many ancestral relationships. Sessile animals, like the sponges, the hydroid polyps, the sea-anemones, the polyzoa or moss polyps, the ascidians, and many others from the higher as well as the lower classes, would be separated from animals having the power of locomotion, and be regarded either as plants, or as forms representing both plants and animals. Where immobility is combined with the branching form, as in the hydroid polyps, the disguise would be complete. Even Linné, the great lawgiver in systematic biology, described such forms in the tenth edition of his "Systema Naturæ" as "plants with animal flowers"; and in the twelfth edition, which concluded his systematic work, he held to the opinion that the stock of the hydroid colony is a true plant, while its "flowers" are true animals. This idea was embodied in the word zoöphytes, plant-animals, a word that has done varied service in systematic zoology from the middle of the 16th century.

The utter insufficiency of external characters as a guide to genetic affinity, is well seen when we come to such forms as the so-called compound ascidians, which are found encrusting the rocks along the shore. At first sight one would not even detect any signs of life here, and appearances would suggest relationship to the lichens sooner than to the vertebrates. If we cut open the fleshy encrustation, and examine under the microscope the contents of some of the little sacks found in it, we discover some minute tadpole-like beings, representing the larvæ of the ascidian. The structure of these remarkable creatures repeats the fundamental features of the vertebrates so perfectly that we are compelled to place them in the same great family. They have a chordal axis with a nerve-tube on one side and the alimentary tube on the opposite, with gill-slits perforating the throat, features common to all vertebrates in early life. Although the adult ascidian bears not the remotest resemblance to a vertebrate, the combination of these characters in its larva proves that it belongs to the vertebrate stock. The larva reaches the adult condition by a process of degeneration. It fixes itself to a stone by its head, then loses its tail, its only organ of locomotion, and sinks into a purely vegetative existence. So completely are its original features obliterated, that its vertebrate nature would never have been suspected, had not embryology brought to light its developmental history. The striking agreement with the development of the curious worm-like fish, Amphioxus, as made known by Kowalevsky, a Russian embryologist, led Professor Haeckel of Jena to regard the ascidian as the ancestor of the vertebrate stock. Startling as such a proposition was, it was favorably received at first, and was approved, though with reserve, by no less a logical and critical thinker than Huxley. Most authorities now concur with Lankester and Dohrn in regarding both Amphioxus and the ascidian as our degenerate vertebrate cousins.

Thus you see how far from the surface the truth may lie, and how, in the systematic position of a single form, we may find a problem which only yields to solution after exhausting the resources of nearly every department of animal biology.

In order to correct and extend the results of surface observation, the investigator appeals first to internal structure, and is thus led into the province of anatomy. Here fundamental features of relationship are brought more clearly into view; and, following the general law that animals or plants of like structure have descended from common ancestors, it becomes possible to outline, in a rough way, a genealogical system. It is here that the investigator would begin to grasp the meaning of those deeper resemblances, called homologies, and learn to distinguish between these and deceptive analogies. But nature has concealed many of her more important homologies under disguises that a study of adult structure could not penetrate. Comparative anatomy, in the hands of such men as George Cuvier, Friedrich Meckel, Johannes Müller, Richard Owen, Thomas Huxley, and Carl Gegenbaur, has accomplished wonders in this direction, but it owes many of its greatest discoveries to the aid of embryology and paleontology. Its greatest achievement was the reduction of the animal world to four great types, and the same high elevation was reached independently by comparative embryology.

But the type system of George Cuvier and Carl Ernst von Baer did not finish the reconstruction of the genealogical tree; for it failed to grasp the full meaning of like development and like structure. Comparative anatomy found ascending grades of organization in the vertebrates of the present; paleontology discovered a corresponding gradation in the vertebrates of the past; and embryology revealed the same serial gradation in developmental stages. The discovery of this most remarkable parallelism between the three series, the anatomical, the paleontological, and the embryological, is one of the most brilliant in the whole history of biology, and one which with pride and admiration we place to the credit and honor of Louis Agassiz. It is remarkable that these three of the leading biologists of the century, after laying the foundation of the theory of transformation, remained to the end its most determined opponents. It was left for Charles Darwin to show that the coincidence pointed out by Agassiz between the geological succession, the embryonic development, and the zoological gradation, held also in the geographical distribution of animals in the past and the present, and to find the interpretation of the fact now universally accepted.

The recognition of so fundamental a truth as that of community of descent, at once raised every department of biology to a new plane, gave new aims to each, and profoundly altered their relations to each other. Descent was seen to be "the hidden bond of connection" so long sought for under the "natural system" of classification. Embryonic development came to be regarded as the epitomized history of ancestral development. As Darwin puts it, the embryo is "a picture, more or less obscured, of the progenitor, either in its adult or larval state, of all the members of the same great class."

"In two or more groups of animals, however much they may differ from each other in structure and habits in their adult condition, if they pass through closely similar embryonic stages, we may feel assured that they are all descended from one parent-form." Thus embryology came to have a higher value in classification than anatomy, and to take the place assigned to it by v. Baer more than half a century ago, as "the true torch-bearer in the investigation of organic bodies."

Embryology and paleontology have become complementary sciences, associated in the common aim of determining the genesis and the history of life. The peculiar charm of embryology is, that it brings us into direct contact with living forms, places us face to face with the phenomena of life, and reveals in the history of the individual the principal events in the history of the race. It holds the key to many a problem that has exhausted the resources of all the sister branches of biology, and promises to contribute more than all the rest towards the solution of the great mystery of life.

In order to illustrate the relative position of embryology, and at the same time the nature of the naturalist's work, let us now look at one of the problems before him.

II. *A Special Problem.*

Naturalists are familiar with the efforts of comparative anatomy to determine the number of segments in the vertebrate head. At the beginning of this century, Germany's great poet, Goethe, and one of her most gifted naturalists, Oken, came independently to the idea that the skull is only an enlarged and otherwise modified portion of the backbone; that is, that it is composed of a number of segments, each of which is the structural equivalent of a vertebra. The idea was suggested by the sutural lines in the mammalian skull, which appeared to mark the boundaries of successive segments. Thus arose the so-called "vertebral theory" of the skull, which was widely accepted and which was made the corner stone of Richard Owen's great work on the comparative anatomy of vertebrates. If the skull could be regarded as three, four, or more modified vertebræ, it followed that the brain might be considered as a portion of the spinal column, and that the cranial nerves were the equivalents of the spinal nerves. It was impossible to settle these questions by compartive anatomy, and the assistance of embryology was invoked. The discovery by Jacobson, that the bony skull is preceded in development by a so-called "*primordial cranium*," consisting of a cartilaginous case, which, although a direct continuation of the cartilaginous basis of the backbone, yet differs from it in not being divided into segments, and the fact that the adult skull is really a *double* brain case, the inner portion representing the primordial cranium and its derivatives, or by bone that has replaced it, while the outer portion consists of the so-called *dermal bones* that have been added externally and secondarily, have been used with great force by Huxley, against the vertebral theory of the skull. If the skull ever consisted of segments comparable with the vertebræ, the proof of this should appear in the primordial cranium, as it is found to-day in the lower fishes, or in the course of its development.

Since the time of Goethe and Oken, we have learned the important lesson, that the place to look for primitive vertebrate characters is in the lower rather than the higher forms, and in the embryos rather than in the adults. The original expounders of the vertebral theory pursued just the opposite course, and were thus deceived by superficial analogies.

This theory, wide of the mark as it was in its original form, contains a germ of truth, which embryology has brought to light. Its fundamental idea, that the head, in whole or in part, is composed of segments morphologically equivalent to those of the body, may now be said to be an established fact. The problem as it now stands is this, — How far is the segmentation of the body carried forward into the head? in other words, how many segments are represented in the head? Let us look a little further into the nature of the problem, and the methods and means of approaching its solution.

The subject is a difficult one to make intelligible to those who are not familiar with the main features of development; but it is so full of instruction, that it cannot fail to yield some points of interest even to a most superficial examination. Possibly the idea of segmentation of the head, or, to use the technical expression, the metamerism of the head, may appear to some of you quite devoid of general interest or importance. The principal charm of the subject of course lies in its environment, if I may use such a term, to express its general relations or bearings. In attempting to decipher the metamerism of the vertebrate head, we are really engaged in tracing the history of the origin of the great vertebrate stock or phylum. It is simply a question of the genesis or the *phylogeny* of the vertebrate type, at the head of which stands man himself. We do not know when nor how this metamerism of the vertebrate arose; but, both embryology and paleontology afford ample evidence that it existed long before it took the form of vertebræ. Among the earlier and extinct forms of fishes are found some without bony vertebræ, but still divided into segments; and in the development of the fishes and other vertebrates of to-day, we find that the vertebræ are preceded and predetermined by a primordial division of the trunk into a series of uniform segments. This division appears very early in the embryo, long before there is any cartilage or bone, and before there is any trace of limbs, or indeed of any distinctive *vertebrate* organ, except the cordal axis referred to in speaking of the ascidian larva. Now this primordial segmentation carries us back to a stage in the evolution or phylogeny of vertebrates, so full of meaning that its contemplation would seem to be enough to arouse the interest of the most worldly-minded.

This is a stage through which every vertebrate passes on its way from the egg to the adult, a stage in which the fish, the amphibian, the reptile, the bird, the beast, and man find a common level, and in which every title to superior rank lies in unexpressed potentialities. But more than this; for it is here that the vertebrate is an invertebrate, and stands beside its prototype, the segmented worm. On the same metropolitan plain, the lobster, the crab, the insect, in short all the members of the great arthropod group, meet and acknowledge their community of descent. Thus, the great branches of the genealogical tree represented in the higher types first defined by Cuvier converge and unite in a common stem, which bears the deep and enduring mark of metamerism.

So much for the general significance of metamerism. Let us now return to the vertebrate head. If the metamerate type of structure precedes and forms the foundation of the vertebrate type, then the question how many primordial segments are represented in the head takes precedence of the question how many vertebræ compose the skull. The inquiry takes us back to that interesting stage in which the embryo becomes divided into a chain of segments. But here we find that the transverse lines marking the boundaries of the segments do not extend into the region of the head, or at most only into its hinder portion. But we are not yet satisfied that the head is a thing *sui generis,* built upon a plan fundamentally different from that of the body. Baffled in the attempt to find *direct* evidence sufficient to demonstrate the unity of plan which we suspect underlies both the head and the trunk, we next resort to indirect or circumstantial evidence, and begin to question whether the records of ancestral development have been perfectly preserved in the embryonic development. It is here that the towering difficulties of the problem come into view, in scaling which investigation rises to its sublimest heights.

Before the division into segments, there is nothing in the embryo to show even approximately where the head ends and the body begins; the part which is destined to become the head forms with the rest a continuous whole, as shown in the external form and in the continuity of like structural elements. The cordal axis before alluded to is the precursor of the backbone, and this structure extends through the greater part of the head region of the embryo, from which we may safely infer that, at least, so much of the primordial cranium as possesses this structure must be regarded as a direct continuation of the vertebral axis, even though no distinct outlines of segments appear in it. In the absence of such outlines, the inquiry turns upon *indications* which may betray their former existence. For evidence of this sort, the investigator continues his search, first of all, in the *posterior* region of the head, since this is demonstrably the least modified. Now it is just here that embryology has been able to demonstrate, in some of the lower fishes, the existence of at least one genuine *vertebral* segment. In a remarkable shark from Japanese waters, which Mr. Garman of Harvard has recently baptized with the name, *Chlamydoselachus anguineus*, as I learn from Dr. Ayers, who has lately studied its cranium, there are unmistakable evidences of from three to five cranial vertebræ. Indications of a considerable number of *primordial* segments, or protovertebræ as they are called, have been discovered in the hind head of the embryo of the amphibian, the reptile, the bird, and even the mammal. In the lowest representative of the fishes of to-day, the much-talked-of Amphioxus, the segments and the chordal axis extend from end to end; and the head merges so completely in the trunk, that the most searching examination has scarcely yet been able to fix any boundary line. Although Amphioxus takes an isolated position, and may have sacrificed some elements of its head in exchange for the material enjoyments of a semi-vegetative existence, still it must be admitted as an eligible witness to the metamerism of the vertebrate head.

We are indebted mainly to recent studies on the development of the nervous system for the views now held on this subject. In the trunk we find each segment provided with a pair of so-called spinal nerves, both of which spring from the spinal cord by two short roots, known as the anterior and the posterior root. The posterior root bears, just before its union with the anterior root, a spinal ganglion, and is thus stamped as something different from its fellow. This anatomical distinction is the basis of a physiological distinction, the discovery of which, by Sir Charles Bell, in the early part of this century, has been regarded as the most important acquisition of physiology since the time of Harvey. Bell determined by experiment that the posterior roots are appointed for sensory, the anterior roots for motor, work. Thus both structure and function suggest that the spinal nerve is not *one* nerve, but two nerves united; and this point is settled beyond dispute, first, by the independent and unlike development of the two roots, and second, by their complete and permanent separation in such fishes as Amphioxus and Petromyzon. Each segment of the trunk may therefore be said to have two pairs of nerves, a sensory pair with ganglia, and a motor pair without ganglia.

Now we come to a question of absorbing interest not only to the embryologist but also to the anatomist and physiologist. Are the metameric arrangement, the division of labor or function, and the mode of development, essentially the same for the cranial as the spinal nerves? The several inquiries into which the question resolves itself have not yet been fully answered; but the investigation of the last ten years has heaped up affirmative evidences until the final answer has been in the main anticipated. Although a Dutch embryologist, Van Wijhe, has shown that Bell's law must be modified for the cranial nerves, yet we know from the researches that started with His, Balfour, and Marshall, that these nerves follow the same general law of development as the spinal nerves. We find posterior nerves with ganglia and anterior nerves without ganglia; and the latter are purely motor as in the trunk, while the former are sensory. Some of these posterior cranial nerves, however, are mixed nerves; that is, they have in addition to the regular sensory fibres motor fibres, and in this respect they appear to depart from the spinal nerve type. But this difficulty, which still remains to be cleared up, loses its force as an objection, when placed beside an overwhelming amount of evidence in favor of the homology of the two sets of nerves. The posterior nerves of the head and trunk have the same origin; and the early development runs so exactly parallel in both cases, that their fundamental equivalence can no longer be seriously questioned. The cranial ganglia, according to the researches of Beard, receive, secondarily, some elements that are not added to the spinal ganglia; but homologies are settled by original conditions, not by adventitious differences, and hence no objection can be raised on this score to the identification of the nerves. That the cranial nerves agree with the spinal in having a metameric arrangement is made evident by their relations to undoubted segmental structures of the head, such as the gill-arches and the head-cavities.

I must now invite you to the very borders of the beaten ground of investigation; and I hope you will have the fortitude to follow me even to the brink of a precipice or two, should it be necessary, in order to get a view of the steep ascent which now challenges further advance in this direction. I have endeavored to give you the salient points in the historical development of the subject, and it remains for me to define the position now occupied, and so far as possible, by way of anticipation, the path which investigation is destined to take in the immediate future.

In the anterior region of the head, into which the cordal axis or "primitive backbone," as Lankester has called it, does not extend, there are two sensory nerves, the olfactory and the optic, which investigation has thus far failed to reduce to the type of the spinal nerves. No corresponding motor nerves exist; and no decisive evidence of metamerism has yet been discovered in their development, or adult condition. Foremost authorities in anatomy and embryology, like Gegenbaur, Balfour, and Kölliker, have declared that here a dividing line must be drawn, separating the head into two distinct regions, one of which bears with the trunk the common stamp of metamerism, while the other is built upon a plan of its own. It is here that Balfour, looking back into the remote ancestral history of the vertebrates for clews, recognized what appeared to him a primitive boundary line, corresponding to what now divides the head and trunk in many invertebrate forms. According to this view, the fore-brain would represent the *whole* of the ancestral brain, while the mid-brain and hind-brain would represent a number of segments belonging originally to the trunk, but now pressed into the service of the head. This conversion of trunk into head, in answer to the greater and greater demands made upon the brain, as the vertebrate line rose in the scale of development, is just that kind of economy which nature everywhere practises, and which we find exhibited in most instructive grades of elaboration in the nervous system of invertebrates. That this has been the history of the mid and hind portions of the vertebrate brain, is a truth resting upon so many convergent lines of evidence that there is no longer room for scepticism.

The fore-brain, in which the problem culminates, is still enveloped in a dense cloud of uncertainty, pierced by so few and feeble rays of light that we are compelled to accept the lead of conjecture, or to abandon the hope of further advance. We are limited to three hypotheses: We may assume with Balfour, that the fore-brain is the unsegmented brain inherited from an invertebrate ancestor; or with Kölliker, that it is a new formation, representing an outgrowth from the unsegmented anterior end of the primitive nervous axis; or with Kleinenberg, that it represents a number of fused trunk segments, in which the ancestral brain — the "head-glanglion" of annelid worms — has either been absorbed beyond the hope of identification, or totally suppressed.

Balfour's view marks the level of investigation ten years ago. Since that time the progress of discovery has been steadily in the direction of Kleinenberg's view. But we have reached a point where direct, demonstrative evidence appears to vanish, and it is only by the circuitous route of circumstantial evidence that we can push onward. The solution we are looking for does not lie in the skull, the primordial cranium, the cranial nerves, the head-cavities, or the gill-clefts, nor, in short, in any one organ or system of organs that could be named in the head. As Professor Dohrn has insisted, both by word and example, nothing less than a complete analysis of the whole head and trunk can furnish a safe foundation for speculation on this subject. But the task does not end with the vertebrates. The present vertebrate head represents the cumulative development of unnumbered æons, and its ancestral history is only very imperfectly recorded in its embryonic development. Our analysis must therefore be extended to the worms, the arthropods, the molluscs, and, as it now appears, even to the cœlenterates. The history of metamerism must be traced upwards, and the lessons of the simpler types must be our stepping-stones to a knowledge of the higher.

There is little prospect of ever knowing precisely how many segments the ancestor of the vertebrates possessed. The number varies in the different branches of a common stock; and we know that this variation is the result of loss in many cases, and suspect that it may be due to addition in others. But we know that this variability in number has very definite limitations in the laws that control the formation of segments. The possibilities in this respect are by no means the same for all regions of the segmented axis. Although the head segments have undergone the greatest modifications in form, *fixity in number is here the rule*, while variation, if we except degenerate forms, is confined to the posterior trunk segments. In the embryo the anterior segments are invariably first in formation, and generally so in definition, the addition of new segments taking place from behind. *There is not the least ground for supposing that a single segment has ever been, or can ever be, added to the anterior end.* If, in the course of development, segments disappear, the loss is borne by the posterior end, as we see when the tadpole lays aside its fish-like tail in rising to the estate of frogdom. The direction of loss is the reverse of that of acquisition, the one travelling away from, the other towards, the head. Thus the point of maximum variability in number is always most remote from the head. Both the laws of development and the conditions of continued existence tend to strengthen the distinction. The head segments developing first, have the advantage in the struggle for existence, and their supreme importance is the guarantee of their permanence.

Although there is not the least probability, and scarcely a possibility, of adding or interpolating entirely new segments in the head region, and although the chances of loss appear to come to a vanishing point a long way behind this region, still the shadow of uncertainty is not dispelled, and we have to acknowledge that we do not yet know how far the transforming influence of functional changes and substitution of organs has here been felt.

In looking around us for a possible foothold, we inquire, first of all, if there are not some structures connected with the fore-brain on which the seal of metamerism has left an indelible impression. One pair of these so-called cerebral nerves, the olfactory, have fast been losing their high claims to a position of isolation, until at last, stripped of one disguise after another, they have been almost, if not quite, reduced to the level of the sensory nerves of the trunk and hind head, through the researches of Marshall, His, Beard, and others. The identification of this pair of nerves with the rest of the segmental sensory nerves, on the basis of development and structural features, is a triumph of investigation so near at hand that it is scarcely premature to proclaim it. The chain of discoveries bearing on this subject has still many links to be supplied, and here is one of the opportunities of the hour.

The optic nerves still hold undisputed possession of the very pinnacle of isolation ; and even to question their claim to such a position may appear to betray a woful superabundance of speculative audacity that would be less unbecoming to a romancing visionary than to the sober investigator. But without hesitation or misgivings, and without any special claim to scientific prevision, I venture to predict that these nerves and their sense-organs will yet fall into line with the other sense-nerves and sense-organs.

I cannot here enter very far into the question of the origin of the vertebrate eyes, but the subject is one of such great interest, that, at the risk of overtaxing your forbearance, I venture to ask your indulgence for a few general remarks. The evidence in favor of the derivation of the organs of the special senses from a common basis, has been growing during the past few years with such astonishing rapidity, that the hypothesis of independent origin has no longer a respectable claim to attention. If the eyes have been derived from some simpler form of sense-organs possessed by the ancestors of the vertebrates, we can only expect to find out what those primitive organs were by searching among invertebrate animals of the ancestral type. By common consent we turn to the annelids, or segmented worms. Here we find sense-organs of a low order, segmentally arranged, and supplied by nerves bearing ganglia, which correspond in position and general relations to the spinal ganglia of vertebrates. That the segmental nerves and ganglia of the annelids are the morphological equivalents of the spinal nerves and ganglia of vertebrates, is a proposition that now admits of little doubt. If the argument holds for the nerves and ganglia, the basis is given for the comparison of sense-organs. But are there any sense-organs in the vertebrates that can be said to agree in structure and function with the segmental tactile organs of annelids? Leydig and Eisig have given an affirmative answer to this question, and their views have already met with general acceptation. The sense-organs of the lateral line of fishes and amphibia, rudiments of which have been found by Froriep and Beard in the higher classes of vertebrates, have essentially the same structure, the same or a closely allied function, and, so far as known, fundamentally the same mode of development.

Allowing then that these organs are the homologues of the segmental sense-organs of annelids, there arises the very important question, is it possible for such organs to develop into those of the special senses, taste, smell, sight, and hearing? In the vertebrates we meet with no serious difficulty until we come to the eye. The sensory impressions received by a visual organ differ so radically from those received by a tactile organ, that it seems almost incredible that cells devoted to one of these functions could ever serve the other. Nevertheless, this marvellous transformation and change of function have actually taken place, and the fact still admits of ocular demonstration in a very large group of annelids. Sometimes all the tactile cells are converted into visual cells; at other times only a part of the cells assume the new function, while the rest continue to serve the old. The result is that we have at one end of the series pure visual organs, at the other end pure tactile organs, and between the two extremes every grade of mixture represented in veritable compound sense-organs. The picture is a revelation that gives swift wings to suggestion. If such is the path of evolution in one case, the best ground is given for suspecting that the same economy has been practised elsewhere. The discovery of these facts in the leeches, led naturally to the anticipation of a similar origin for the eyes in other annelids and in those groups that have had a common origin with the annelids, before all the arthropods and vertebrates. The existence of segmental sense-organs, as I have said, is well known in other annelids than the leeches, and the origin of eyes from them is fairly well indicated in many cases. It is a most promising subject of investigation, which, like a thousand others, still waits for the encouragement which the wealth of this country will not long, I trust, refuse to supply.

The close relationship between the annelids and arthropods rendered it probable that in the latter the eyes were also derived from segmental sense-organs, and the probability was strengthened by the arrangement of the eyes in successive pairs, as in the larvæ of many insects.

My anticipations seem to have been in the right direction, so far as I can judge from the observations of Dr. Patten, which have been carried on during the last three years through the generous support of Mr. Allis, of Milwaukee.

So far then, as we now understand the genesis of sense-organs, both in the vertebrates and in the invertebrates, the evidence all points to the derivation of the paired eyes of vertebrates from segmental sense-organs. The development of the vertebrate eyes has never been studied from this stand-point; but the subject is a most inviting one, and offers a broad field for observation and reflection.

The existence of an unpaired median eye in vertebrates, which has been claimed by a number of recent investigators, is rendered doubtful by Professor Leydig's careful researches. If the pineal organ turn out to have been a visual organ, it will present a difficulty not easy to dispose of on the hypothesis of derivation from segmental sense-organs. All such sense-organs are *paired*, and a single median eye could arise from them only through the fusion of at least one pair of eyes. We have examples of such fusion in the invertebrates; but it might be extremely difficult to find any evidence favoring a double origin of the pineal organ. Investigation must lead with a searching analysis of structure and development in every group of vertebrates, while keeping up the search for a homologous structure in the invertebrates.

We have now followed the subject of the metamerism of the vertebrate head far enough to get a clear idea of its essential features and general bearings. We started with a special problem and found it to be the centre of inquiries, leading in all directions into the unknown. So it is with all special subjects in biology. The farther we pursue them the broader and more interesting they become. Nothing could be farther from the truth than the idea that such questions are isolated, and devoid of interest to all except the specialist.

THIRD LECTURE.

SOME PROBLEMS OF ANNELID MORPHOLOGY.

By EDMUND B. WILSON.

I SHALL endeavor in this address to consider, in an elementary way, some of the broader morphological questions that are suggested by a study of the development of annelids. It is a subject that has a very special and technical side; yet it is also, as I shall try to show, a subject that at every step suggests wider and deeper problems, some of which extend so far beyond the limits of the particular group of annelids as to stand among the most interesting general questions of comparative zoology. They are, moreover, questions which I believe may be made intelligible and suggestive to those who are not specialists — who, I had almost said, are not even zoologists. To this end, however, it is of primary importance to indicate the point of view from which the subject is considered and the pathway by which it is approached. And hence I may perhaps be pardoned for a few introductory remarks on the purposes and methods of morphological inquiry, and the considerations that lend interest to the group of annelids from a general point of view.

Of the numberless genealogical inquiries raised by the theory of organic evolution, none has a higher interest or has attracted more general attention than the derivation of vertebrates, involving, as it does, the origin of all the highest manifestations of vital structure and action. So long as the evolution theory remained an unproved and comparatively vague hypothesis, as it was left by Lamarck and St. Hilaire sixty years ago, the origin of vertebrates, like other genealogical inquiries, could have no more than a speculative interest, and could produce little direct effect upon morphological investigation — which indeed had quite enough to take care of at home, without following speculative zoology in her erratic excursions. When, however, the field of action had been cleared by such pioneers as von Baer, Johannes Müller, Remak, and Kowalevsky, when speculative zoology had been redeemed and vitalized by Darwin, and the theory of organic descent established on a firm footing, morphological research entered upon a new phase. A broad foundation of known facts had been laid; a splendid working hypothesis had been found. The central question in every morphological investigation became twofold; it was no longer simply *what is?* it was also *how came it to be?* And this second question, be it observed, is not properly a speculative matter at all, but an historical one; it relates not to an ideal or hypothetical mode of origin, but to a real process that has actually taken place in the past and is to be determined like any other historical event. "Speculative zoology" thus, by slow degrees, became the guide and leader of research, and every morphological inquiry became, in the last analysis, a genealogical one.

Now, under the evolutionary interpretation of nature, every higher and more complex form has arisen from a lower and simpler one, presumably now extinct, but possibly more or less similar to forms still existing. In any case the key to the genealogy of higher forms must be sought in the organization of lower but related forms. In morphology, as in every field of research, the interpretation of complex phenomena must be sought through the study of simpler phenomena. And so it comes about that the indispensable basis for every inquiry respecting the derivation of vertebrates is an accurate knowledge of those invertebrate forms, if any there be, that possess any features in common with the vertebrate type. I scarcely need to add that no zoologist would look for the actual progenitor of vertebrates among existing invertebrates. We seek only for forms more or less nearly similar to the ancestral proto-vertebrate. The character of the ancestral type must be largely a matter of inference, not of direct observation.

Now, what are the most fundamental and interesting features of the vertebrate body? Let us leave aside such characters as the presence of a corda dorsalis, the relation of the central nervous system to the alimentary canal, and the double-tubular composition of the body — all of which are peculiar to the vertebrates or their immediate allies. Let us consider only those broader characteristics on which the distinctive vertebrate features are, as it were, moulded.

I think most morphologists will agree that the most striking feature of the vertebrate body as regards structure is its *metamerism* (or segmented structure); and its most remarkable feature as regards development is the fact that growth takes place mainly at one end (the posterior) of the embryo, differentiation becoming more marked as we proceed forwards along the antero-posterior axis of the body. For the sake of brevity, this may be called *apical* or *unipolar* growth. To these fundamental morphological peculiarities we may add a third — that in all vertebrates the body appears to be built up, in a greater or less degree, by the union along the median line of parts that are laid down in the embryo as separate bilateral foundations. This I shall term *concrescence.*[1] Vertebrate morphology therefore presents three fundamental problems for solution, viz., the origin of (1) metamerism, (2) apical growth, and (3) concrescence; and these three lie at the root of all others.

Let us now turn to the invertebrate types. Do any of these possess the three characteristics in question? There are two such types, namely, the *arthropods* (insects, arachnids, crustacea, etc.) and the *annelids* (earthworms, leeches, and a great number of marine worms). The arthropods may, however, be left aside, since the annelids are in every respect simpler and less specialized, and there is strong reason to believe that the leading features of arthropods are inherited from annelid-like ancestors. The annelids have a typical metamerism and they are the lowest of segmented animals; apical growth appears among them in its clearest and simplest form; the phenomena of concrescence are nowhere so

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[1] The term is here used in a wider sense than is ordinarily employed. The occurrence of concrescence in the more restricted sense among the vertebrates is not generally admitted to be a fact, and very eminent authority can be cited both for and against it. However, this very division of opinion in regard to so deep-lying a question only serves to render its investigation more interesting and important.

striking, nowhere less open to dispute. It is therefore clear that from a comparative point of view a peculiar interest attaches to these animals. It is nearly certain that they are closely related to the ancestors of the arthropods ; many zoologists regard them as closely approaching the progenitors of the vertebrates. In any case, no one who wishes to gain any insight into the morphology of the higher segmented types can afford to pass by the annelids, even though their remarkable similarities to the higher types in organization and development be regarded merely as analogies and not as evidence of direct genetic connection.

The importance of the annelids is heightened by another remarkable fact. All annelids, in the course of development, pass through a larval stage (Fig. 2) known as the *trochosphere* or *trochophore*, often disguised but always present in some form. This larval type, under many different modifications, occurs in many other groups of invertebrates, though nowhere so clear and typical as among the annelids. Its significance is one of the most vexed questions of comparative morphology, and opinion is at present nearly equally divided between two opposing schools. According to one view the trochophore is the embryological (or ontogenetic) representative of an ancestral (phylogenetic) type, the "Trochozoön," from which all forms passing through a trochophore stage have actually been derived by evolution — just as a bird, for instance, is supposed to have arisen from a fish-like ancestor because it passes through a fish-like stage of development within the egg. If this view be well founded, and if (observe the double condition) the similarities between annelids and vertebrates indicate real affinity, then the trochophore larva must be taken to represent, in a certain sense, the ancestor of all the higher forms of life. According to a second school, however, the trochophore has no such remarkable significance, but is a "secondary" or "adaptive" larval form — *i.e.*, one secondarily interpolated into the development and representing no ancestral group; as is the case, for example, with the larvæ of insects. Whichever view be taken, a precise knowledge of the trochophore is essential to the investigation of the general problems indicated; and I shall show further on that the study of this remarkable larva raises a number of very singular questions regarding the nature and origin of the higher forms of life.

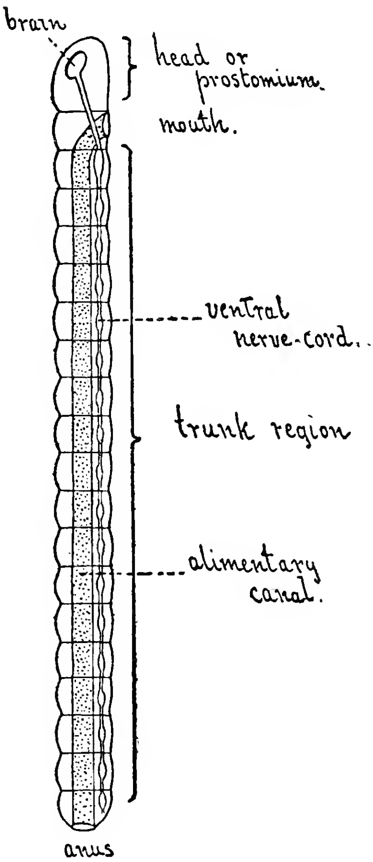

FIG. 1.

I trust that this introduction will suffice to make clear the general considerations which, in my opinion, render the annelids, and particularly their trochophore larvæ, worthy of especial attention; and which give value to the investigation of every detail of their morphology. We turn now to a more special account of the annelids.

The body of an annelid (Fig. 1, which may be taken as a diagram of the common earthworm) is divisible into two widely different regions, though the grounds for making the division do not very clearly appear until the embryological development is taken into account. The first, known as the *head* or *prostomium*, lies anterior to the mouth. It is unsegmented, contains no organs of reproduction, excretion, or circulation (minute blood-vessels excepted), and is devoted to the higher functions of sensation and coördination. It contains the brain (cerebral ganglia), and is often, though not always, provided with eyes, antennæ, or other highly organized sensory apparatus. The second portion, known as the *body* or *trunk*, lies posterior to the mouth. It is much larger than the head, and forms an elongated cylinder divided into a large number of segments (*metameres* or *somites*). The trunk is segmented internally as well as externally, nearly all of the internal organs being divided into segments, or repeated in the successive somites throughout its whole extent — as for example, the ribs or the spinal nerves are repeated in a vertebrate. As regards function, the trunk is in the main given over to nutrition, circulation, excretion, motion, and reproduction; its actions are, however, regulated by a series of ganglia, a pair to each somite, that form a "ventral nerve-cord" along the middle line of the body. It is also, as a rule, provided with sense-organs; these, however, are in most cases less highly organized than those of the head. It has been proved that, in many cases at any rate, the brain exercises a directive action over the other ganglia; so that from a physiological point of view the body may be regarded as subordinate to the head. We shall find a somewhat similar morphological subordination of body to head in studying the development of an annelid.

Upon this simple plan all annelids are constructed, though they are almost as varied in the details of their organization as the vertebrates themselves. The head may be provided with the most elaborate lobes, tentacles, cirrhi, branchiæ, eyes, etc.; or it may lose all of these special organs and become reduced to an insignificant rudiment, as in the earthworm. The trunk is no less diversified; sometimes a simple jointed cylinder, sometimes provided with lateral appendages of the most diverse character in different forms and performing many functions — locomotion of many varieties, respiration, sensation, etc.

Let us now turn to the development; I select *Polygordius*, a form generally regarded as one of the simplest and most primitive of the annelids. *Polygordius* has a perfectly typical trochophore larva (Fig. 2), shaped

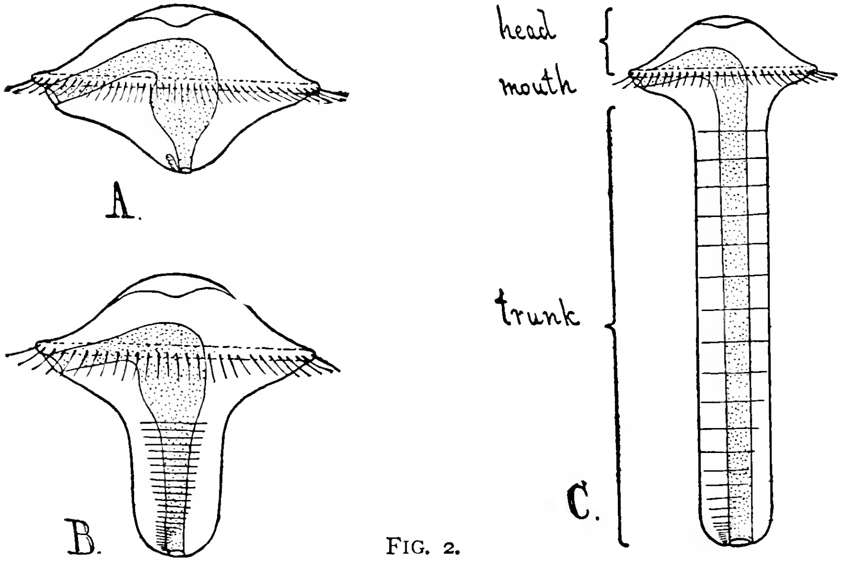

FIG. 2.

almost like a bi-convex lens, with a circle of powerful cilia (prototroch) running around the edge, a mouth at one point near the edge, a retort-shaped alimentary canal (dotted in the figure) and a brain (cerebral ganglion) at the upper pole. The trochophores of other annelids have the same general structure as this, but are often more rounded in form, sometimes being nearly or quite spherical, with the prototroch at the equator. The anus is always at the opposite pole from the brain.

The subsequent history of this larva reveals the singular fact that the parts thus far described become, almost entirely, converted into the *head* or prostomium of the adult. The trunk is a later formation, growing down from the lower pole of the larva — like a bud, as it were — and becoming divided into segments. (Fig. 2, *B* and *C*). At the posterior (lower) end of the body there is a kind of growing point, like the terminal bud of a plant, at which rapid cell-formation takes place, so that the tip is carried further and further down and the body steadily elongates in one direction. The segments are formed successively, those in front being the oldest while new segments are continually in process of formation, one after another, at the growing point. This is a typical case of apical or unipolar growth. Examining the structure of the growing point more narrowly we find that the internal tissues (mesoblast) are arranged in two widely separated lateral bands, which, as the trunk grows older, widen out and grow together along the median line, ultimately giving rise to muscles, blood-vessels, excretory organs, reproductive organs, etc. This process is a form of *concrescence ;* but this mode of growth will be seen more clearly in the development of the leech, described further on. The newly formed trunk ultimately becomes so large that the original substance of the trochophore forms the head only,[1] which is in *Polygordius* scarcely larger than one of the trunk-segments. The cilia of the prototroch disappear, the animal sinks to the bottom, burrows into the sand, and assumes the adult condition.

Let us examine the significance of these facts. It appears that the head is the oldest part of the body, and that in a certain sense the trunk is its offspring, — as a branch is an offshoot from a tree. In other words, the egg develops into what we may regard as a free-swimming head, and this after a while buds off the body — an afterthought, as it were. Observe now the genealogical question that is at once raised. If this mode of development be in any manner a repetition or representation of the ancestral development, then the ancestors of the annelids, and of all the higher metameric types, are represented to-day in the head. And the head must, therefore, be historically, as well as embryologically, the oldest part of the body, and the trunk is a later acquisition.[2]

We may go farther than this. The trunk, I have

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[1] This statement demands some qualification, since the extreme lower pole of the larva, bearing the anus, is carried down with the growth of the trunk, and remains as the so-called telson of the adult. It is, however, unnecessary to complicate the discussion by bringing in this fact.

[2] The "head" of arthropods and vertebrates probably represents the prostomium plus a certain number of trunk somites, closely united and devoted to special functions. Indeed, these somites have so far usurped the functions of the original prostomium that it is doubtful whether this can any longer be distinguished in the arthropod or vertebrate embryo. This, however, does not affect the essence of the historical question under consideration.

said, appears to be budded off from the head. How? By the successive formation of a series of somites, each of which contains its own segment of the alimentary canal and of the circulatory apparatus, a pair of excretory organs, a pair of ganglia and nerves, and in some cases gills, locomotor organs, sense-organs — eyes, it may be — tactile organs, and the like. Each somite has a complete, or nearly complete vital apparatus of its own; and in some annelids (though these cases are rare) the somites may become separate, lead independent lives, and develop finally into complete individuals like the original worm.

These facts irresistibly suggest the question: is not the trunk to be regarded as a linear colony of sexual individuals, successively budded off from the asexual head? — precisely as sexual medusæ are budded off from the asexual scyphistoma,[1] or as proglottides are segmented off from the scolex of a cestode worm. If this question be answered in the affirmative, then all metameric animals, vertebrates and man included, must be colonial organisms, comparable, in point of individuality, with a hydroid or polyp colony. A number of eminent zoologists do not hesitate to accept this conclusion. One of the latest and best students of annelid development (Kleinenberg) regards the trochophore as being simply a modified asexual medusa (!). He finds in it the characteristic medusan nerve-ring, the modified velum (prototroch), the umbrellar and sub-umbrellar regions. He does not state definitely his conception of metamerism, which we are left to infer; but other morphologists have not hesitated to interpret his views in accordance with the colonial theory.

This theory of metamerism is an old and familiar one; it has been adopted by many eminent morphologists, both of the older and the newer schools. That it is a plausible and fascinating hypothesis must be admitted. Yet there is strong reason to doubt whether it can be sustained, either on general or on special grounds. I have not space for a discussion of the objections to the theory, but I will mention a few of the principal difficulties. We do not, as a matter of fact, find in the lowest and most primitive annelids, as we should find if the theory were true, that the somites show clearly marked individuality, or any tendency to become separate individuals. On the contrary, the metamerism of these forms (*Polygordius*, etc.), is less pronounced than in higher forms. It is in the highly organized Polychæta that the repetition of similar parts is most marked, and in the highly modified Oligochæta that the independence of the somites is greatest. A second, and much more fundamental difficulty, is that the trochophore, according to Kleinenberg, has at first no middle germ-layer (mesoblast). How then is it possible, on any theory of budding, to account for the origin of the trunk-mesoblast? Again, as a recent writer (Meyer) has pointed out, if the somites are budded off successively from the head, the anterior somites should be the youngest, which is the reverse of the truth; and finally, the somites are not strictly homodynamous, since the alimentary canal of the anterior and posterior somites (stomodæum and proctodæum, respectively), differs entirely from that of the middle section. These various objections, with others that might be given, are in my opinion fatal to the entire theory.

It is not my intention to review the various theories that have been put forward in place of the colonial theory. Some of them are exceedingly ingenious; none of them are adequate explanations of metamerism. But I wish to show that the study of this question is very closely bound up with that of certain others which need to be carefully studied in the embryology of annelids, and which offer a very inviting field for investigation. The segmentation of the trunk first arises in the internal parts of the embryo — *i.e.*, in the mesoblast — and upon this internal segmentation the external segmentation is, as it were, moulded. Now, the mesoblast, as every embryologist knows, arises in all annelids in two separate lateral masses (mesoblastic bands) that extend lengthwise along nearly opposite sides of the trunk and sooner or later join each other both in front and behind, so as to form, as it were, a longitudinal ring, lying between the two primary germ-layers. In all cases the bands grow mainly at their posterior ends, where, in many cases, each terminates in a large pole-cell (or "teloblast") from which the entire band is derived (see Fig. 6). As development proceeds the two bands widen out, forcing their way between the ectoblast and entoblast, and ultimately grow together along the median line, first below and afterwards above the alimentary canal, which is thus entirely surrounded (Fig. 3, *A.*, *B.*, and *C.*). Metamerism, I repeat, first appears in these mesoblastic bands, and is only secondarily extended to the other parts. And it is interesting to observe, further, that the segmentation of the bands is perfectly distinct long before they unite in the median line. Each somite, therefore, is formed by the union in the middle line of two halves, which are at first completely separate, *i.e.*, by concrescence. And each band grows at its posterior tip, the somites being progressively developed from this point forwards, *i.e.*, by apical growth.

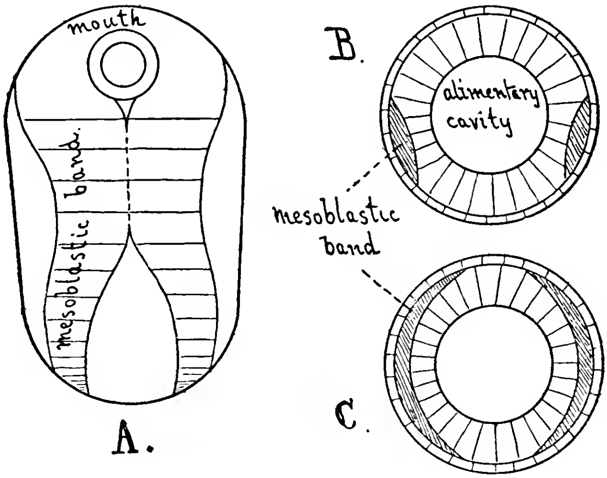

FIG. 3.

I think it must be clear, therefore, that the investigation, from an embryological point of view, of metamerism, of apical growth, and of concrescence is inseparable from the study of the whole series of phenomena relating to the mesoblast formation; and that a close study of the origin of the mesoblast in annelids is of great importance to comparative embryology. If we turn now to the literature of the subject, we find the utmost confusion, the most extraordinary differences of opinion among the various authors, respecting almost every detail of the subject. We find the mesoblast described by one author as arising wholly from the ectoblast, by another as arising from the entoblast, by others as arising from both layers, or again as arising from neither directly, but being differentiated in the course of cleavage. It is described as arising from a single pair of pole-cells, from several pairs of pole-cells, from no pole-cells at all — and so on through a long list that might be given did space suffice. It is, in short, simply impossible, at present, to reconcile the various modes of mesoblast-formation in annelids as described by various good authorities, and there is scarcely a more confused subject in comparative embryology, or one which more pressingly demands revision. It is no wonder that Kleinenberg, who has been largely influenced by the study of annelids, attempts to cut the Gordian knot by denying the very existence of the mesoblast as a "germ-layer" — "es gibt gar kein Mesoderm." Nevertheless very few forms have as yet been adequately studied. Indeed, scarcely a single case has been exhaustively worked out; and while this is the case, we need not despair of reducing the various modes of mesoblast-formation to a common type. Until this has been accomplished, however, it will, I believe, be premature to speculate on the origin and meaning of metamerism.

We may come now to closer quarters with the problem of concrescence and the meaning of the trochophore, questions that have thus far only been alluded to in passing. I am obliged to treat this part of the subject in a more technical manner, though I fear it will be at some sacrifice of intelligibility to those not especially interested in the subject. If we examine the embryo of a leech (*Clepsine*), in the middle period of development (Fig. 4, *A*.), we find that the future alimentary canal is represented by three macromeres (yolk-cells), distended with food-yolk, on the top of which the remaining parts are spread out in a flat disc, the margins of which are notched at two opposite points. These notches mark, respectively, the anterior and posterior ends of the future body; and it is therefore possible to distinguish the right and left sides of the embryo, even at this very early period. The margins of the disc are thickened on each side to form a structure known as the *germ-band.* The germ-bands join anteriorly above the notch to form the head; posteriorly each ends in a group of five large pole-cells which form the growing point of the band. As development proceeds, the disc extends over the yolk-cells and finally encloses them completely; its edges grow together in a seam (the beginning of which is shown in Fig. 4, *B.*), which extends along the median ventral line of the embryo. The body is formed by the fusion of the two germ-bands, which are at first completely separate except at their foremost ends. But more than this, a close examination of the germ-bands shows that each consists of several distinct elements. Each is covered by the outer ectoblast; it contains a cord of nervous matter, from which the corresponding half of the ventral nerve-cord is derived; it has a cord of cells which appears to be concerned in the development of the excretory organs (nephridia); and each contains internally a mesoblastic band like that of

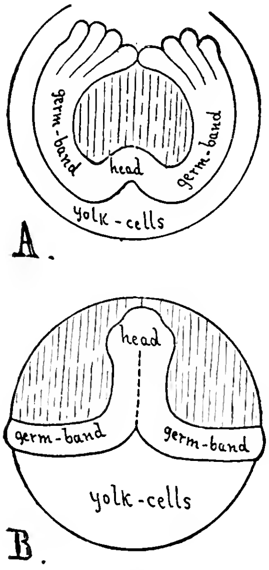

FIG. 4.

Polygordius, which gives rise to muscles, blood-vessels, etc., and which, by segmentation, first blocks out the metamerism of the trunk. Thus, with exception of the alimentary canal, every system of the body — circulatory, excretory, muscular, nervous, reproductive — is laid down in two completely separate halves. And the union of the two germ-bands, which form the two halves of the trunk, is a typical and unquestionable case of concrescence. This extraordinary phenomenon is exhibited in its greatest perfection in the leeches and some of the fresh-water annelids ("naids"). It occurs in a striking form in the development of the earthworm, though modified by the very different structure of the gastrula. In *Polygordius* the two halves of the body are never as completely separated as in the leech, yet the primary separation and subsequent growing together of the mesoblastic bands is clearly enough a simplified form of the same general phenomenon; and the same is true of many other marine annelids. Among the arthropods complete concrescence, — *i.e.* the complete separation of the two halves of the body on the ventral side — has been observed in a single case only; but a partial concrescence, comparable with that of *Polygordius*, probably occurs throughout the entire group. Whether complete concrescence occurs among the vertebrates or not is still a disputed question. It is asserted, on very high authority, to take place in some of the lowest vertebrates (sharks and bony fishes) in nearly as typical a form as among the leeches, but this is disputed by many observers. It is, however, unquestionable that a partial concrescence — that for instance in the mesoblast and the central nervous system — takes place throughout the group, and the phenomena are in some cases nearly as striking as in the annelid types.

What is the interpretation of concrescence? Is it a secondary adaptive mode of growth, necessitated by some mechanical condition of development? Or is it a primary, ancestral process, which means that all unpaired organs (such as the heart or the spinal cord) now formed by concrescence were originally double? Both sides of this alternative have their adherents. The first view, which is represented by very eminent authority, regards concrescence as a process of restoration (to use Professor Whitman's apt expression) by which the two halves or the embryo, which have been mechanically separated in the course of development, are brought together again. I have not time to go fully into the nature of the causes that are supposed to have produced this separation. Broadly speaking, however, the main cause is supposed to have been the excessive accumulation of food (yolk) in the lower and middle part of the egg, for the use of the developing embryo. This mass of food, lying as it does in the median line, is supposed to have temporarily bisected the embryo, as it were; so that a subsequent concrescence became a mechanical necessity in the construction of the body. According to the second view concrescence has a far deeper meaning, though the probability is not lost sight of that accumulation of yolk may have modified its character or heightened its effect. The origin of concrescent growth is to be sought, from this point of view, in the origin of bilaterality itself — an inquiry which brings us to a deep-lying problem concerning the mode of derivation of bilateral animals from the radiate (cœlenterate) forms, which by common consent are considered to have been their progenitors.

At present, apparently, the data do not exist for a trustworthy decision between these two conflicting views; though, as a matter of fact, most practical embryologists adopt one or the other as a working hypothesis. Speaking for myself alone, and judging from the development of annelids, the view that concrescence is a wholly secondary process seems inadequate and opposed to many important facts. There are forms — the earthworm, for instance — in which there is little food-yolk, and yet a nearly typical concrescence takes place. Furthermore, a nearly complete series may be traced, from such typical cases of complete concrescence as *Clepsine* or *Rhynchelmis*, to the opposite extreme of *Polygordius*, in which there are no "germ-bands" and no concrescence save that of the mesoblastic bands. It is precisely these bands, however, that form the most important element of the germ-bands in *Clepsine*, etc., inasmuch as the development of the other parts is, as I have said, moulded upon them. There is no logical justification for making any fundamental distinction between complete concrescence (*i.e.* of the germ-bands), and partial concrescence (*i.e.* of the mesoblastic bands). The latter process is, however, one of the most characteristic features in the development of all annelids, whether possessing food-yolk or not; and this, in my opinion, is fatal to the theory in question.

Let us turn, therefore, to the second view. If it be true that the origin of concrescence goes back to the origin of bilaterality, then our inquiry must be extended to include the genealogy of the Bilateralia — *i.e.* of all forms above the Cœlenterata. It is generally agreed that the bilateral type of structure arose by the modification of a radial type, but as regards the mode of transition two totally different views are maintained. Under the older view, still maintained by some morphologists, the long (or principal) axis of the radiate body — *e.g.* of a *Hydra* or a sea-anemone — corresponds to the long or antero-posterior axis of the bilateral body; and hence the oral face corresponds to the anterior end, and the aboral face to the posterior. The mouth must therefore correspond in the two cases, and the anus of Bilateralia is a new formation. Under the more recent view — which is held by the greater number of morphologists — the long axis of the bilateral body corresponds to one of the *transverse* axes of the radiate body, and the oral face of the latter is represented by the ventral aspect of the former.[1] The justification of this view — which to me appears the only possible one — lies in the facts of embryological development. The gastrula stage of development is all but universally regarded as being, in a broad sense, the embryonic representative of the radial, two-layered, ancestral type. The blastopore (or gastrula mouth) represents the ancestral mouth (or protostome). Hence the mode of transition from the radial gastrula to the bilateral adult should give us decisive evidence in regard to the ancestral transition. Now, it has been shown in the clearest manner that, in the great majority of cases, at any rate, the blastopore occupies

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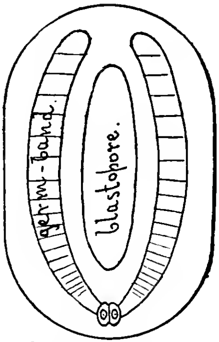
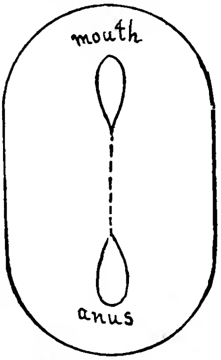
[1] This applies, of course, to the bilateral invertebrates only. The vertebrates are left out of consideration, as having, in all probability, arisen from forms to which the statement would equally apply.

the ventral surface of the embryo (Figs. 5, 6), and that the elongation of the body takes place approximately in the plane of the blastopore—*i.e.* that the long axis of the adult coincides with one of the transverse axes of the gastrula. This appears with especial clearness in the development of annelids (Fig. 5), where the bilaterality is thrown back, in a measure, upon the gastrula itself, and the blastopore is more or less elongated, its anterior part persisting as the mouth; or in that most primitive arthropod, *Peripatus*, where the elongated blastopore closes in the middle, the two openings thus left persisting as mouth and anus respectively (Fig. 6).



Earthworm



Peripatus.

FIGS. 5 AND 6.

In these facts lies, as I believe, the key to the problem of concrescence. We see from such cases as the earthworm and *Peripatus*, that the separation of the two sides of the body (germ-bands), may be caused, not by a mass of food-yolk, but by the blastopore itself, and *concrescence is a sequence of the closure of the blastopore*, modified more or less extensively by accumulation of yolk. In forms like the leeches or vertebrates concrescence is modified and exaggerated by the fact that the region of the blastopore is occupied by the enormous mass of yolk. But this should not blind us to the fact that the primary cause of concrescence lies in the position of the blastopore, not of the food-yolk. From a genealogical point of view I believe this must be taken to mean that bilateral animals have arisen from radial forms by elongation in one of the transverse axes of the latter, the oral face becoming the ventral aspect, and the aboral face the dorsal. The mouth, meanwhile, shifted its position so as to lie near the anterior extremity of the new long axis, and the lateral portions, growing together more or less completely along the region formerly occupied by the mouth, gave rise to the process of concrescence in the ontogeny. What, then, was the origin of the anus of bilateral forms? Here again the answer of embryology appears to be nearly or quite conclusive. The blastopore gives rise sometimes to the mouth, sometimes to the anus, sometimes to both. The only possible interpretation of these facts would seem to be that the blastopore originally gave rise to both mouth and anus, the case of *Peripatus* being an interesting and apparently isolated remnant of the ancestral mode of development, or perhaps a reversion to it. Under any other view, as has often been pointed out, we should be reduced to the absurdity of regarding the mouth of one animal as homologous with the anus of another, perhaps closely related, form; or we should be involved in other difficulties, equally great. The original mode of closure of the blastopore has been secondarily modified in the great majority of cases, but the mesoblastic bands and the neural cords still follow the original mode of development, being laid down separately on either side of the region of the blastopore, and growing together along its line of closure.

Let us now turn, in the last place, to the significance of the trochophore. A very little consideration will show that if the foregoing discussion of concrescence has any weight the trochophore cannot possibly be an ancestral larval form, but is one that has undergone very great secondary modification. For concrescence takes place throughout the trunk-region; and if the line of concrescence represent the original line of closure of the protostome the trunk cannot be of later origin than the head, since, by the hypothesis, the ancestral radiate body gave rise, by transverse elongation, to both head and trunk. From which it follows that the suppression of the trunk-region, which is the essential feature of the trochophore, must be a secondary matter. In other words, the anterior part for some reason develops more rapidly than the posterior part, which lags behind and only makes its appearance after the anterior part has acquired highly developed organs of locomotion, sensation, and coördination. Strong confirmatory evidence of this view appears to me to be afforded by the following facts: If the suppression of the trunk region be a secondary character, we should expect to find in the larva some rudiment of the trunk, present, but in an undeveloped state; and, in point of fact, I believe such a rudiment is always present. If we examine the posterior portion of the trochophore we find on each side of the body, near the end of the alimentary canal, a small group of cells — or, it may be, a single cell ("primary mesoblast"), lying in the cavity of the body. It is this cell or group of cells that in later stages gives rise to the mesoblastic band — *i.e.* to the basis of one-half of the trunk. The trunk is not present, but its germ is; and hence it is not strictly correct to say that the trochophore represents the head alone. It is a highly developed, individualized head, which carries within itself a minute, rudimentary trunk — just as in a seed two huge modified leaves, the cotyledons, carry between them the minute germ of the stem, root, and foliage-leaves. If the cells in question can be shown to be always present the trochophore is not a diploblastic organism, but a triploblastic one, and Kleinenberg's comparison of the trochophore to a medusa falls to the ground. Kleinenberg asserts that the trochophore consists at first of the ectoblast and entoblast alone, the mesoblast being a later formation. This conclusion is based upon the study of *Lopadorhynchus*, in which the mesoblast is apparently not present at the start but is afterwards split off from the ventral ectoblast. This result has always seemed a very puzzling one, which could not be harmonized with what is known of the mesoblast formation in the earthworm, the leeches, and many other forms. I have recently been able, however, to examine the development of an annelid (*Nereis*) which I believe solves the puzzle and shows how *Lopadorhynchus* is connected with the other forms. The early trochophore seems to be diploblastic, as in *Lopadorhynchus* — *i.e.* to consist of ectoblast and entoblast only, without any trace of mesoblast. In later stages the mesoblast arises from the anterior ventral portion of the outer layer ("ventral plate"). A study of the early stages of development however — which Kleinenberg did not succeed in following — shows that the cells of the ventral plate are differentiated from the remaining outer layer cells almost from the beginning of development, and even without the use of reagents can be easily distinguished from the remaining outer layer cells in the fully established "diploblastic" trochophore. *These cells have* *the same ontogenetic origin, in the cleavage-process, as the mesoblast in other annelids.* In other words, the mesoblast is differentiated during the cleavage in essentially the same way as in other forms, but is not removed from the surface until a very late period. It forms, in fact, a part of the outer layer of the larva, which has accordingly a deceptive appearance of being two-layered. In reality the third layer is already present; and it constitutes here, as elsewhere, the germ of the trunk.

It appears, therefore, that in all cases the trochophore contains a rudiment of the trunk, the presence of which means in my opinion, that the larva once possessed a fully developed trunk, which is now temporarily reduced in favor of the head. A somewhat analogous case is that of the Nauplius larva of the Crustacea. This larva has but three pairs of functional appendages, which become highly organized and of great functional importance while the remaining appendages are represented by mere rudiments, or, it may be, by mere groups of cells near the posterior extremity of the larva. Now, it is nearly certain, in the opinion of the best authorities, that the Nauplius is a secondary form; that the posterior appendages formerly developed in uniform succession to the three anterior pairs; and that their temporary suppression in the Nauplius has been secondarily brought about. This case, though not entirely parallel to that of the trochophore, will serve to illustrate the general character of the change which I believe the latter form has undergone.

Let us finally pass in brief review the principal points we have considered. Of the three main problems suggested by the development of annelids, only one can at present be brought under a satisfactory working hypothesis, and this solution is one that many embryologists would be unwilling to accept. I think the great majority of morphologists will agree that no satisfactory explanation of metamerism has yet been given; and the problem of apical growth is still farther from a solution. Concrescence stands on a very different footing, since clear and definite causes for it can be assigned; yet even here a complete solution of the problem will only be possible when comparative embryology has advanced far beyond its present standpoint. As regards the trochophore, opinion is still divided; and I am giving only a personal view in stating that the accumulating evidence seems to favor, in the main, the view that it is a secondary larval form, which gives no clue to the ancestory of the segmented animals. To those whose interest in science lies in the consideration of its positive results only, the outcome of this discussion will doubtless seem rather unsatisfactory; and it must be admitted that in some respects the fundamental problems of annelid and vertebrate morphology seem to be as far from a solution as in the time of von Baer. To the investigator, however, it is the unsolved problems that call forth the deepest interest. It is the very vagueness and uncertainty of the subject that impress upon us how much remains to be done in the embryology of annelids, and arouse the interest with which we look forward to the results of future investigation in this field of study. That the problems of metamerism and apical growth will ultimately be solved, there can be little doubt; but the present need is for new facts, not for new theories. When the facts are forthcoming, the theories will take care of themselves.

FOURTH LECTURE.

THE GASTRÆA THEORY AND ITS SUCCESSORS.

BY J. PLAYFAIR McMURRICH.

WHEN morphological science had emancipated itself from the influence of the Cuvierian doctrine of types, a result mainly due to the publication of Darwin's "Origin of Species," morphologists turned their attention to the problem of tracing out the phylogeny of the various animal groups and forms. During the last thirty years much has been accomplished along this line, but one of the greatest of the difficulties which presented themselves in the way of a completion of the phylogenetic scheme, was the lack of facts upon which to base a satisfactory explanation of the manner of origin of the Metazoa from the lower unicellular organisms.

From time to time, however, theories have appeared which attempted an explanation, but, with a single exception, they have been weighed and found wanting. These theories may be classed in two groups, (1) those which take for their starting point a multinucleate protozoan, such as *Opalina* (von Ihering), and (2) those in which a colonial flagellate is regarded as the ancestral form (Haeckel, Lankester, Balfour, Bütschli, and Metschnikoff).

Von Ihering suggests[1] the possibility of the transformation of a multinucleate protozoan into a metazoan by the segregation of the protoplasm around the various nuclei, whereby the organism becomes multicellular, the original Infusorian mouth becoming the mouth of the multicellular animal, and the contractile vacuole its excretory system. This theory, however, has not been received with any degree of favor, inasmuch as it lacks confirmation from the developmental phenomena of the Metazoa, the cases in which the segmentation results in a syncytium (Crustacea, Insecta) being evidently a secondary modification due to the accumulation of food-yolk. There can be little doubt but that the segmentation of the ovum and the resulting formation of a morula or blastula are most readily comparable to the development of a colonial protozoan, and the theories based upon this idea are more worthy of consideration than that advanced by von Ihering.

The first of these theories in point of time, and the one which has had the greatest influence upon embryological investigation, is Haeckel's well-known Gastræa theory. This made its appearance in 1872, and was the outcome of the researches embodied in the classic "Monograph of the Calcareous Sponges." The simplicity of structure of the lowest calcareous sponges, and their apparent similarity to the gastrula of the higher forms, a similarity all the greater to the mind of Haeckel on account of his erroneous conception of the structure of

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[1] H. von Ihering. Vergl. Anatomie des Nervensystems und Phylogenie der Mollusken. Leipzig. 1877.

the sponges, were the leading causes in the evolution of the theory. Haeckel entirely overlooked the presence of the flattened ectodermal layer (first discovered by F. E. Schulze in 1875, and since demonstrated by other investigators in many different groups of sponges), and homologized with the ectoderm of the Cœlenterata and of the Gastrula the mesoglœa, or rather the mesoglœa *plus* the unobserved ectoderm of the sponges. Thus a sponge was to him a diploblastic organism, the *Olynthus* being "nur eine festsitzende Gastrula."

A complete exposition of the theory and of the facts upon which it was based is to be found in the Jenaische Zeitschrift.[1] The starting point in the line of evolution, according to the theory, was a simple mass of protoplasm destitute of a nucleus, the *Monerula*, a representative of which is found in *Protamœba*, and the disappearance of the nucleus of the ovum previous to its division to form the polar globules, was considered to be the reproduction of this stage in the individual development. It is probable, however, that the nucleus is represented in *Protamœba* by scattered particles of chromatin disseminated through the cytoplasm and not yet aggregated into a definite mass, in which case the Moners, as Haeckel understood them, do not exist. Granting the disappearance of the nucleus in the ovum, the explanation that it is a return to an ancestral condition is most unsatisfactory. The

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[1] E. Haeckel. Die Gastræa-Theorie, die phylogenetische Classification des Thierreichs und die Homologie der Keimblatter. Jenaische Zeitschr. Bd. viii. 1874.

E. Haeckel. Die Gastrula und die Eifurchung der Thiere. Jen. Zeitschr. Bd. ix. 1875.

E. Haeckel. Nachträge zur Gastræa-Theorie. Jen. Zeitschr. Bd. xi. 1877.

ovum is a cytode, the next stage in the process of evolution according to Haeckel's scheme, and that it returns for a few minutes to a lower grade of organization simply to indicate its ancestry is certainly an idea at variance with all morphological principles. Thanks, however, to our more perfect technique, we now know that the original nucleus of the ovum does not disappear but is the direct ancestor of the nuclei of all the cells composing the organism resulting by development, and there is therefore no Monerula stage in the developing ovum.

The next stage of evolution was the formation of a nucleus, by which the Monerula was converted into a cell or cytode, the ancestral form being a *Cytula* equivalent to the existing *Amœba.* Following this came the *Morula,* represented ontogenetically by the morula stage which occurs in the development of certain forms, and during which the embryo consists of an undifferentiated solid mass of cells. That this stage can be considered primitive, and the early appearance of a segmentation cavity which is found in so many forms a secondary condition seems however very doubtful. The evidence at our disposal points the other way. No living representative of the morula stage is known, and to fill this gap Haeckel proposes an hypothetical ancestor, the *Synamœbium.*

The fourth stage is the *blastula,* a hollow sphere produced by the usually contiguous cells of the morula secreting a fluid, which, passing to the interior, forces the cells to the periphery. The hypothetical ancestor corresponding to this ontogenetic stage is termed the *Planœa.*

The fifth stage is the *gastrula,* formed from the blastula by the invagination of certain of its cells, and represented ancestrally by the hypothetical *Gastræa.* This forms the last stage common to all the Metazoa; from it various paths branch off: "sie führen von der monaxonien Gastrula einerseits zu den monaxonien Spongien und den stauraxonien Acalephen, anderseits zu den dipleuren oder bilateralen Bilaterien; und zwar zunächst zu den Würmern, aus denen sich die vier typischen Stämme der Mollusken, Echinodermen, Arthropoden, und Vertebraten erst später hervorgebildet haben."

Such is in outline the Gastræa theory, the first attempt to plan out from embryological data the phylogenetic origin of the Metazoa. One of the greatest difficulties in the way of its acceptance is the occurrence of delamination; that is, the conversion of the monoblastic blastula into a diploblastic organism, not by invagination, but by the separation off, by karyokinetic division, of the inner ends of the blastula cells. Some of Haeckel's followers have endeavored to overcome this difficulty by rejecting as improbable Fol's observations on the delamination in *Geryonia,* but renewed study of the development of the Trachymedusæ by Metschnikoff and Brooks have incontestably demonstrated the occurrence of the process. Haeckel, however, met the obstacle more fairly, and, relying on the fact that in comparatively closely related forms both modes of endoderm formation may be found, held the view that delamination is a secondary condition derived from invagination, failing however to explain *how* it has been derived, and thus leaving the difficulty as great as before.

Shortly after the publication of the Gastræa theory Ray Lankester brought out his *Planula* theory, the key-note of which is the formation of the endoderm primarily by delamination, invagination being thus a secondarily acquired phenomenon. Thus Lankester's views stand in direct contrast to those of Haeckel.

Like Haeckel, Lankester attempts[1] to give the different historical phases recapitulated in ontogenetic development. He starts with the ovum, the *Monoplast*, corresponding to Haeckel's second stage, the Cytula. This is succeeded by the *Polyplast*, equivalent to Haeckel's third and fourth stages, for Lankester recognizes two different forms of Polyplast, — one in which it is solid, the Morula, and another in which it is hollow, the blastula, derived from the morula in the manner indicated by Haeckel. Up to this point the only difference between the two authors is the omission by Lankester of the Monerula stage. To the Polyplast succeeds the diploblastic *Planula*, for which Salensky's more convenient term *Diblastula* may be employed. This is a two-layered vesicle without a mouth, the inner layer of cells (endoderm) having been formed by delamination. The cavity of the blastula (*blastocœl*, Huxley) has now become the digestive cavity, or archenteron, the cells lining it having gradually acquired a digestive function while they still formed the inner ends of the blastula cells, the acquisition of the function leading to their differentiation from the non-digestive or ectodermic portion.

Delamination is, however, a relatively unusual occurrence, invagination replacing it in a large number of cases. How can its occurrence be explained on the basis of the Planula theory? The changes which led to the

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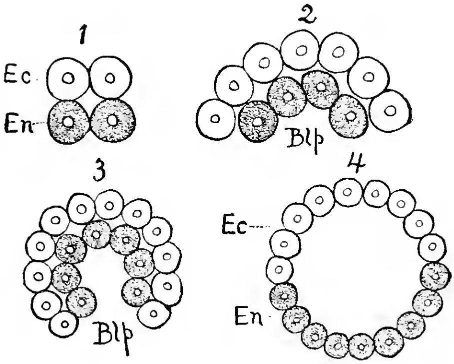
[1] E. Ray Lankester. Notes on Embryology and Classification of the Animal Kingdom, etc. *Quart. Journ. Micr. Sci.* vol. xvii. 1877.

formation of the diblastula must be regarded as having been primarily adaptive, but later became dependent upon heredity. The physiological molecules composing the ovum tended to become differentiated earlier and earlier in the ontogenetic history, those destined to form the entoderm being early set apart for that purpose. This is Lankester's doctrine of precocious segregation, equivalent to the law laid down by Haeckel as "heterochrony in the palingenetic phenomena of ontogeny." Lankester supposes that in invaginate types the segregation of the endoderm extends to the first division of the ovum, one spherule containing the ectodermal molecule and the other the entodermal (Fig. 1). By the continued division of these spherules a number of cells are produced, the entodermal ones arranging themselves within the ectodermal, a gastrula being thus formed (Figs. 2, 3) without the intervention of a blastula. This structure, which occurs so frequently in the typical formation of an invaginate gastrula, Lankester considers to be an altogether different structure from that which precedes the diblastula, and to have been secondarily acquired by the mechanical accumulation of fluid between the cells of the forming gastrula, whereby the endoderm cells are forced out from their position within the ectoderm, and a cavity is thus formed between the two layers (Fig. 4). This cavity is, however, not equivalent to that of the



FIGS. 1–4.

delaminating blastula, inasmuch as it does not become the archenteron on the formation of the endoderm, but is obliterated by the invagination. It is necessary then to distinguish between the delaminating blastula and the invaginating "pseudo-blastula," and between the archenteric blastocœl of the former and the "pseudo-blastocœl" of the latter.

The ingenuity of this theory is its strong point, but simplicity can hardly be considered one of its characteristics. It has not met with the general acceptance which greeted its predecessor and rival, nor has it had the same influence on embryological investigation, — a result owing to the fact that no evidence in support of such an origin of the gastrula can be found.

A third theory is due to Balfour, and may be termed the *Amphiblastula* theory.[1] It is founded upon the peculiar blastula of the calcareous sponge *Sycandra*, the cells of which at one pole are columnar and ciliated, while those of the other pole are larger and granular. Balfour thinks it possible to consider this larva as a colony of Protozoa one-half of the individuals of which have been specialized for locomotor and respiratory purposes, while the others are essentially nutritive. In the later stages, however, the ciliated cells become invaginated within the granular ones, a fact which seems at variance with the theory if the granular cells are to be homologized with the endoderm of other forms, but which Balfour explains in the following manner. On the settling down and fixation of the sponge embryo the ciliated cells, being partly locomotor in function, become, to a

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[1] F. M. Balfour. A Treatise on Comparative Embryology, vol. i. London. 1880.

great extent, useless, and are therefore invaginated, the nutritive granular cells being thus able to expose their full surface for the acquisition of food particles. The ciliated cells are enabled to carry on their respiratory function by the formation of an osculum and pores.

According to this idea the nutritive function ought to reside in the ectodermal cells of the Sponge, and in the flat cells lining the walls of the canals which Balfour took to be derived by invagination from the ectoderm, and the collared cells of the ciliated chambers should be purely respiratory, and Metschnikoff's researches appeared to confirm this view to a large extent. The recent extensive observations of von Lendenfeld[1] are, however, in direct opposition to it, demonstrating that it is the collared cells which are ingestive, thus confirming the earlier statements of Carter. In addition to this, the fact that the development of *Sycandra* cannot be regarded as primitive, and therefore as throwing light on the ancestry of the Metazoa, indicates that the *Amphiblastula* theory is not founded on a secure basis.

The speculations of Bütschli, which led to what that author has denominated the *Plakula* theory,[2] had their starting point in a study of an existing flagellate, *Gonium*, which consists of a single-layered plate of cells. The transverse division of all the individuals of such a colony would result in the formation of a two-layered plate which Bütschli terms the *Plakula*. At first in all probability there would be no difference in

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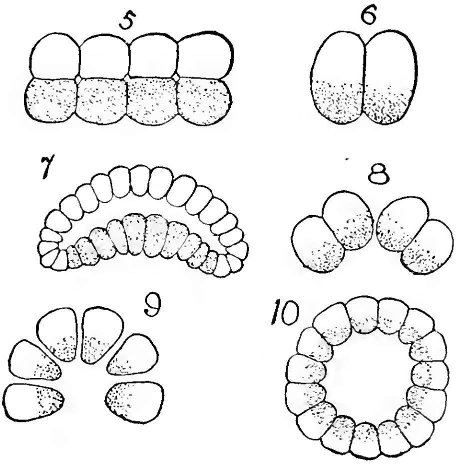
[1] R. von Lendenfeld. Experimentelle Untersuchungen über die Physiologie der Spongien. Zeit. für wiss. Zool. Bd. xlviii. 1889.

[2] O. Bütschli. Bemerkungen zur Gastræa Theorie. Morph. Jahrb. Bd. ix. 1884.

the cells of the two layers, but later one layer might specialize for nutritive purposes, and the other for locomotor (Fig. 5). From such a condition, by the gradual bending of the plate so that the nutritive layer becomes concave (Fig. 7), a gastrula could readily be produced, and in this connection Bütschli points out that the concavity would be useful to the colony, serving as a trap for food-particles and also allowing a larger number of cells to come into contact with a larger food body.



Figs. 5–10.

The blastula which so frequently precedes invagination could be produced from this by the accumulation of fluid between the two layers; and furthermore, delamination may have been brought about by the plate, while still one-layered, becoming concavo-convex (Figs. 6, 8 and 9), and finally a hollow sphere (Fig. 10), the transverse division of the constituent cells then taking place.

Unfortunately for this theory it does not find general support in embryological phénomena, nor any more than the Planula theory does it explain the formation of the blastula in a manner in accordance with the actual facts.

There is a series of phenomena which none of these theories attempt to explain. Many of the authors who have recently contributed to our knowledge of Cœlenterate development have felt strongly the insufficiency of these theories to explain the phenomena occurring in the early stages of the ontogeny of forms belonging to that group, and have been led either to throw doubt upon their applicability to these cases (Brooks, von Lendenfeld, Goette), or have exhibited considerable intellectual elasticity in endeavoring to bring about a harmony. Let us glance at the methods of formation of the diploblastic embryo in the lower Metazoa, before passing on to a consideration of the next theory.

In Sponges there seems little room for doubt that the solid embryo or planula, as we may call it, is of much more frequent occurrence than the invaginate gastrula. In *Ascetta* a blastula results from segmentation, and by the migration of cells situated at one pole of this structure, a solid central mass of cells is produced, and a similar process (perhaps assisted by delamination) probably occurs in *Halisarca*, *Reniera*, *Esperia*, and other forms; at all events, there is nothing in the formation of the central cells of the embryos of these forms which indicates the occurrence of invagination. This process is exceptional in the Sponges, and so far as is known at present occurs only in some of the simpler calcareous sponges and in *Oscarella*, and in these cases presents some peculiar characteristics which throw doubt upon the homology of the Gastrula of these forms with that of such a form as *Sagitta*.

In the Cnidaria the absence of an invaginate gastrula is quite as striking as in the Sponges. It is unknown in the Hydrozoa, in which migration of cells of the blastula resulting in the formation of a solid planula may be regarded as the rule, though in the Trachymedusæ delamination may produce a hollow diploblastic embryo without the intervention of a solid condition. The formation of a solid morula during segmentation which occurs in such forms as *Hydractinia, Clava,* etc., may readily be regarded as a precocious immigration, finding its counterpart among the Sponges in *Chalinula.* (Kellar).

In the Scyphomedusæ some forms such as *Pelagia, Cyanea,* and *Chrysaora* have long been considered to have an invaginate gastrula. Regarding *Pelagia* there is no doubt that this is really the case, and Metschnikoff has described the occurrence of invagination in *Nausithoe.* As regards the other forms, however, the observations are not sufficiently complete to render the occurrence of this process certain. Sections are absolutely necessary for a correct determination of the processes which occur, and Goette's observations on *Aurelia* and *Cotylorhiza* show that a structure exactly resembling an invaginate gastrula may be produced from a solid planula formed by migration. My own observations on *Cyanea arctica* demonstrate the occurrence in its development of a solid planula formed apparently by immigration, and it seems probable from Claus' figures that such is also the case in *Chrysaora.*

Among the Anthozoa it is very doubtful if invagination ever occurs. In the majority of forms investigated delamination is the process by which the inner cells are formed, but invagination has been stated by Kowalewsky to occur in *Cerianthus membranaceus* and *Actinia,* sp. (?) In *Metridium marginatum* I have found what renders doubtful the statements of that author, who studied optical sections only. A hollow blastula results from segmentation; delamination then occurs, producing a diblastula. At the same time, however, or even previous to the delamination, a certain amount of disintegration of the inner ends of the cells takes place, the central cavity becoming more or less filled with granules of food-yolk. These are later on either absorbed, or pass out through the mouth-opening, which is formed later, and we get a structure resembling closely in general appearance a typical gastrula. The fact that Kowalewsky found some food-yolk in the supposed gastrula cavity of *Cerianthus* seems to indicate that we have in that form not an invagination, but a delamination such as occurs in *Metridium*.

To sum up briefly, in the lowest Metazoa there is produced a solid embryo, either by immigration of certain of the blastula cells or by delamination, a hollow diblastula being formed in a few cases by the latter process, and still more rarely invagination occurs. Accordingly the difficulties in the way of the Gastræa theory are very great, and the other theories fail to explain the immigration phenomena. It is hardly logical to take phenomena occurring in comparatively few cases to be the most typical, and consequently we must assume that the formation of a solid planula and a subsequent hollowing out of the central mass is typical in the Porifera and Cnidaria.

The Parenchymella or Phagocytella theory proposed by Metschnikoff[1] seems much more in accordance with the facts than any of the theories hitherto discussed. He starts with a spherical hollow colony of flagellate Infusoria similar to *Volvox*, and supposes that in it "cer-

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[1] E. Metschnikoff. Embryologische Studien au Medusen. Wien. 1886.

tain of the superficial cells became amœboid and migrated into the interior of the colony just as we find them doing to-day in *Protospongia*, and that, in addition, certain other cells divided transversely, one of the cells so formed passing into the interior, while the more peripheral one retained its position at the surface. . . . While transverse division became predominant in some forms, longitudinal division and consequently the immigration of superficial cells prevailed in others. In this manner from mixed delamination, primary delamination branched off on the one hand, and multipolar immigration on the other."

Is it necessary though to assume that this "mixed delamination," *i.e.* a mixture of delamination and immigration, was characteristic of the ancestral flagellate colony? May we not claim that immigration is the more primitive method, and that delamination has been secondarily acquired after the group Metazoa had been well established? There is evidence in the colonial Protozoa in favor of such a view; as, for instance, in *Protospongia* in which cells, originally seated superficially in the jelly in which the individuals of the colony are imbedded, pass to the centre, losing their flagella and collars, and becoming, according to Saville Kent, reproductive. *Volvox* again, when mature, is a hollow sphere with reproductive cells lying freely in the central cavity; these cells were originally at the surface, but, losing their flagella, they migrated to the centre. The same process too is found in the sponges in *Ascetta*, and Metschnikoff has demonstrated its prevalence over delamination in the metagenetic Hydromedusæ.

If this idea be accepted, however, how can delamination be explained? Metschnikoff imagines that both delamination and immigration have arisen simultaneously as a natural sequence of the modes of non-sexual multiplication found in the Flagellata, where transverse division and longitudinal division both contribute, sometimes one sometimes the other occurring, or, as in certain Chlamydo-monadinæ, both processes occurring together, colonies being thus built up. If in the lower Metazoa longitudinal division predominates, we get immigration, but if transverse division also occurs delamination results. This seems, however, hardly to explain what happens; it does not explain why longitudinal division, *i.e.* the division in a plane perpendicular to the outer surface of the blastula, prevails exclusively during the conversion of a large-celled blastula into one with columnar narrow cells, the transverse division then suddenly appearing. It seems quite possible to explain the origin of delamination in another way. We know that in many ova food material may be aggregated at one pole, and if such a polar storing-up of food should have occurred in the various cells of the blastula, or of an ancestral form corresponding to it, it is easy to understand how it would be to the advantage of the organism for the inner portion of its cells to divide off, to delaminate, instead of migrating *in toto.* A certain amount of migration might accompany this process, as in *Cotylorhiza* and *Aurelia*, or the new delamination might entirely replace the earlier process as in *Renilla* and *Metridium*, and if this specialization were carried a little further, typical delamination such as occurs in *Geryonia* and *Liriope* would result, the embryo in these cases being not a solid planula but a hollow diblastula.

Invagination can readily be deduced from immigration. Metschnikoff points out that immigration may take place irregularly over the entire surface of the blastula (multipolar immigration), or may be confined to the posterior extremity, especially in free-swimming blastulas (unipolar immigration). It is interesting to note, in this connection, that according to recent observers there is a tendency towards unipolar immigration in the case of the sexual cells of *Volvox*. From the polar immigration Metschnikoff deduces invagination. In the Hydroid *Laodice* a few cells at the posterior extremity of the blastula are clearer than the rest and gradually migrate into the interior. If these cells should migrate *en masse*, instead of individually, we should have such an invagination as occurs in *Nausithoe*, the alteration of the manner of migration being an abbreviation of the original process.

The simplicity of this explanation recommends it, and it serves to clear up the sporadic appearance of invaginate gastrulæ in the Sponges and Scyphomedusæ. But the occurrence of these gastrulæ suggests the question, when once the invaginate gastrula has been established, does invagination continue to be the mode for endoderm formation, other processes, such as epibole, being derived from it? A negative answer to this question involves the assertion that the invaginate gastrula may have been developed several times independently. Is this impossible?

We have invagination occurring in the Sponges and in the Discomedusæ. The gastrula of *Sycandra* cannot be regarded as having been the cænogenetic ancestor of the gastrula of *Oscarella*, and neither of these that of

Pelagia. Too many forms with the characteristic cœlenterate solid planula intervene phylogenetically, to say nothing about the individual differences of the gastrulæ. If the Sponges are included among the Cœlenterata it is necessary to homologize the osculum of such a form as *Olynthus* or *Sycandra* with the mouth of a Cnidarian. This being the case the gastrulæ of *Sycandra* and *Oscarella* cannot logically be considered homologous with the gastrula of *Pelagia*, since, whereas in the latter the blastopore becomes the mouth of the adult, in the Sponges it closes, the embryo settling down upon it, and a new mouth (the osculum) breaking through at the opposite pole of the embryo.

The relation of the gastrulæ of *Pelagia* and *Nausithœ* to the invaginate gastrula of the higher Metazoa is also highly improbable. Whatever scheme of Cœlenterate ancestry for the higher Metazoa we accept, whether the Actinozoan, the Ctenophoran, or the Medusan, it is improbable that such a form as one of the higher Discomedusæ ever came into the series.

Is it probable too that the invaginate gastrula of *Eupomatus* is without genetic relation to that of *Arbacia*, of *Sagitta*, and of *Amphioxus?* Let us try the phylogenetic method of solving this question also. What form of gastrulation is most prevalent among the lower forms, and how far can it be considered ancestral?

Some years ago, while studying Molluscan embryology, I was struck with the similarity which exists between the segmentation and gastrulation of certain forms of that group, and what has been described as occurring in the marine Turbellarians. The conclusion suggests itself that the epibolic gastrulation which is found in these two somewhat widely separated groups can hardly have arisen independently, and that its occurrence is due to its having been the mode of gastrulation in the ancestors of both groups. It is also to be found in members of other groups, such as the Annelida, having been first described by Kowalewsky in *Euaxes*, and it occurs more or less typically in many Polychætous forms. I endeavored to express this idea in the following statement: "The modes of segmentation of the Platyhelminths, Annelida, Mollusca, and Molluscoidea, can be referred to a common type, indicating that the ovum (so to speak) in all these groups has been derived from an ovum possessing a considerable amount of nutritive yolk aggregated more or less completely at one pole." A necessary corollary of such a proposition I also stated as follows: "The regular and equal segmentation which occurs in certain forms in several of these groups cannot be considered the original mode, but has been secondarily brought about by the loss of a food-yolk originally present."

It would not be suitable in a lecture of this kind to review the various accounts of segmentation in these groups, but I would simply point out that if this idea is correct it follows that epibolic gastrulation is more primitive than embolic, the latter having been derived from the former by the loss of food-yolk. Can epibole have arisen from immigration? It can be regarded as a process of migration, the migrating cells being specialized very rarely in the development, having stored up within them a large amount of yolk. The protoplasm separates more or less from the large yolk spherules, forming the micromeres, and the large spherules project into and fill what would otherwise be the blastula cavity. In consequence of this there can be no immigration, but the same result is achieved by the micromeres growing round and enclosing the large micromeres. An indication of the possibility of such a process can be seen in some of the Hydromedusæ as *Laodice*, where the migrating cells are much larger and of a different structure than their fellows, and Metschnikoff has also described a more pertinent case in *Polyxenia*, in which the segmentation is as a rule equal, resulting in the formation of a morula by precocious immigration, but occasionally the segmentation becomes decidedly unequal, so much so that the process of endoderm formation resembles closely epibole. I have noticed in *Cyanea*, in which the segmentation is apparently equal, an exceptional case in which one pole of the rotating blastula consisted of a few large cells, while the other was formed by a number of smaller ones.

The invaginate gastrula I do not then consider to be a phylogenetic form—the Gastræa never existed. The ancestor which must take its place is the Parenchymella. This ancestor is perhaps reproduced in the ontogeny of the Metazoa in the structure which results from the closure of the blastopore. This is a phenomenon which frequently occurs, which is difficult to explain under the Gastræa theory. It is on the other hand what might be expected from the Parenchymella theory, as I have endeavored to extend it. Where epibole occurs, owing to the nature of the process, the breach made in the walls of the blastula by the immigration is not closed at once as in typical immigration.

A large section of the blastula wall migrates at once, and it takes some time for the opening so made to be obliterated. This obliteration is the "closure of the blastopore." The stage succeeding this is the Parenchymella stage, though owing to cænogenetic modifications and acceleration in the development of organs, the comparison is not perfect, but the embryo consists of an ectodermal layer with a central mass of cells in which differentiation has commenced. The blastopore or prostoma of the Turbellarians and Gasteropods has no exact counterpart in the Cnidaria; it is the result of the method of enclosure of the central cells. It is the later formed mouth, or mouth and anus, which corresponds to the Cœlenterate mouth, and just as the mouth forms in the Cœlenterates at the pole where the immigration occurred, so in higher forms the mouth, or mouth and anus, appears at the pole of the embryo formerly occupied by the larger yolk bearing cells. In embolic gastrulas, where the invaginated inner layer of cells forms a hollow sack, the archenteron, it may be to the advantage of the embryo, little or no food-yolk being present, for the blastopore to persist, complete closure never taking place, a portion of the blastopore being converted into the mouth or anus as the case may be. Even in the Echinodermata, however, in which as as a rule the blastopore persists as the anus, a complete closure of it occurs in the Crinoids.

This view of the relation of the blastopore to the mouth and anus does not necessarily conflict with the theory first advanced by Bütschli, and later supported by Adam Sedgwick and E. B. Wilson, to the effect that the mouth and anus of the higher Metazoa correspond to the two extremities of the mouth of the Polyps, but a discussion of this theory would occupy an undue amount of time.

I have hitherto omitted all reference in this discussion to the Arthropoda and the Vertebrata. In the former group a considerable amount of study of the early stages of development is still necessary before the processes of formation of the germ layers can be homologized with accuracy with those of other Metazoa. In one group, however, that of the Arachnida, the researches of Metschnikoff on *Chelifer*, and Morgan on the Pycnogonids, demonstrate the formation of an inner layer of cells by delamination, and it seems not improbable that typical centrolecithal segmentation may be derived from such a process by the extensive accumulation of food-yolk in the inner portions of the blastula cells.

As regards the Vertebrates there is an almost universal concensus of opinion among embryologists that the peculiarities of their endoderm formation are to be explained on the hypothesis of an ancestral invaginate gastrula. It seems quite possible that invagination secondarily derived from epibole may have become so impressed upon the ontogeny of the Vertebrate ancestors as to leave its imprint on the development of the later groups.

There is still another point to be considered in connection with the Parenchymella theory, viz., the causes which operated to bring about the transformation of the solid planula into the hollow gastrula. Metschnikoff's views on this are as follows: — It is clear that it would be to the advantage of locomotor colonies of more or less similar cells, that those individuals which were laden with food matter should not remain at the periphery, but should pass to the centre, not only to equalize the weight of the various parts of the colony, and to allow the more active cells free action at the periphery, but also to permit these food-laden cells to carry on their assimilative functions without disturbance from external conditions.

"For a long time the individuals of any colony probably differed only quantitatively; the locomotor cells attracted food particles by the movement of their flagella and also absorbed some of the smaller particles, just as the ectoderm cells in some Cœlenterates of to-day occasionally ingest food-matter. The inner amœboid cells, however, were on the other hand capable of swallowing larger food particles. Probably when so engaged the amœboid cells approached the periphery, and gained possession of food particles lying on the surface of the colony by means of the numerous pores between the cells of the superficial layer. . . . Gradually the differentiation in this direction progressed; the locomotor cells lost more and more their food-ingesting function, which concentrated itself in the amœboid phagocytes; the occasional fine pores between the locomotor cells enlarged and became openings similar to those so numerous on the surface of a sponge. . . . With the increased activity of the Metazoa, now provided with two primitive organs, there must also have been an increased necessity for food, and larger plant and animal organisms must have served as prey. To make this possible one or more larger openings arose, which led to the formation of a mouth."

According to this scheme the central cells are digestive and ingestive *ab initio.* It seems strange, however, that cells specializing themselves for a purely digestive function should withdraw themselves from practically all contact with the surrounding medium, the source of the food supply, and there seem to be mechanical difficulties in the way of the central cells obtaining particles of food, larger than those which could be ingested by the locomotor cells, and through minute pores many times smaller than the ectodermal cells. Furthermore the explanation of the formation of the mouth is not at all in harmony with its ontogenetic development.

The cells which migrate are well nourished and therefore in a suitable condition for reproduction. This is actually their function in *Volvox*, and in *Protospongia,* which Metschnikoff cites, the only observations we have indicate that the cells which leave the periphery of the colony become reproductive. May this not be the original function of the migrating cells, the formation of the parenchymella being regarded as the migration to the centre of eutrophic cells capable of being reproductive? It does not necessarily follow that all the cells which migrate must become reproductive; some of them may become specialized along other lines; but the idea is simply that primarily it was cells in a condition suitable for reproduction that migrated, and when only a few cells underwent this change of position they all became reproductive, but when a large number migrated some might become differentiated to subserve other purposes.

It seems to me that what we find in the development of such a sponge as *Halisarca* indicates the manner in which the solid embryo becomes converted into a hollow organism with a mouth, endoderm, and mesoglœa, and also gives a clue to the causes which have brought about the change. The central cells of the hollow planula become transformed into the mesoglœa and endoderm, the number of cells contributing to the latter layer being relatively few. The mesoglœal cells have various functions, some producing spicules or horny fibres in some sponges, but a large number remain indifferent or unspecialized to a greater or less extent, some becoming reproductive.

We find too that the endoderm becomes differentiated from the central mass long before the cavity it encloses has any communication with the exterior, and cannot very efficiently function as a nutritive layer since it is separated from the outside world not only by the thin ectoderm, but also by the thick mesoglœa. It is necessary that respiration should be carried on throughout the entire mass of the sponge. While it is small this is readily effected through the ectoderm, but as it grows, the mass increases so much more rapidly than the surface, that this simple method no longer suffices. Cavities appear here and there in the mesoglœal mass, and later communicate with one another, the cells lining them becoming ciliated to produce a more rapid circulation of the water. A large central space into which the various cavities finally open makes its appearance, and last of all this space breaks through to the exterior, forming the *Osculum*. The water which at first reached the cavities by filtration through the tissues, later on has ingress by pores, and the complicated canal system of the sponge is established.

In its first inception, then, the canal system and the ciliated chambers with their collared cells are respiratory in function. The recent observations of von Lendenfeld, however, demonstrate that the collared cells are ingestive, and that ingestion takes place in them solely. Even so, however, they are also the cause of the currents of water which pass in through the pores, bringing them food particles, and are therefore also respiratory in function. It seems quite possible that their ingestive function has been secondarily acquired, they being in the best situation for obtaining food.

As we pass higher in the scale of animal life we find a greater and greater differentiation of the function of the cells corresponding to the central mass, and we find the endoderm cells assuming more and more a purely digestive function. Except in a few cases the reproductive cells arise from the mesoderm or endoderm (in the Scyphozoa), both of which structures may be considered as derivatives of the central mass of the solid planula.

Instances having an important bearing upon the idea here proposed are offered by the Orthonectids and Dicyemids. As is well known, in these forms there is a single layer of ectodermal cells enclosing a mass of reproductive cells, or, in the case of the Dicyemids, a single large "endodermal" cell which is the source of the reproductive elements. In development this cell is separated off very early, and is enclosed by the ectodermal cells by a process of epibole. The stage preceding the complete enclosure of the central cell is generally spoken of as the gastrula stage, but under the present view a Dicyemid or an Orthonectid would be regarded as an adult parenchymella, whose central cells retain their original function, being entirely reproductive.

Other cases might be given having a more or less direct bearing on this question, but the time at my disposal prevents a fuller treatment of the subject. I would like, however, to refer to one case, namely, Grobben's account of the development of the Phyllopod *Moina*. We have in this form three distinct invaginations: (1) an invagination of certain cells to form the endodermal midgut; (2) of certain cells to form the general mesoderm; and (3) of four cells to form the reproductive organs. Only one of these, however, the first, can be considered a true invagination; the others are more correctly immigrations. The entire process can, I think, be referred to the formation of a parenchymella in which there has been a precocious segregation of certain important organs. The germ plasma has been early segregated into a certain spherule of the developing ovum and accordingly immigrates independently of the general mesoderm cells, whose perfect segregation, like that of the endoderm, is postponed to a slightly later period, these two last-named structures likewise immigrating independently.

There are some cases, however, which seem to throw serious obstacles in the way of the view as to the origin of the endoderm and the reproductive elements which I have advanced. In the Hydrozoa and Ctenophora, the reproductive cells have been shown by Weismann, and the Hertwigs especially, to be derived from the ectoderm. The latter authors endeavored, on this account, to associate the Hydrozoa and Ctenophores together as distinct from the Scyphozoa, in which the reproductive cells have an endodermal origin. Other structural peculiarities, such as the presence of an ectodermal stomatodæum, seem to indicate, however, that the Hydrozoa and Ctenophores have little in common and must be regarded as two widely divergent stocks. If this be so, the occurrence of an ectodermal origin for the reproductive cells in these two groups cannot be regarded as a primary arrangement, but for some unexplained reason has been secondarily acquired. We have seen that in certain lower Crustaceans the "Keimplasma" may become very early specialized, and immigrate quite independently of the mesoderm and endoderm, the other constituents corresponding to the central cells of the Cœlenterate planula. We may perhaps conceive of a somewhat similar segregation of the germ-plasm occurring in the Hydrozoa and the Ctenophores, the cells containing it, however, remaining in the ectoderm, and not migrating with the other cells, which are to form the mesoglœa cells and the endoderm.

In conclusion I must express my admiration of the masterly manner in which Metschnikoff has treated the exposition of his theory. Probably no one has such an acquaintance with the embryological phenomena of the Cœlenterates, or has contributed so extensively to our knowledge of these phenomena, as Professor Metschnikoff, and few possess that insight into the bearings of facts which he has exhibited in all his studies. The Parenchymella theory places our ideas of the relationships of the Protozoa and Metazoa upon an entirely new basis and enables us to overcome many great and perplexing obstacles. It is founded on facts and explains them satisfactorily.

The ideas advanced in this lecture which are not embodied in Metschnikoff's statement of his theory do not modify it in its essential points in the least. They are merely suggestions which have developed during the consideration of the application of the theory, and must be regarded simply in that light. For a complete exposition of them much more detailed description, unsuitable for an occasion of this kind, would be necessary, and I present them here merely in the hope that they may incite to more thorough and perfect acquaintance with the problems connected with the early development of invertebrated animals, and the bearings of the ontogenetic phenomena on the question of the origin of the Metazoa and of their organs. I cannot do better than quote in conclusion from Metschnikoff, "*Es musste gerade im Bereiche der niederen Metazoen ein fester Boden für das Verständnis der primitiven Organe gewonnen werden.*"

FIFTH LECTURE.

WEISMANN AND MAUPAS ON THE ORIGIN OF DEATH.

By EDWARD G. GARDINER.

HEREDITY and Variation are among the most interesting subjects which attract the attention of naturalists, and any theory which attempts to explain these phenomena is worthy of consideration.

Why is it that all organisms tend to repeat themselves in their descendants, and why do the offspring always differ somewhat from their parents? That this invariably occurs has long been a matter of common knowledge, and yet a satisfactory explanation of why it should occur is still to be sought.

Darwin founded his theory of evolution on the facts of Heredity and Variation, but the explanation by which he sought to account for these phenomena was offered more as a "provisional hypothesis" than as a complete theory.

Many valuable modifications of, and additions to, his theory have been proposed from time to time by different authors, but the main idea of gemmules from all the different cells of the body aggregating in the generative glands, and being thus transmitted to the young, seemed too cumbersome and complex for general acceptance.

Quite recently Professor Weismann of Freiburg has advanced a theory of Heredity which seems by far the best hitherto offered. This theory is the culmination of a train of thought which he has put forward in essays from time to time during the last few years. These show the gradual growth and development of the theory in the mind of the author, and though some of the facts from which he argues may be open to dispute, yet the ideas which he suggests are so interesting that they are entitled to consideration, even though subordinate to the main plan of his theory.

In one of his earlier essays he points out that the manner of reproduction among the Protozoa is such that death does not normally occur in this group, for the animal reproduces by merely dividing itself into halves. Thus an adult animal ceases to exist as such, by becoming two animals instead of one. It does not die during this process, for there is no corpse, but the whole animal as such has completely disappeared, and in its place we find two individuals so similar that it is impossible to regard them as parent and offspring. Indeed, they cannot be parent and offspring, for they are of the same generation, — it is more natural to call them twins. They are both young animals, for they increase in size, and when adult each of them ceases to exist by dividing itself into two new young ones, and so on indefinitely.

Hence it would appear that the life-history of such an animal may be divided into two periods, — youth and adult life. There is no old age; there is no death. Clearly, then, since these forms do not die, they may be said to be potentially immortal. The living matter of which they are composed passes over without break into a younger generation, and in it life is continued. These facts have long been known, and earlier investigators have pointed out the potential immortality which this mode of reproduction implies; but Weismann was the first to develop this knowledge into a scientific theory which may throw light on other facts.

When Weismann calls these animals immortal he draws a proper distinction between the terms immortal and eternal. Eternity reaches back into the past as well as out into the future. With eternity he has nothing to do. Neither does he use immortality in the sense in which it is used in theology, — as applied to something which can never die, but must exist through all future time. His claim is not that the life of a Protozoön is such that it must under any circumstances exist forever, but that it will exist as long as the proper physical conditions exist; in other words, that death is not inherent in life.

He compares the life cycle of a Protozoön to the circulation of water which evaporates, gathers in clouds, and falls to the earth only to evaporate again. There is no inherent cause in the physical and chemical properties of water which will bring this cycle to an end. As long as the present physical conditions exist the cycle must continue. So it is, he claims, with the life cycle of a Protozoön; *i.e.* division, growth by assimilation, division again — and so on without end; there being no inherent cause in the constitution of the protoplasm which will cause it to fall short of its cycle, and to physiologically decline. He does not mean that such unicellular forms cannot be starved to death, crushed out of existence, devoured, or killed by disease. These are rather accidental than natural deaths. He claims only that since life has existed in these forms, it has passed unbroken from one generation to another down to to-day. The material of which the individual is made may change, but in all cases it is animated by the same life.

Now no one doubts that the Metazoa have at some time in the remote past been evolved from such potentially immortal Protozoa. But the life of all of the Metazoa may be divided into *three* periods, — youth, adult life, and old age, during which latter there is clearly a physiological decline in vigor, which is terminated normally by death.

Old age and death then would appear to be something which have been acquired with the development of the Metazoa from the Protozoa.

Exactly for what purpose, and how, death has been instituted are questions which Weismann endeavors to answer.

But first let us compare the life-history of a Metazoön with that of a Protozoön, and see whether there is anything in the Metazoa which is comparable to Protozoa immortality. All Metazoa start their individual lives from an ovum, which is a single cell, and may well be compared to a Protozoön. After fertilization this cell or ovum divides into two, then into four, then into eight cells, and so on, thus giving rise to a very large number of cells which, as development progresses, differentiate to form the tissues and organs of the embryo. Now of these cells in the embryo, Weismann distinguishes two different kinds; viz. the germ-cells which lie in the generative glands of the animal, and the somatic cells, which form all other organs and the body itself. During early youth the germ-cells remain dormant. When, however, adult life is reached, they develop, and under proper conditions, such as fertilization, etc., each one is capable of producing a new organism, with germ-cells and body, while the body itself grows old and dies.

The germ-cells of the second generation do not die, but produce a third, and the third a fourth generation, and so on. The body of each of these generations must grow old and die, but the germ-cells themselves, if allowed the proper physical surroundings, do not. They go on germinating, and so produce generation after generation.

Hence it would appear that the germ-cells of the higher organisms are comparable to the entire body of unicellular forms, and like them are endowed with potential immortality; and that this immortality has never been broken by death since life has existed on this earth. In other words, a Metazoön equals a colony of Protozoa *plus* a perishable body.

This theory he calls the "continuity of the germ-plasm." He compares the germ-plasm of the Metazoön to the rhizome of a fern which runs along underground, the perishable body to the green frond which grows up, withers, and dies, without affecting the life of the rhizome from which it springs.

Death, then, is something secondary; an adaptation which has been acquired through natural selection during the evolution of the Metazoa from the Protozoa. Whether this conclusion is just is to a certain extent a side-issue to the theory of the continuity of germ-plasm, and further on the matter will be more fully discussed.

Among the Protozoa it is very evident that the young must resemble the forms from which they spring, for they are a part of the same stuff. Furthermore, if during life an individual becomes changed by its environment, this change must become an hereditary trait.

Now we may assume that the Protozoa may be affected by the physical conditions under which they live just as much as are the Metazoa. It is a well-known fact that the bodies of the higher forms may be changed by food and exercise. The muscles of a blacksmith or a sailor are stronger than those of a dude.

A Paramæcium which lives in a strong-flowing stream would be apt to acquire stronger cilia than one living in a stagnant pool. The young which spring from a Paramæcium with strong cilia must inherit this character. Indeed, the cilia of the young are the identical cilia which by constant use have been lengthened and strengthened. In every case of reproduction by fission, the whole body of the parent continues its existence in the younger generation. If the parent is strong and vigorous, the young are so likewise; if the parent is decrepit and feeble, the young must likewise be decrepit and feeble. Hence all modifications which any unicellular organism may acquire must be transmitted to its young.

Among the Metazoa, however, the case is somewhat different. In all the higher forms the germ-cells which contain the potential immortality of the organism have no function but that of reproduction, and are so well protected from the environment that they must be difficult to affect.

The old idea that an animal which strengthens its legs by severe labor will have offspring with stronger legs than one which has not so exercised is hard to comprehend. If this be so, then we must imagine that the strain put upon the muscle cells of the legs has changed the molecular structure of the germ-cells. This seems a monstrous supposition. Of course when Weismann says that no acquired character can be inherited, he does not mean that half-starved animals may not give rise to stunted young. This is, however, a case of direct action on the young itself, for before birth the young is fed from the tissues of the mother, or the mother supplies food in the form of the egg-yolk.

Certain diseases are known to be hereditary. These, however, may perhaps be ascribed to the direct passage of the Bacterium from the parent to the germ-cell or to the embryo. Other diseases which are due to structural malformation may, of course, also be inherited. The isolated cases where scars or other such acquired characters are said to have been inherited, are never so well authenticated that their accuracy is beyond doubt. Certain it is that where wholesale experiments on animals have been carried on, no inheritance of mutilations has been observed. Generations of horses and dogs have had their tails docked without affecting their young. The Chinese women deform their feet, yet the young are not affected. Mutilation, among savages, of the nose, face, and ears has been carried on for generations, yet no traveller has reported that either the mutilations or the scars are inherited. All these facts should be borne in mind when it is claimed, as it still is by many, that acquired characters may be and are inherited. Weismann admits that the long-continued effect of climate and food may to some extent act on the germ-cell; but the idea that species can have originated through the inheritance of the peculiarities acquired by their ancestors, is contrary to his theory.

Now the young of the Metazoa inherit the main characters of their parents, for the same reason that the young Protozoön resembles the form from which it springs, — they are made of the same stuff. Germ-cells and body-cells arise from the same germ-cell. During the development of the individual the immortal portion of the germ-cell is set aside to form the next generation. The characters which the body of the individual may acquire during life must be very fundamental to affect these germs. A young Metazoön is a part of its parent, because the stuff of which it is made is a part of the germ-cell from which its parent was made. It may also resemble a grandparent or a great-grandparent, for its parent sprang from a part of the same germ cell which built its grandparent. Its great-grandparent was in turn a part of its great-great-grandparent. Thus every individual is made up of the same material as its ancestors, in degrees varying with the different generations. In ten generations an individual may have 1024 ancestors, of all of whom the individual itself is a part. If the theory of the continuity of the germ-plasm be accepted, there is no difficulty in understanding why heredity should occur. Ancestors, parent, and offspring are all a part of the same stuff.

Now in regard to variation, and why it should occur. Every individual is the result of the union of the male and female germ-cells, and Weismann holds that the minor characters are due to the manner in which these cells are mixed. He assumes that these cells are of the most complex molecular structure, so that when they unite it is impossible that exactly the same arrangement of the molecules should be repeated. Put a handful of currants into two loaves of bread, and after baking see whether there is exactly the same number and arrangement in the fifth slice of each. The chances against this are enormous.

All variations which occur in nature, — size and shape of the features, organs, stature, color of skin or hair, — depend on the molecular combinations formed in the union of the two germ-cells. If a single germ-cell should develop without so uniting with another, the young would be the exact duplicate of its parent, for it would be composed solely of the germ-material of which its parent was composed.

In essence the male and female germ-cells are identical. Each is potentially capable of producing an embryo by itself, if the proper physical conditions could be secured. Weismann says that if it were possible to bring about the conjugation of two ova, fertilization would be accomplished, and development pursue its normal course. Indeed, this, or something very similar, has been done. Boveri succeeded in removing the nucleus of an echinoid ovum, and then induced this ovum to develop by introducing spermatozoa. A new nucleus was then formed by these, and the ovum developed into a free-swimming larva.

If before sexes were fully established, two germ-cells of different origin were to unite, the embryo would have a dual origin, and hence would differ from both parents. If the variation thus introduced were favorable, survival of the fittest would preserve it. The germ-cells of this form would, of course, inherit the tendency to unite with another germ-cell. In this way natural selection would establish sex, to ensure the combining of two germ-plasms in each individual. Without such combination no variation in the Metazoa could occur. Hence all sexual characters — even to the higher mental attributes — are due in their origin to the necessity of establishing variation. Variation, then, is a consequence of the union of two sexual germ-plasms, and not something inherent in protoplasm.

At first thought it seems strange that variations are not more numerous and marked than they are; that for thousands of years the germ-plasm of every species of animals has undergone so little change that each species still retains all its specific characters. It would seem that if animals are not suited to the environment, they are not modified, but exterminated. Yet when advantageous variation has occurred, and the race has been preserved by natural selection as a different species, this must have been brought about very slowly. It is thus evident that the plasm is very conservative and difficult to change; that the conservative forces far outweigh all tendencies to vary.

Now to return to the question whether death is inherent in germ-plasm. Weismann attempts to show that to the species death is an advantage. All animals are liable to accidents, and if animals were to live on for all time, many would be maimed and useless. By far his strongest arguments, however, are based on other facts.

Favorable variations in nature are seized on by natural selection and preserved, whether they be an advance towards greater specialization or retrogressive. Long since, Darwin pointed out that small wings were an advantage to insects living on islands where strong winds prevail, for those which had large wings would be more apt to be blown out to sea, and so lost to the race. Hence a survival of the fittest has maintained short-winged varieties. Small eyes buried in fur are an advantage to burrowing animals, such as the mole; hence this variety has been preserved. So, also, the complete disappearance of the limbs of snakes which squirm through small holes and clefts. Limbs would be a disadvantage and a hindrance.

When, however, degeneration of disused organs confers no benefit on the individual, the explanation is different. Thus the eyes of insects, crabs, fishes, and amphibia, which live in caves, have undergone degeneration; yet this can hardly be of advantage to them, for they could live quite as well in the dark with well-developed, as with rudimentary, eyes. The efficient eyes of allied forms living in the light have been maintained in their perfection by the survival of those only having good eyes. Is it not evident that when such animals come to live in darkness, natural selection will cease to act, and deficient eyesight result? If those with imperfect eyes intermingled with those with perfect eyes, the eyes of the whole race would begin to degenerate. Take another case, such as is offered by birds of prey, which are possessed of exceedingly sharp sight. If some of these birds happened to come into the world with defective eyes, they would starve to death, or at least be less likely to succeed than their brethren which were more fortunate in this respect. Hence sharp sight is maintained by the continued operation of natural selection, which tends to exterminate those with defective sight. But let these birds come to live under conditions in which those with defective sight got along as well as those with keen sight, — say in a dark cave, — and it would seem more than probable that the eyesight would degenerate. Those which varied in the direction of defective eyes would survive as well as the others. Hence they would breed with the keen-sighted ones, and thus gradually the general average would be lowered. Another example must suffice. Short-sightedness is not at all uncommon among civilized races, and is generally believed to be hereditary. Short-sighted men succeed in life as well as those with normal or very keen sight. Neither natural selection nor any other selection compels keen sight. But a short-sighted hawk or antelope, or even a short-sighted Indian, would be placed at so great a disadvantage that short-sightedness would soon be eliminated from the race.

In these last-mentioned forms natural selection compels the eyes to come up to a certain standard, while among civilized men and cave animals there is no such necessity. Natural selection maintains only what is an advantage, and when it neglects an organ, that organ tends to degenerate.

Weismann urges that through the neglect of natural selection immortality has been lost to the Metazoan body. Among the Protozoa, since the whole body is the germ-cell, immortality is inevitable. Among the Metazoa, the body is merely a protector of the immortal germ-cells, and immortality is not essential to the body; hence natural selection has failed to maintain it. He suggests that the Metazoa have been evolved from small colonies of Protozoa which formed clusters. In such groups those on the outer side must obtain food more readily than those in the centre; hence the colony would become gradually differentiated into feeding cells on the outer side and reproductive cells on the inner side, the feeding cells supplying the reproductive cells with nutriment just as the digestive cells of Hydractinia supply the rest of the colony.

The cells that are thus supplied with food would have no use for mouth, cilia, etc.; hence they would lose them, but might retain their reproductive powers. If these central cells retained their immortality, there would be no necessity for the feeding cells doing so also; and if natural selection does not compel the retention of a physiological character, it degenerates just as a useless organ degenerates.

Certain of the lower forms, such as Volvox, suggest this manner of evolution of the Metazoa from the Protozoa. Volvox is a hollow sphere of cells, each of which is provided with a couple of long flagella, by means of which the colony swims. Some of these cells pass to the centre of the sphere, and there undergo certain changes in form, becoming, in fact, the reproductive cells of the colony. When they are ripe the rest of the colony withers up and dies. Hence we find in Volvox the first approach to a differentiation into germ and somatic cells.

Since Weismann made this startling assertion, that death is not an attribute of all living organisms, much opposing evidence has been brought forward. Most prominent and recent among his opponents is E. Maupas, of Algiers, who, after extensive study of some of the Infusoria, asserts that degeneration and death occur as normally among the Protozoa as among the Metazoa. Before entering on his experiments, Maupas first determined very carefully the habits of the different species which he chose for study. He found out the temperature to which they were best adapted, and the kind of food on which they throve best. Then he took a single individual, and isolated it on a glass slide, on which it could be studied. This slide was kept over a dish of water in a warm, damp chamber in which the air was so thoroughly saturated with moisture that evaporation was reduced to a minimum. During its confinement the animal was fed on its favorite food, and in every particular what seemed to be the most suitable conditions were maintained. He found that at the end of seven days there were no less than 935 Infusoria in his culture. One of these 935 he isolated and kept as he had the first. In four days this single one had increased to 230. One of these was isolated in the same way, and this process of isolating and confining one individual of each brood was continued through a large number of generations. He shows the rapidity of increase to be something almost incredible. Calculations show that in six and a half days a single Stylonichia might produce by fission a mass of protoplasm which should weigh one kilogram, and that in thirty days the number of kilograms would be represented by 1 with forty-four zeros, or a mass of protoplasm a million times larger than the volume of the sun.

Cultures were made of no less than twenty different species of Infusoria, and were maintained during periods of time varying in different cases from two weeks to between four and five months. He found that after from fifty to one hundred generations had been produced by fission, there was clear evidence of a physiological decline, which seemed to indicate the approaching extinction of the culture. He withdrew some of the Infusoria from the culture and allowed them to mix with others of a different origin. With these they conjugated, and their full vigor seemed restored. If, on the other hand, they conjugated among themselves, observation showed that decline was so far advanced that the culture was doomed.

Soon, the animals produced by fission were smaller — often being less than half the normal size. At the same time what might be called pathological changes began to appear. The cilia were absent on parts of the body, and the infusoria seemed weaker and less able to digest food. In some species the micro-nucleus underwent changes, finally falling to pieces, a phenomenon which not unfrequently occurs in the cells of the Metazoa when the tissue is undergoing degeneration. Also the macro-nucleus was found to undergo marked pathological changes, finally breaking down and disappearing.

When this degeneration, which Maupas calls senile degeneration, has reached its maximum, nutrition becomes impossible, and death follows. Thus it would appear that the life of these animals is cyclic. During the period of reproduction, which is the adult life of the animal, a sort of physiological decline takes place, and this decline can be repaired only by conjugation.

Now if during these experiments the animals have not been injured or poisoned, it would seem that Maupas had proved that death may occur normally among unicellular forms.

Weismann, however, is not ready to admit this. He claims that conjugation is a necessary condition of the animal's life, just as fertilization is a necessary condition for the survival of an ovum, and if conjugation is denied, the death in consequence is accidental and not natural; further, that the fact that conjugation is necessary does not imply that the protoplasm is not potentially immortal. He seems, however, to overlook the fact that a certain physiological decline has taken place, and that if there is any physiological decline the cycle of life is incomplete; therefore the seeds of death must exist inherent in the life of the animal. It is, then, for the present, impossible to speak of the Infusoria as potentially immortal, and to claim that that portion of the Metazoa which undergoes physiological decline has no equivalent in these forms. Nevertheless, it is too soon to declare that the idea that death is an adaptation is altogether erroneous.

In many well-known unicellular forms, neither a physiological decline nor a process of rejuvenation has been observed. The Bacteria, the Cyanophyceæ, and Yeast increase by budding, spore building, and fission, and unless their life-history is much less well known than bacteriologists and botanists think, these forms are potentially immortal. The Infusoria are the highest and most differentiated of unicellular forms. They have organs of locomotion, mouth, pharynx, some sort of excretory apparatus, myophanes (muscle-like structures), trichocysts, etc.; while in the lowest organisms none of these organs are to be found. Further, the Infusoria have a macro-nucleus which Maupas shows is vegetative in its function, and a micro-nucleus which is generative. If the macro-nucleus is lost, nutrition fails, and if the micro-nucleus is lost, conjugation is impossible. In the lower Protozoa no such differentiation has been observed. There is merely one nucleus, which is surrounded by a mass of protoplasm.

In a recent article Bütschli maintains that in the Bacteria the whole body is the nucleus, and that the surrounding mass of protoplasm, such as characterizes the Rhizopods, is absent. Between the Bacteria and Infusoria there is a wide gap in the zoological scale. Now is it not possible that as the Infusoria were evolved from lower and simpler forms, the process of conjugation was first acquired? That when, in the cycle of metabolic changes the protoplasm fell short of the point from which it started and to which it should return, this deficiency was made up by foreign substance obtained from an individual of different origin, and therefore of different material? Those of the primitive forms which retained their original immortality have left lineal descendants which we know to-day as Bacteria. Those which in a measure lost that power have either become extinct or else acquired a habit of rejuvenescence by conjugation. In other words, those to which it was an advantage to retain their immortality have retained it, and those which varied in such a manner that immortality could be advantageously replaced by rejuvenescence have, by the action of natural selection, undergone this modification. If this is so, Weismann's error is not in claiming that death was an adaptation, but in asserting that all unicellular forms are immortal.

Still another and earlier opponent of Weismann has urged serious objections to this theory of the origin of death. Professor Charles S. Minot was the first to maintain — and many have taken up his suggestion — that Weismann is fundamentally wrong in comparing the life-history of a Metazoön, which is a complex colony of cells, with that of a Protozoön, which is a single cell. Minot urges that an individual Metazoön is comparable to a colony of Protozoa, not to a single cell. If this be so, then the death of a Metazoön (a colony of cells) has its only homologue in the degeneration and death of a culture of Protozoa. The Metazoön colony is the product of a single germ-cell, as is also the whole culture of Infusoria.

This comparison seems safe between the Metazoa and those forms of Protozoa which conjugate, and in which senile degeneration occurs. But how is it when we bring those which do not conjugate under consideration? If this view be correct, then a single Metazoön is equivalent to all of a species of Bacterium which may arise through generations of fission. As far as our knowledge goes, these Bacteria are immortal and their numbers almost infinite. We know, on the other hand, that nothing but the germ-cell of the Metazoa possesses this immortality and vast power of reproduction.

But to return to Weismann's views. If death is not something which is inherent in living matter, but which is acquired, how is it that the length of life differs so markedly in different species? Weismann answers that the age which an animal may attain has been determined by natural selection, and also that the power of reproduction and length of life are correlated. In order to understand this view it is necessary to compare the length of life and reproductive powers of different animals. Birds, as a rule, live to a surprisingly great age. Even the smallest singing-birds live for ten years, while some live for twelve or even eighteen years. A partridge lives from twenty to twenty-five years. A pair of eider-ducks were observed nesting in the same place for twenty years, and it is believed that these birds often reach the age of a hundred. The same cuckoo was recognized by its peculiar note in the same forest for thirty-two consecutive years. Birds of prey become much older, for they outlive more than one generation of men. A white-headed vulture was kept in a zoological garden in Germany for one hundred and eighteen years; and many examples of eagles and falcons reaching an age of over a hundred years have been recorded. Humbolt mentions a parrot from the Orinoco, of which the Indians told that none could understand it, for it spoke the language of an extinct race.

Now let us compare the length of life and reproductive powers of the partridge and an eagle, and see if there is any reason why one should live longer than the other. The partridge lives a little more than twenty years, and each year lays about twenty eggs. Hence a pair of partridges may produce about four hundred eggs in their lifetime. This is at the rate of two thousand in a hundred years. Yet, since the number of partridges in the forest does not increase, three hundred and ninety-eight of these eggs, or young, must be destroyed in twenty years, while but two survive to take the place of their parents. The eggs and young are destroyed by beasts and birds of prey. If these enemies increased very much in number, the partridge would become extinct unless it laid more eggs.

It would appear, then, that the partridge lays just eggs enough to ensure the continuance of its race, and this being accomplished, death removes it. Many species have doubtless become extinct through the insufficiency of their reproductive powers. The number of offspring which, under ordinary conditions, would have ensured perpetuation, has proved insufficient when their enemies increased or the environment became unfavorable. The supply must be equal to the demand.

Now for the eagle. The eagle is one of the most powerful of birds, and builds its nest on such inaccessible cliffs that eggs and young are comparatively safe from marauding animals. Many, however, are destroyed by late frosts and snows. To be on the safe side, let us fix the duration of life of the eagle as sixty years, and of this ten years is spent in immaturity. Hence there are fifty years of its life during which it reproduces. If the eagle lays but two eggs a year, a pair of eagles would produce one hundred during their lifetime. In a hundred years two hundred eggs against the partridge's two thousand; therefore the partridge produces ten times as many young as the eagle, and it is safe to say that the partridge has ten times as many enemies. If the life of either were shortened, the race would die out unless the power of reproduction were increased or the struggle for existence became less severe.

Many sea-birds, such as the petrel, auk, and gannet, lay but one or at the most two eggs a year. Any one who visits a locality where these birds breed must be struck with the enormous number of eggs or young which are destroyed. The eggs are often laid on the bare rock on projecting ledges of a cliff, so that the slightest movement will precipitate them to the beach below. Every disturbance among the breeding birds is marked by a small avalanche of eggs or young, so that the beach below is strewn with broken eggs and mangled remains. If these birds were not long-lived they would soon become extinct. Now all of these birds live much longer than mammals of a much larger size. The lion lives thirty-five years, the sheep fifteen, the fox fourteen, the squirrel or mouse about six. Most of these animals are much more fertile than the birds, and the young are much less exposed to dangers. The bird's egg is exposed from the time it is laid, while the young mammal is protected during its development.

Only the very largest of the mammals, such as the whale, the elephant, and possibly the rhinoceros, live as long as these birds. The elephant may live for a hundred or perhaps a hundred and fifty years, and reaches maturity when about thirty. A pair produce but a single calf about every ten years; hence, during their lifetime, a pair of elephants contribute but ten or a dozen young to the race.

Wallace shows that we are living now in a zoologically impoverished world. Almost all of the largest and strangest forms have recently become extinct: in Europe the great Irish elk, the sabre-toothed tiger, cave-lion, rhinoceros, hippopotamus, and elephant; in North America equally large felines, horses, and tapirs larger than any now living, a llama as large as a camel, mastodons and elephants, besides a large number of huge megatherians; in South America an even greater number of megatherians, huge armadillos, a mastodon, large horses and tapirs, large porcupines, two kinds of antelopes, numerous bears and felines, beside the sabre-toothed tiger.

Remains of all these are found in the recent deposits, and these animals lived till shortly before the northern continents were encased with the ice of the glacial epoch. It is possible that a change of climate, due to the growing cold from the encroaching ice-belt, affected the flora. This would, of course, affect the food supply, and so tend to lessen the reproductive powers, and shorten the lives of the individuals. Lessened reproductive power and shortened lives of the individuals would surely result in the extinction of the race, and in this way the destruction of these forms may be accounted for. The starvation of the individual is therefore synonymous with the starvation of the race.

The main features of Weismann's theory may be summed up as follows: *First*, The continuity of the germ-plasm. *Second*, Variation is due to the different molecular combinations formed in the mixture of the male and female germ-plasm. *Third,* Death is an adaptation, and the duration of an animal's life has been determined by natural selection, and is correlated with its power of reproduction.

Whether this theory will endure and receive even fuller acceptance in the future than it does to-day, time alone can show.

SIXTH LECTURE.

EVOLUTION AND HEREDITY.

By HENRY FAIRFIELD OSBORN.

I WANT especially to direct your attention to the relations between our present knowledge of the evolution process and the problem of Heredity. The mere truth of the origin and succession of life by evolution may now be demonstrated in every branch of Biology, the arguments from palæontology, embryology, and morphology being equally convincing, but the theory of the evolution process is inseparably connected with some theory of inheritance. If new individuals were simply repetitions, like coins struck from a species mint, there would, of course, be no evolution possible, and we should perforce return to the Miltonic conception of creation, at the same time greatly reducing the number of difficulties in the heredity problem. While in zoology the repetition phenomena are perhaps the most conspicuous, in palæontology, or, in other words, in the succession of life in time, the variation phenomena are more striking, and we come to realize that the how, why, and when of the variations give zest to the study of the fossil series and furnish the crucial test for any heredity hypothesis.

Yet men were slow to see this relation. Lamarck did not study heredity as a special problem in itself, but he boldly postulated the only theory which fitted his views of evolution. Darwin really gave it a comparatively small share of his thought, and only after he had modified his views of the omnipotency of natural selection,[1] did he begin to feel the absolute necessity for a working hypothesis of inheritance. But now the heredity problem is no longer the subsidiary one, in fact, just at the present time, it is the chief one, for the whole accepted theory of the process of evolution has been overthrown by a brilliant student of heredity; and there are two parties, each attempting to throw the *onus probandi* upon the shoulders of the other. It is clear enough that when we have reached an heredity theory which will explain the phenomena of inheritance, the method of evolution will itself be a problem of the past. No such explanation can be reached, however, so long as students of heredity take only a partial view of the facts of evolution. The present temper of Weismann and his English followers is apparently somewhat exclusive; the same is equally true of some of our friends on this side of the Atlantic.

What then is necessary in a complete theory of heredity? It must account for the repetition phenomena; these were the first to attract attention, for we are always more struck by the features in which the offspring resembles the parents than by those in which it differs. Under this head are included "reversions."

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[1] This change of view becomes most evident in his Animals and Plants under Domestication, in the closing part of which *Pangenesis* is proposed.

Second, it must account for the non-repetitive phenomena, or the appearance of new characters, to the importance of which Darwin first directed our attention. It is clear that anthropology, zoology, botany, and palæontology give an ample field for the above. Thirdly, there are the physical transmission phenomena, the peculiar field of the embryologist. We may approach heredity through either of these channels, but the test must be by the data afforded by them all.

Thus we find Lamarck, Darwin, Galton, Spencer, Brooks and others coming to the problem chiefly from the study of living adults in past and present time, while Weismann has come to it from the side of embryogenesis. There are great difficulties in the embryological problem ; we have to do with particles of protoplasm of minute size, largely composed of water, yet suspending invisible molecules which we must suppose are the actual vehicles of inheritance, for, under the ordinary conditions of nutrition, they will repeat chapter after chapter in the history of the race, and finally take the form of the adult — they are indeed microcosms. We have to consider the part played by the male and female element. And the relation of these specks of protoplasm to the life history of the individual.

Democritus, who offered the first hypothesis, supposed that the sperm was secreted from all parts of the body of both sexes at the time of impregnation animated by a bodily force, like parts producing like. When Darwin proposed his provisional hypothesis of pangenesis he embodied in it a somewhat analogous conception, but he was aided by the well advanced stage of embryological and physiological science. The older views of "evolution of the germ," or the expansion of a minute pre-formed individual, as opposed to Harvey's "epigenesis,"or growth by addition, had given way to a modification of both ideas: "That development, which, in its superficial aspect, is *epigenesis*, appears in essence to be *evolution* or the expansion of a potential organism according to fixed laws."[1] Darwin's views were thus stated:[2]

> "It is universally admitted that the cells of the body increase by self division thus forming the various tissues. Besides this, I assume that the cell units throw off minute granules which are dispersed through the entire system; these may be called *gemmules*. They are collected from all parts of the system to form the sexual elements, and their development in the next generation forms the new being. They are thrown off by every unit, not only during the adult stage but during each stage of development of every organism. Hence it is not the reproductive organs or buds which generate new organisms but the units of which each individual is composed. Gemmules are capable of transmission in a dormant state to future generations and may then be developed."

Notice two main features of this hypothesis: that there is no difference of character in the elements conveyed by the two sexes; second, that the vehicles of hereditary characteristics are broken down, scattered through the system, and *re*-collected from the soma or body of each individual to form the germ of the new one. There are, therefore, postulated countless numbers of gemmules corresponding to the constantly changing cells of the body; these gemmules being also imaginary elements. Their migration to and from the body cells is in contrast with the fixity of the repetition of parental

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[1] Huxley, Art. Evolution, Enc. Brit., p. 746.

[2] Variation of Animals and Plants under Domestication, vol. ii., p. 369.

and ancestral traits, and does not accord with the facts of the early appearance and isolation of apparently complete germ cells. Moreover Galton's well known experiment of the transfusion of the blood of eighteen silver-gray rabbits with that of other varieties showed that the gemmules, if existent, do not circulate in the blood, for this transfusion of blood was not accompanied by the slightest interchange of characteristics.

Passing by Haeckel's suggestion of *Perigenesis*, which invests the molecules of organized matter with some of the lower faculties of mind,[1] let us look at Brooks's ingenious attempt to modify Darwin's hypothesis. His postulates were the actual existence of the gemmules, but not quite as conceived of by Darwin, for there is a fundamental difference between the male and female elements of reproduction. The ovum is conservative, reproducing cells like itself and a storehouse of hereditary tendencies, giving rise directly to new ova, while the spermatozoan is the progressive element, the repository of the gemmules. Nor are the gemmules thrown off at random by all the cells of the male body, but especially by those which are disturbed in their conditions by a change in environment. Variability, therefore, is most rapid when external conditions are disturbed, and it springs from the union of the ovum and spermatozoan. This system is open to most of the objections which can be raised against the original of Darwin, but is moreover opposed by the rapidly accumulating evidence for the essential similarity of the ovum and spermatozoan.

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[1] See Brooks's Heredity, p. 37. "Unconscious memory is the most important characteristic of organized matter. Heredity is the memory of the plastidules; variability, their power of perception."

Observe that all these hypotheses sprang from the evolution standpoint, and were constructed to account not only for the repetition phenomena but for what was by each author considered a prime factor in evolution, namely, the transmission of acquired characters, or the inheritance by the offspring of some of the influences which environment and habit have exerted upon the body cells of the parent. All reasonable hypotheses, as these certainly were, have their value in stimulating research; and the main service rendered to science by the pangenesis doctrines has been a negative one, namely, they have shown that it is extremely *difficult to construct even an a priori working-hypothesis of heredity which will explain the transmission of acquired characters.*

Weismann is the most brilliant of the post-Darwinian writers, and no one at the present time has so great a following or is exerting such a wide influence. He approached the heredity problem purely from the embryological side: "How is it that a single cell of the body can contain within itself all the hereditary tendencies of the whole organism?" There can be but two alternatives, either the substance of the germ cells is derived from the body of the new individual, or directly from the parent germ cells. His theory of the "continuity of the germ plasm" supports the latter alternative according to which the germ cells of the parent must give rise to "somatic" cells forming the body of the offspring, and to "germ" cells. Each generation has an identical starting-point in cells of the latter kind which are in a sense immortal, the individuals being mere offshoots from the continuous germ plasm stem. Some of the details of Weismann's views are, that the nucleus of the germ cell is the sole bearer of the hereditary tendencies; that the expulsion of each of the two polar bodies of the ovum has a distinct meaning, the first expelling the ovogenetic nucleoplasm, the second reducing the ancestral germ plasm by one half, and thus rendering the nucleus ready for the accession of the germ plasm of the spermatozoan which has previously been correspondingly reduced. While these subsidiary hypotheses, if correct, would strengthen Weismann's position, I do not see that his theory is dependent upon them.

Now look at his main propositions, first, as against Brooks, there is no fundamental distinction between male and female germ cells; second, as against Darwin and Lamarck, the early separation and isolation of the germ plasm from the somatoplasm, renders it highly improbable that acquired characters can be inherited, for the changes in the body can exert no definite influences upon the germ cells. It is at once evident that this theory explains admirably the repetition-phenomena, and is strong upon the embryological side. Before criticising it from the non-repetitive or evolution standpoint let us examine the views of Galton.

It is certainly very remarkable that there are so many points of agreement between Weismann and Galton, when we consider their diverse fields of research. Galton was the pioneer, and the fact that Weismann independently reached similar conclusions from entirely different data, affords a strong presumption in favor of their common grounds of opinion — that the physical vehicle of heredity is continuous and feebly or not at all influenced by changes in the individual which conveys it. Some of the special biological problems which Galton[1] set before himself to solve by anthropology, were: (1) The share contributed to the offspring by each of its several ancestors. The nearness of kinship of different degrees of relation. (2) The causes of stability of type observed in large populations through many generations. (3) Nature *v.* Nurture, or the share contributed by inheritance and environment respectively to personal characteristics.

1. Stature is an heritage which blends[2] and which therefore enables us to determine with precision the contribution of each ancestor. We find that the mid-parent contributes $\frac{1}{2}$ the total heritage (= father $\frac{1}{4}$, mother $\frac{1}{4}$ with transmutation for sex). The mid-grandparent (= grandfather $\frac{1}{32}$, grandmother $\frac{1}{32}$) contributes $\frac{1}{16}$, etc. There is in every one an unused or "latent" heritage as shown by the fact of his transmitting ancestral peculiarities he himself does not exhibit, but the store of latent heritage is not necessarily from all or even from many of his ancestry. As the personal heritage from each parent is but one quarter, the total being one half, it follows that both the personal and latent heritages must be reduced by one half. 2. In hereditary inquiry we must study fraternities and compare all the members of one generation with those of another. The main line of hereditary connection unites the set of elements out of which both the parent and the child are evolved. *The main line is a chain of which the personalities are pendants.* Stable forms represent the groupings

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[1] See his "English Men of Science," "Inquiries into Human Faculty," and "Natural Inheritance."

[2] Eye color is an example of characters which do not blend.

of characteristics which have the firmest hold upon the race; as illustrated by a polygonal block with unequal sides: the chances are that the block will fall upon its longest side, yet it may fall upon its shortest side and represent a new type, which, nevertheless, possesses some small stability of its own. Against such stability, however, works the *law of regression*, viz. that upon the whole the stature of children will be more mediocre than that of their parents; that the more exceptional an individual is, the greater are the chances that his offspring will be unlike him, *i.e.* nearer to the race type. Nearness of kinship must therefore be computed in degrees of regression. 3. In the life history of the individual the influences of nature, or inherited constitution, greatly preponderate over those of nurture, or environment and education. It has been generally held that the study of man affords the most striking examples of the law of inheritance of acquired characters. Yet Galton says, in doubtful terms, that such inheritance should be looked for not in the first but in the second and third generations; that acquired faculties, if at all, are transmitted with dilution; that the actual evidence for such transmission is not very conclusive.

It appears to me that if Weismann's system had been especially built up *a posteriori* for Galton's anthropological laws it could not have been better adjusted, but since he makes no allusion to Galton's work we know this was not the case. The balance between variation and stability, the element of certainty and of chance in the mingling of heritages, the reduction of parental and ancestral characteristics are all explainable by Weismann's views of physical transmission. Upon the question of inheritance of acquired characters, they are almost but not quite in accord; Galton is in doubt, Weismann thinks it improbable if not impossible. From the standpoint of evolution, or non-repetition, however, there is one point in which Galton's results are decidedly adverse to Weismann as we shall see.

There is thus strong evidence for the "continuity of the germ plasm" theory. This does not seem to be necessarily antagonistic to the Lamarckian idea for we can conceive that the germ plasm is continuous and still influenced in definite ways by the body which contains it. Yet Weismann holds that this is not the case: that no special or local life changes in the body can in any way reach or influence the germ cells in such a manner as to be inherited. This view throws the whole burden of evolution upon the natural selection or survival of those individuals which possess, by blending or otherwise, that germ plasm which represents the bodily constitution and structure best fitted to environment.

In this manner the principle of inheritance of acquired characters, from being one of the dogmas of science has been first questioned, then thrown in doubt, and finally rejected by a large body of zoologists. We really owe it to Weismann that this principle, which forms the mainstay of Lamarckism, was adopted by Darwin as a most important factor in evolution, but has never been critically examined from the heredity side, should now be thoroughly investigated. The existence of this principle in inheritance is the focal point of a discussion in which the authority of Lamarck, Darwin, Spencer, Eimer, and the greater number of American biologists may be quoted in the affirmative, while Wallace, Weismann, Lankester, and the majority of the younger English biologists take the negative. Darwin's later views in this matter are most clearly stated in his correspondence with Moritz Wagner: "In my opinion the greatest error which I have committed has been not allowing sufficient weight to the direct action of the environment, *i.e.* food, climate, etc., independently of natural selection." I quote this because Lankester has tried to show in a letter to *Nature* that Darwin never adopted the views of Lamarck.

The general drift of my own views is that upon the side of evolution, or non-repetition in inheritance, the Lamarckians have much the best of it; while upon the side of repetition and of embryology, their opponents are strongest. It has been said, "Heaven deliver us from our friends," and I must confess that, upon carefully analyzing the arguments of some of the neo-Lamarckians, I find almost as much against as for the principle they are advocating. The palæontological evidence appears to be the least vulnerable. For example, the evolution of the horse's foot seems to afford conclusive proof of the inherited effects of use and disuse; yet when we consider the enormous period of time which the reduction of the second and fourth digits has required since the lower Miocene period, when they became absolutely useless, the force of the argument is somewhat invalidated. Again, in the teeth, the evidence for kinetogenesis is not without exceptions. We require more accurate observation and more logical reasoning, especially directed to the facts of transformation in their bearing upon inheritance.

What is your opinion upon the nature of variations? All my own observation in the field of palæontology goes to show that they are not fortuitous, but along certain definite lines, as early claimed by Gray and Nägeli. Discard the principle of the inherited influences of habit and environment, and you are apparently left without any explanation of this fact. The fortuitous mingling of germ plasms must result in random variations. Granting that they may be of sufficient value to be selected, we still have to eliminate the swamping effect of interbreeding, and the fatal force of the law of regression to race type which, according to Galton, acts even in the offspring of a pair, both of which possess the advantageous variation.

In addressing this association of the Marine Biological Laboratory, I chiefly advocate, not so much my own views, as a liberal and generous spirit of discussion, for there is little prospect of a solution of these irreconcilable opinions in the temper which characterizes both sides at present. I claim, if the Lamarckians can demonstrate by palæontological or other evidence, that acquired characters are inherited, it rests with the embryologists to furnish a theory of physical transmission. On the other hand, embryologists may show conclusively that such inheritance is impossible. In the meantime let us keep in view, without prejudice, all classes of facts which bear upon this most important biological problem.

SEVENTH LECTURE.

THE RELATIONSHIPS OF THE SEA-SPIDERS.

By T. H. MORGAN.

AMONGST the Hydroids and sea-weeds on the piles of the wharf of the Fish Commission, living below the tides, and clinging tenaciously by means of the long jointed legs to the surrounding stems, are to be found abundantly small whitish spider-like creatures. And if the sea-weeds, etc., dredged in the "Hole" be examined, a similar but larger animal may be found.[1] The group to which these belong is known technically as the Pycnogonida, or, as Professor Dohrn of Naples has proposed to call them, Pantopoda. Fortunately we have a good enough English equivalent for the terms — Sea-Spiders.

It may not be out of place to say here a few words about the structure of the adults of these sea-spiders, as the group is a small, isolated one, and only short accounts are given in the ordinary text-books. The accompanying figure (1) may aid us in understanding some of the principal structures of the group.

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[1] Phoxichilium maxillare.

At the anterior end of the body we see the large forwardly-projecting proboscis, with the triangular mouth opening at the anterior end. Above and on each side of the proboscis lies the first pair of appendages — the mandibles so-called — each with a pair of forceps at its end — the chelæ. Behind the mandibles and somewhat on the dorsal side of the animal lies the second pair of appendages — the palps. The next pair of

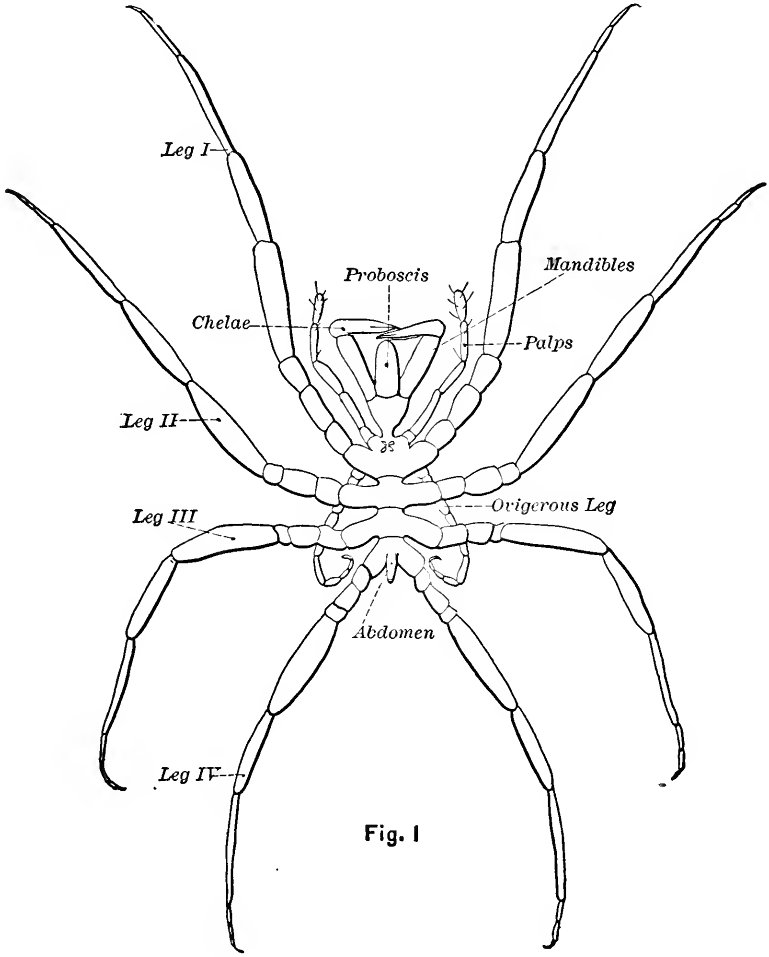

Fig. 1

appendages following the palps is situated more ventrally than either of the other two, and hangs down from the ventral side of the animal. These are the ovigerous legs. These anterior three pairs of appendages are followed by four pairs of walking-legs. The first pair of walking-legs is attached to what we may call the first body segment. To the same segment are attached the proboscis in the anterior middle line, the pair of mandibles, the palps, and the ovigerous legs. In the middle of the dorsal surface of the same segment lie the four small simple eyes.

The second pair of walking-legs (the fifth pair of appendages) is attached to the second body segment, the third pair of walking-legs to the third body segment, and the fourth pair to the fourth body segment.

The body of the animal ends posteriorly in a small process pointing upwards and backwards, which carries the anal opening at its distal end, and is known as the abdomen or rudimentary abdomen.

Turning now to the internal structure, we find a brain — dorsal to the œsophagus — followed by a ventral chain of five pairs of ganglia for the middle region of the body and a pair of small ganglia, continuous with those of the trunk, within the abdomen. The first pair of appendages is innervated from the brain; the palps and ovigerous legs from the first pair of ventral ganglia. This first pair of ganglia is in reality the partially fused first and second pairs. Each of the four pairs of walking-legs has a pair of ganglia in its segment, which supplies it with nerves; and there is, as I have said, a pair of ganglia in the abdomen. The digestive tract runs as a simple straight tube through the body, beginning at the anterior end of the proboscis and ending at the tip of the abdomen. As it passes through the body it sends out long diverticulæ into the appendages — the mandibles and the legs — and an anteriorly directed pair into the base of the proboscis. These diverticulæ are the most characteristic and interesting structures in the group.

The reproductive organs likewise extend from the body into the walking-legs, and have their openings on the second (proximal) joints of these appendages. There is a simple tubular heart lying dorsal to the intestine, which receives the blood through lateral ostia to pump it over the body.

These are the more important structures of the Pycnogonids, or at any rate those which we will need in our comparisons.

The gallantry of the males must not pass unnoticed. Each during the breeding season carries on its ovigerous legs the developing eggs, which have been received, as soon as laid, from the females. Curiously enough this fact led naturalists into a most amusing blunder, inasmuch as it was tacitly assumed that those individuals which took charge of the young and eggs must be the females, and were described as such.

The problem, and possibly its solution, which I wish to present to-night, is the relationship of the Pycnogonids to other groups; and the point of attack is to be largely from the side of the embryology of the group. There have been endless speculations as to the position — zoologically — of these animals, but until within recent years little was known of their anatomy, and practically nothing of their embryology.

Speaking in general we may say that prior to 1880 the group was placed either amongst the Arachnids (spiders, scorpions, etc.), or else amongst the Crustacea. Recent work has shown Crustacea to be out of the question, I think, but at the same time, the alternative was not believed to be the Arachnids. The group has been independently monographed by Dr. Hoek in a report of the *Challenger* Expedition, and by Professor Dohrn in a volume of the Naples Fauna and Flora. Each of these authors concludes that we are to believe the group to have arisen, independently of other Arthropods (Crustacea, Spiders, Insects), from the Annelids. While their work has been very complete as regards the adult anatomy, and inasmuch as any speculations about the inter-relationships of animals must take into account largely the adult structure, yet there remained unworked another equally valuable source of knowledge; viz. the study of the changes which the animal undergoes in its development from egg to adult. Information from this source must take equal rank at least with that from adult anatomy and histology, and may throw light upon hidden relationships which could not otherwise be obtained; and I wish to give hurriedly a few facts about the embryology of these animals, choosing those which seem to me to bear directly upon the relationship of the Pycnogonids to another group to which a study of the development has led me to believe the sea spiders to be allied.

Without a series of figures to illustrate these stages of development, it will be impossible to do more than merely mention, in the briefest possible way, those points which are to be used in our comparison. Moreover, there are two types of development within the group, and only to one of these have I paid, so far, special attention.

The first type is that represented by the genus Tanystylum, and is to be regarded as the more primitive of the two, which I shall describe.

The egg of Tanystylum undergoes a regular equal segmentation into two, four, eight, etc., resulting in a solid mass of cells, each cell pyramidal in shape, with its apex at the centre of the egg, and the base at the surface. Every cell contains a single nucleus lying nearer to its base; that is, to the outer part of its cell.

Each of these cells then divides — the nucleus dividing into two at the same time — into an inner and outer half, so that there results a solid two-layered embryo. This change has been effected by a process of multipolar delamination. The inner cells, or at least some of them, go to form the endoderm of the adult; the outer form the ectoderm.

I have not followed in detail the changes which take place after this, so that we must pass to a stage of development when the young embryo has broken through the egg membranes and has begun to lead an independent life. At this stage it is totally different from the adult, although, as we shall see later, it contains many of the essential characteristics of those parts of the adult which it represents. Figure 2 gives an outline of a larva at such a stage. We see it has three pairs of appendages, of which the first is chelate, and the second and third pairs are simple uniramous structures, which are used in crawling around amongst the hydroids. The first pair are three-jointed, — counting the movable claw of the chelæ, — the second and third appendages on each side are two-jointed. These last two appendages represent the palps and ovigerous legs of the adult. The body ends anteriorly in a rounded proboscis. The digestive tract, beginning at the mouth at the distal end of the proboscis, passes through the proboscis as a tube triangular in cross-section and opens out into the wide stomach within the body proper. There is no posterior opening to the digestive tract, but from the stomach runs forward into the mandibles a pair of diverticulæ. The larva has a brain lying dorsal to the œsophagus, which is connected by two commissures with a pair of ganglia ventral to the digestive tract. There are in all two pairs of these ventral ganglia, the pairs more or less fused together; and behind these, and completely detached from them, is a thickening of ectoderm which indicates the commencement at this place of a third pair. The larva has no heart nor reproductive organs at this stage.

PANTOPOD-LARVA

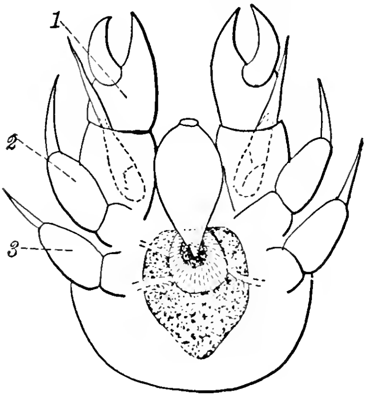

Fig. 2

It is needless to follow here the changes which this Pantopod-larva (Dohrn) undergoes as it is metamorphosed into the adult. The body elongates, new appendages appear seriatim, the proctodæum invaginates and puts the digestive tract posteriorly into communication with the outside world, and the second or third pairs of larval appendages change into those of the adult — the palps and ovigerous legs.

We may now take up another type of development found in the group, and represented by the genus Pallene, which, I may say in passing, is to be regarded as a much modified and abbreviated development of a form like the last — Tanystylum.

The egg has one hundred and twenty-five times the volume of the preceding species. Corresponding with the increase in the size of the egg is a decrease in the number, and correlated with the addition of food-yolk to the egg is the abbreviated development; so that the young leaves the parent — not in an immature state as in Tanystylum — having almost all of the structures of the adult.

The segmentation of the egg is holoblastic as in the last case, but the first cleavage furrow divides the egg into a small cell — the micromere — and a larger one. The protoplasm surrounding the nucleus is free from yolk in all cases; but from this purer protoplasm, processes ramify all through the yolk. It is needless to follow, for our purposes, the egg through the series of segmentation phases which follow, and it will be sufficient for us to know that the result of these changes is a solid mass of cells much as in the case of Tanystylum. There is this difference, however, that in Pallene the cells covering one pole of the egg — those which have come from the micromere — are smaller than those over the rest (two-thirds) of the egg. It is in the region of these smaller cells that the first indications of the embryo appear.

After the segmentation is completed follows, as in the former case, multipolar delamination ; but owing to the large amount of yolk, the delamination begins first in the region of the micromeres, — each cell of which delaminates into an inner and an outer cell, — and this process progresses slowly over the surface of the egg, each cell, both micromere and macromere, delaminating just before it joins the edge of the ever-widening blastoderm. The outer cells of the blastoderm form a somewhat flattened columnar layer, under which lie the nuclei and protoplasm of the inner cells. To the inner cells would belong properly all of the yolk of the pyramidal cells ; but as a matter of fact, all traces of cell-outlines are completely lost in the yolk at this time, so that the blastoderm, with its two layers, lies at the surface of a yolk-mass. Soon after this there can be seen at the surface of the embryo a round opaque spot, which I shall call the primitive cumulus. The ectoderm is thickened in this region, and in the centre of the thickening lies the triangular invagination of the stomodæum, and around the latter appear the first traces of the mesoblast.

There next appear at the surface of the embryo other opaque areas, which are the beginnings of the brain, the ventral ganglia, and four pairs of appendages ; — viz. the first, fourth, fifth, and sixth. The embryo still retains its spherical shape.

The next stage is shown in ventral view by Fig. 3. By reference to the figure the more important structures can be seen. The proboscis projects forward ; on each side of this are the mandibles. On each side of the ventral median line lie five pairs of appendages, and to the sides of the last three are three pairs of walking-legs. The second and third pairs of appendages are absent from the embryo at this stage. If we had cross-sections through the body of such an embryo, we should find, lying at the base of each of the walking-legs, a small cavity with a definite boundary of mesoderm cells; this cavity is the body-cavity. Such sections would further show us that the digestive tract had begun already to push out into the appendages, and *each pouch contains yolk*, as does also the whole of the mid-gut.

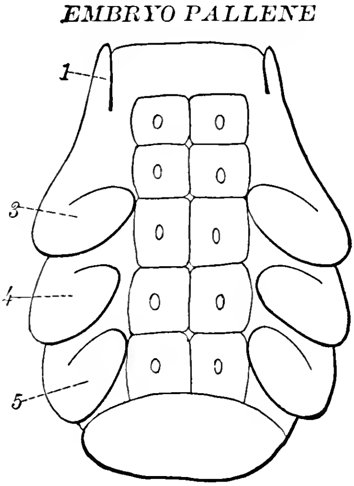

Fig. 3

It is not necessary to follow the later stages of development of such an embryo, as we have already seen those peculiarities which are to be used in the comparison of the Pycnogonids with other groups.

Now in the briefest manner possible I wish to point out the importance of these embryological facts, and their bearing upon the relationship of the Pycnogonids to the group of the Arachnids.

First there is the multipolar delamination, which is such a striking feature in the development of the Pycnogonids; so that when we come across an exactly similar series of phenomena in the false-scorpions (Metschnikoff) and in the spiders (Balfour), we have found a strong point for comparison in the development of the two groups. We find in the spiders the first external appearance of the embryo to be a round opaque area on the surface — the primitive cumulus; beneath this the first traces of the mesoderm are found, and further, this is the point where the stomodæum soon invaginates. We have seen an exactly similar series of changes in the embryos of the Pycnogonids. We also find body cavities lying at the bases of the legs of the embryo spider, in an exactly similar position to those which we have seen in the sea-spiders. The digestive pouches found in both the adult and in the embryos of the Pycnogonids, which contain yolk in the young, furnish us with another point of comparison with the Arachnids. In the latter, we have these for a time in the developing young; and, moreover, in the false-scorpion they contain yolk from the mesenteron.

Lastly, I must call attention to the structure, innervation, and origin of the first pair of appendages. These are chelate, as in many Arachnids, and the free movable joint of the claw moves outwards and downwards as in the Arachnids generally (and not upwards and outwards as do the chelæ of the Crustacea). Again, these appendages are innervated in the sea-spiders from the brain, and finally in the embryo the appendages are seen to arise at the sides of the stomodæum, and subsequently move forward and dorsal to it. In both of these last characteristics we can compare the two groups directly together.

So much for the embryology: I leave these comparisons to speak for themselves.

And now let us turn to the adult structures of the two groups under comparison.

I do not believe any general definition of the group of Arthropods can be made, which, if based on fundamental characteristics, will not of necessity include within it the Pycnogonids. We have the segmented body with its segmented appendages, typically a pair to each segment. There is a supra-œsophageal ganglion — the brain — connected by commissures with a double ventral chain of ganglia. Digestive tract, circulatory apparatus, and to some extent[1] the generative organs, fall into line with the other Arthropod characteristics.

Comparing the adult structures of the sea-spiders with the Arachnids, we find many common characteristics; and I must point out that many of these similarities are in structures which we must believe the primitive ancestors of the Arachnids to have had more fully developed than the living forms to-day.

First, we may consider the digestive tract. In the adult sea-spiders we find long diverticulæ from the mid-gut into the appendages; and we find in the early stages of development of both (false) scorpions and spiders similar pouches.[2] The heart, too, with its lateral ostia resembles that of spiders, though the resemblance is not more striking than to Arthropods in general, and I have spoken above of the resemblance between the chelæ and their innervation in the sea-spiders and Arachnids. Further, the external openings of the reproductive organs in Limulus lie on the base of the first

[1] The opening of the ducts of the reproductive organs are not as difficult to account for as I had at first supposed. We may imagine them to have secondarily shifted from the body to the legs, and we see in Limulus ("An Arachnid") the external reproductive orifices on the base of the first pair of abdominal appendages.

[2] The structure and arrangement of the so-called livers of Limulus and Scorpions is interesting, inasmuch as they may represent ancestral abdominal pouches.

abdominal appendage, so that the difficulties arising from the existence of similar openings in the Pycnogonid, on most of the appendages, is partially at least overcome. I have also examined the structure of the adult eyes of the Pycnogonid, which seem to furnish, perhaps, an explanation to the early inversion of the eyes of the Scorpion and other Arachnids.

Let us turn finally to an examination of the appendages of the Pycnogonids, where we meet with a stumbling-block in the way of our acceptance of the relationship of the sea-spider and Arachnid.

If we arrange in two series the appendages of the two groups, beginning with the first pair in each, we get the following table: —

Pycnogonid.		*Spider, Scorpion, etc.*
Mandibles	1st pair	Cheliceræ.
Palps	2d "	Chelæ.
Ovigerous legs	3d "	1st walking-legs.
1st walking-legs	4th "	2d " "
2d " "	5th "	3d " "
3d " "	6th "	4th " "
4th " "	7th "	. . . . .

In the Pycnogonids there are seen to be seven pairs of appendages, while the spider, etc., have only six pairs in all. There are four of these pairs used by each as walking-legs, and in the Pycnogonids three pairs lie in front of these, and two such pairs in the spiders.

We may get out of this difficulty of numbers in either of two ways. In the first place, we may assume that the four pairs of walking-legs are homologous in the two groups, and at first sight this seems very plausible.

Then the mandibles of the one group seem undoubtedly homologous with the cheliceræ of the other; so also do the palps of the one and the chelæ of the other; therefore the trouble lies with the ovigerous legs.

Schimkewitsch tried to solve the problem by suggesting that this third pair came in as greatly developed exopodite, or endopodite — I forget which — of either the second or third pairs of appendages, and was therefore not equivalent to the other appendages. This was ingenious, but wrong. The development of the appendages shows that the third pair is formed in line with, and independently of, the other pairs; and, moreover, it has a separate pair of ganglia from its earliest appearance.

But there yet remains another possible explanation for this third pair of appendages of the sea-spiders, viz. that the spiders have lost a pair of appendages (and ganglia?) between the chelæ and the first pair of walking-legs. Here the objection arises that, although the development of spiders has been quite fully studied, no evidence of such a loss of appendages is forthcoming, and therefore, for the present at any rate, we have to reject this solution.[1]

The explanation which seems most plausible is, that we cannot properly bring into line all the pairs of walking-legs and compare them, pair for pair, but that the first pair of walking-legs of the spiders corresponds (as in the table given above) with the ovigerous legs of the sea-spiders, and, therefore, the second pair of legs of the

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[1] Perhaps the development of spiders will bear re-examination in this respect, and more especially should the first pair of ventral-ganglia be examined to see if it is a single or a double pair.

spiders with the first of the sea-spiders, the third with the second, and the fourth with the third, leaving over the fourth pair of legs of the Pycnogonids as a pair not found in the spiders. If this be true the position to which we are forced is obvious, — that the last segment of the body of the sea-spiders, and its appendages, correspond to the first segment of the abdomen of the spiders. Such a transfer of segments is not uncommon amongst Arthropods, and there is nothing unusual in such a process. It here carries with it, however, the assumption that the fusion must have taken place at a time when the abdomen still bore appendages serially homologous with those of the thorax. We may imagine, if we like, that this took place at a time when the third pair of appendages appeared and began to carry the eggs, so that the body, by utilizing the first legs as egg-carriers, retained a pair of the abdominal legs for purposes of locomotion.

I must confess, however, that although this last view seems far the more probable, in the present state of our knowledge, yet the idea is a very attractive one, — that the four pairs of walking-legs are homologous in the two groups, and that therefore the spiders have lost a pair of appendages between the chelæ and the first pair of legs.

I have, in the above comparison, left to one side the Crustacea, nor is there need to say much in regard to their possible relationship to the Pycnogonids. The characteristics which the two groups have in common are only those of Arthropods in general. Other than this there seem to be few homologies, with the possible exception of a six-legged larval form of which I shall speak later. And these points of difference in the development may be mentioned. There is no primitive cumulus or its homologue in the Crustacea, and the first invagination of the surface ectoderm of the embryo goes to form the mid-gut, and its point of origin corresponds, approximately (perhaps entirely), with the permanent anus. Further, there is nothing corresponding to the gut-pouches so characteristic of the Pycnogonids and, to some extent, of the Arachnids.

If we turn to the insects, which form by themselves so well-defined a group, we see little or nothing new for comparison with the Pycnogonids.[1]

Returning again to the Arachnids, we have found that the Pycnogonids have, in common with them, not only the general characteristics of the Arthropods but many peculiarities of development and many structures common in the adults. If we accept this we have gone perhaps as far as the facts at present at our command will allow. For it is impossible to say at just what point the Pycnogonids have branched off from the phylum of the Arachnids; but, inasmuch as several of the adult characteristics of the sea-spiders are found in the embryos of higher Arachnids, we may fairly believe that the group arose quite far down amongst the primitive Arachnids, to have retained many of their primitive structures, and to have lost others which the ancestral form possessed becoming simplified, specialized, and degenerate.

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[1] If Heider's and Wheeler's accounts of the early formation of inner yolk nuclei from the outer (ectoderm) nuclei be true, it looks exceedingly like multipolar delamination for the insects.

There is another problem, which must arise in any discussion of the affinities of the Pycnogonids, and which may be treated as a corollary to what has gone before. I refer to the presence within the group of a free-living larval form — the Pantopod-larva which we must believe typically to belong to all the species of the order.[1] Was the ancestral form from which the group has arisen similar to this Pantopod-larva, hence its presence as a stage of development to-day ; or is it a purely secondary larval form, an interpolated stage, therefore, unimportant from a phylogenetic point of view ?

Before attacking the problem directly, let us understand clearly the possible conditions under which such a larval form, or any larval form, may occur within a group of animals. There are at least, two, and perhaps three, such conditions generally recognized. We have first what is known as a primary larval form, by which we mean the young form represents approximately the structure possessed by the ancestor from which the group has arisen. In Fig. 4 this is shown diagrammatically by *A*. The *X* marks the place at which a species *x* expanded into a group, and after the group has been evolved each young form in that group first reaches *X*, and then each in turn develops the peculiar features of its particular family, genus, species.

Again we may find all the animals of a group possessing a common larval form, but which need not necessarily ever have been an ancestor of the group, but may have been *interpolated* quite early in the history of the

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[1] Such exceptions, as Pallene for instance, show an abbreviation of this development, and at one time they or their ancestors must have had a free-larval form.

group before it (the group) diverged into those forms existing to-day. In Fig. 5 such a condition is shown by B. At *X* in this figure we may suppose, by some means or other, a stage of development (not an ancestral one), to have appeared, and the young to have become adapted to an independent existence, or to have been fitted by a process of natural selection to lead a free life. Now since the adult form, which developed this secondary larva, subsequently was the starting-point for a group of animals, we would expect each species to retain this secondary larval form. Thus in diagram *B*, Fig. 4, we may suppose a larval form *a* to appear, and afterwards as the group arose giving *x*, *x*, each to have retained the larva *a*.

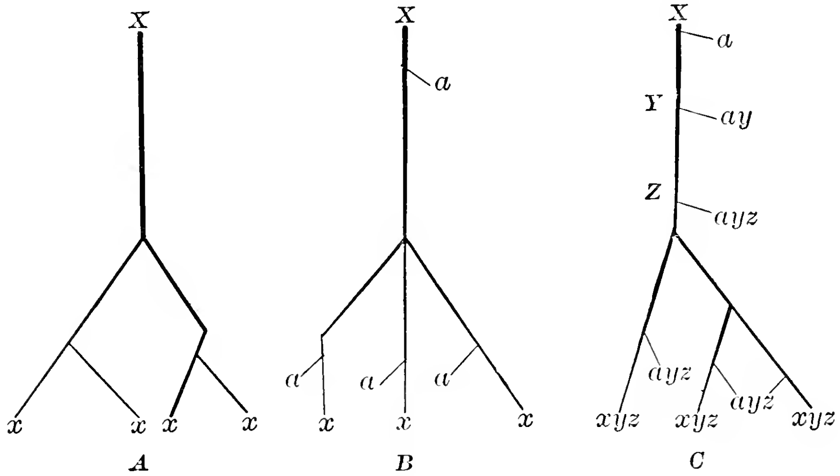

Fig. 4

There is possibly a third condition by which a larval form may appear within a group. Briefly put, it is something like this, an adult animal which subsequently gives rise to a group, may have had at its starting-point a free larval form of its own (whether primary or secondary is immaterial), and as the group arose, through divergence of the adult animals, the larval form was itself affected by the new characters of the adult, and so changed into what I shall speak of as a *transformed larva*, or, to put it differently, we may suppose the newly acquired characters of the adult to be thrown back upon the larval form already present. This is shown by diagram *C*, Fig. 4, when *a* is changed gradually to *ay*, *az*, as the adult *X* changes into *Y* and *Z*.

There may be many modifications of these three conditions I have sketched, but for our present purposes these will suffice.

To restate the problem before us: we wish to find out, if possible, in which of these ways the larval form in the Pycnogonids has been evolved. Professor Dohrn believes, and his theory is the natural outcome of the position he has taken as to the origin of the group of the sea-spiders, that the larva of the Pantopoda is a transformed larva, and therefore the explanation of its appearance within the group to be represented by Fig. 4, *C*. Dr. Hoek, on the other hand, believes the embryo to be a primary larval form, and therefore its presence to be accounted for in some such way as represented by Fig. 4, *A*. Professor Dohrn further believes that the Trochophore of Annelids represents the first larval form which became modified into the Pantopod-larva; while Dr. Hoek believed that the Pantopod-larva of the Sea-spiders, the Trochophore of the Annelids, and the Nauplius of the Crustacea, have each given rise to their respective groups, and to each represent a primary larval form; and moreover, he thought these larval forms themselves to have been inter-related at the time when they diverged into Sea-spiders, Annelids, and Crustacea. My own view of the question is that we have here a condition represented by Fig. 4, *B*, or, in other words, that the Pantopod-larva represents purely a secondary larval form.

I wish now to bring forward the reasons which have led me to such a belief, and at the same time the objections to the views of Dohrn and Hoek.

Let us stop for a moment and examine the structures of the three larval forms under discussion.

NAUPLIUS

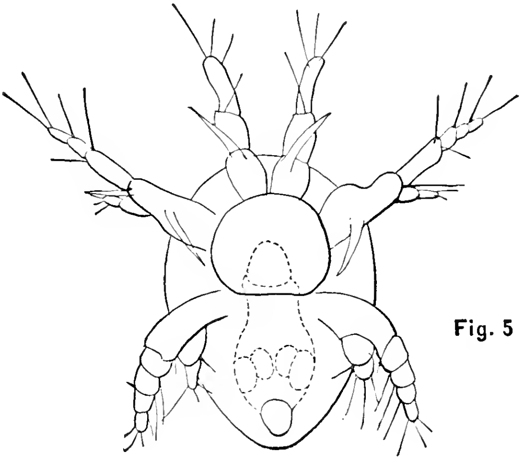

Fig. 5

The Nauplius of the Crustacea is shown in Fig. 5. The body is oval in outline, and unsegmented; it has three pairs of appendages arranged along the sides of the body. The mouth lies under a large upper-lip, a little anterior to the centre of the body, and leads into the œsophagus which in turn opens into the stomach or mid-gut; then follows the proctodæum with its external opening at the posterior end of the body. There is a brain (supra-œsophageal ganglion) dorsal to the œsophagus, connected by commissures with the first pair of ganglia of the ventral chain. An eye lies in the mid-dorsal line over the brain. The first pair of appendages is simple and uniramous and receives its nerves from the brain. The second and third pairs of appendages are each biramous, and the first and second pairs are innervated from ventral ganglia. These I believe are the essential features of the Nauplius. It swims freely in the water, and lives a perfectly independent life in those forms in which it is best represented.

TROCHOPHORE

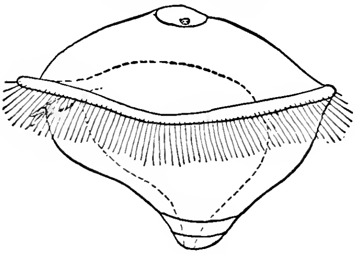

Fig. 6

The Trochophore of the Annelids is likewise a free-swimming pelagic animal, and is diagrammatically represented by Fig. 6. The larva has a large oval anterior end, and a somewhat funnel-shaped posterior part. In the centre of the head-region lie two eye specks, and under this the beginnings of the brain. The middle of the animal is encircled by a band of ciliated cells which form the locomotor apparatus. Just beneath this band, or where the band is double within it, is the large mouth opening. The œsophagus is short and leads into the large mesenteron, and from this runs posteriorly the proctodæum to end in the anus. Beneath the mouth, and lying between it and the anus, is a bilateral plate of cells which is to form the nervous system. In the earliest stages the Trochophore represents a single segment —

the head segment.[1] Soon, however, other segments appear in the anal region, so that we see at one time three segments, two besides the head, and it is at such a stage we may compare the Trochophore with the other forms.

The characteristics of the Pantopod-larva have been already described on page 148, and reference to Fig. 2 may serve to recall its more important features.

We have seen that Hoek holds the Pantopod-larva to be a primary form, and that Dohrn believes it to be neither primary nor secondary, but what I have called a transformed larva.

It is exceedingly difficult to combat these theories, but this much must be against Hoek's position, viz. that the same objections which are nowadays being brought against the Nauplius theory of the Crustacea, must tell at every step against his Pantopod-larval theory for the Pycnogonids; and I believe morphology is outgrowing the Nauplius theory. To-day it seems to be on its last legs — or rather more legs have been forced upon it than it could conveniently carry. Some of its earliest and most brilliant advocates, including Hatschek, Dohrn, and Claus, have at last thrown it over, so that it seems superfluous to repeat the same arguments against the Pantopod-larva that have been brought against the Nauplius theory.

Turning now to Dohrn's theory, we cannot but grant that it at least is a theoretical possibility, even if the Pycnogonids be related to Arachnids. It only remains to examine the facts which we have and see if they

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[1] This is not quite exact, for the posterior part of this segment contains the rudiment of the future body.

furnish sufficiently good grounds for rejecting such a theory as exceedingly improbable.

First, I must insist upon the fact that those characteristics which the Pantopod-larva has in common with the Trochophore are only those features which any two Arthropods have as common characteristics of the first three segments; or, if we go further and include the Annelids, we may say which any two Articulates possess as common characteristics. They are these: a brain and ventral chord, united by commissures around the œsophagus; serial appendages corresponding in number to the number of segments; a digestive tract with stomodæum, mesenteron; and — and here lies the difficulty: not a trace of proctodæum does the Pantopod-larva possess, while both Nauplius and Trochophore have the digestive tract open posteriorly. In the young Pantopod-larva we have, so far as it goes, a fully formed and presumably functional digestive apparatus, and no reasonable account can, I believe, be given to explain how this posterior opening could have become lost in the transition of Trochophore into Pantopod-larva as Dohrn has supposed. If it be urged that in the young form the anus may have become functionless, and hence not developed, it will not mend matters, since we have every reason to believe that in the adult Pycnogonid the proctodæum is to a large extent useless.[1]

I think these facts must prejudice us strongly against the position taken by Dohrn; but let us go further and examine into the other features of the Pantopod-larva.

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[1] It has been suggested that it may serve for purposes of respiration, but no evidence for this is forthcoming.

The chelæ are identical with those of the adult, and pass over during the metamorphosis without change into the first pair of adult appendages. The ventral ganglia arise in the young larva, as do the later ones, by a peculiar process of invagination, and differ markedly from the origin of similar ganglia in the Trochophore; and lastly, the ectoderm and its sense organs are the same as those of the adult. Now while, as I have said, it is just possible all of the things (with the exception of the Proctodæum!) may, as Dohrn believes, have been thrown back upon the larva, such a process seems improbable in itself, and, I think, is an entirely unnecessary supposition.

For the necessity of believing that the young forms, in such groups as Annelids and Crustacea, more nearly resemble each other than do the adults seems to me an entirely unwarranted supposition. On the contrary, I think *a priori* we should expect to find exactly the reverse of this, — that is, that the adults are nearer together ancestrally than are the larvæ.

If we stop to recall the fact that most of these animals lay great numbers of eggs and that almost all of these are destroyed during the larval stages, and out of several thousands only a few reach the adult condition, then I think we must see that the battle for existence amongst the larvæ as compared with the adult is as a thousand to one; and hence, when there is this vigorous process of natural selection going on, we must expect the embryos to become changed, or adapted to new conditions, with great ease and rapidity.

And now if we remember that during the time in which the groups of Annelids and Crustacea have been evolved that the larval forms themselves have been acted upon in an increased degree, there seems every reason to believe that the young may have been much more acted upon and suffered far greater changes.

On the other hand, when we see in such a group as the Vertebrates that in the higher forms the young have been removed to a large extent from the action of surrounding conditions, — as, for instance, by being enclosed within a shell as in the Sauropsida, or retained within the uterus in mammals, — then can we understand why the young resemble each other more closely than do the adults, for the obvious reason that the adults have had to adapt themselves to more numerous external conditions while the embryo has remained fixed.

Indeed this may be pushed a step further, it seems to me, and explain why such young retain the characteristics of lower forms while the adults have lost such structures. This may be due to the young having been removed to a greater extent than the adults from a process of active selection. Hence in such a group, when we say that the Ontogeny tends to repeat the Phylogeny, we mean that the embryos have retained more of the ancestral features than have the adults.

But in such groups as the ones we are discussing, — Annelids, Crustacea, etc., — we ought to expect, if what I have said be true, the reverse of what we find in such a group as the higher vertebrates; viz. that the young forms diverge far apart, and the adults come nearer together.

This will tell strongly against the position taken by Hoek (also against the Nauplius theory), and render unnecessary or even improbable that we need bring together such forms as the Trochophore of the Annelids and the Pantopod-larva of the Pycnogonids. And although on this supposition we might suppose so great a transitional change as Dohrn believes to have taken place, yet it also carries with it the assumption that a new larval form may have been acquired with ease within such a group independently of any previous (ancestral) stages. Hence we are left in an unprejudiced position to choose between these two possibilities! And for my own part I am led to the conclusion, from the foregoing facts of development, that the Pantopod-larva is neither a primary form, as Hoek supposes, nor represents a much modified Trochophore, as held by Dohrn. And it seems to me far simpler and much more in accordance with the facts to believe that we have here a clear case of a secondary larval-form.

EIGHTH LECTURE.

ON CARYOKINESIS.

BY S. WATASE.

IT has been said that one of the greatest discoveries of modern times is the generalization that all animals, however complex their structure, arise by the division and subdivision of a single, nucleated cell. The Cell doctrine in its original form, which had its origin in the comparative study of adult tissues, appears in a new light when viewed from the standpoint of the embryological history of these tissues, arising as they do, as the direct products of egg-cleavage, each segment being the exact copy of the original egg-cell, in so far as its general, superficial features are concerned.

Here arise two important problems : —

(1) How does one egg, which is a single nucleated cell, and which gives rise to one animal, differ from another which gives rise to an entirely different organism ?

(2) What is the essential method of cleavage by which an apparently homogeneous ovum becomes converted into a complicated organism ?

The first problem is well-nigh beyond the range of our present means of research. Take an egg of a starfish and that of a jelly-fish ; raise them under exactly the same conditions. Both will undergo division and subdivision, but the process will end in the production of two entirely different organisms. The difference in result cannot, therefore, be attributed to difference of conditions under which they develop, but to something inherent in the ova themselves. In other words, the egg-cell of a jelly-fish must have had from the beginning the potentiality of becoming a jelly-fish and nothing else ; and similarly, the starfish ovum must have been a potential starfish from the beginning. To imagine, therefore, that all protoplasm is identical, because no difference is recognizable by any means at our disposal, must be an error. Deep within the two particles of protoplasm which give rise to two different organisms, there must be a corresponding difference which lies at the bottom of all differences. In short, the eggs of two different animals must be supposed to differ in their elementary constitution, as much as their adult organisms differ in anatomical structure. "From general scientific principles," says Professor Sachs, "we must assume that for each visible external difference of organ, there is a corresponding difference in its material substance, exactly as we regard the form of a crystal as an expression of the material properties of the crystallizing substance." And again, says the distinguished German botanist, "Even the different shapes of the two sexual cells — of an antherozoid or a pollen grain compared with the oosphere — indicate plainly, that both are constituted differently as to material, since the external form as well as the internal structure of any body is the necessary expression of its material constitution. Difference of form, always indicates difference of material substance." This doctrine of "Form and Matter," or of "Mechanism and Function," as expressed in the language of physiology, is the basis of our biological inquiries. As is clearly expressed in the words of Professor Burdon Sanderson, we must assume that "*every appreciable difference of structure corresponds to a difference of function;* and conversely, each endowment of a living organ must be explained, if explained at all, as springing from its structure"; or in short, "*living material acts by virtue of its structure*, provided we allow the term structure to be used in a sense which carries it beyond the limits of anatomical investigation, *i.e.* beyond the knowledge which can be attained either by the scalpel or the microscope." Given protoplasm of definite structure, and we have its definite function or property. Or conversely, we observe a certain property in a given mass of protoplasm and we regard it as springing from a definite structure. When structure varies, the function must vary also; and when we observe certain peculiar properties we must ascribe them to peculiarities in structure.

One rational answer to our first inquiry is possible, viz. the protoplasmic structure of the egg which gives rise to one organism, must differ from that of the egg which gives rise to another different organism, the differences between the two being relatively as great as those which the two adult organisms display in their anatomical relationships.

If the similarities of two organisms must be attributed to the corresponding similarities of the protoplasm of the fertilized ova from which they respectively arise, the source of similarities in the latter must be sought for in the community of their hereditary antecedents. Hence, one way to place the doctrine of phyletic kinship of two or more organisms upon a scientific basis, would be to demonstrate the molecular or structural affinities of their tissues, or what amounts to the same thing, to demonstrate the molecular or structural affinity of their germ-cells. The embryological phenomena of a developing organism may be expressed in the terms of protoplasmic metamorphosis. Two organisms at the same stage of development would represent the same stage of protoplasmic structure. The budding of a new cell or the formation of a new organ would correspond to the birth of a new phase in the course of the metamorphosis of the original protoplasm of the egg.

To turn to our second problem. What is the cleavage of the ovum? What is accomplished by it? Is it "the mere sundering of material which has no more reference to the future organization of the embryo than the snowflakes bear to the size and shape of a future avalanche"? Or is it a "histogenetic sundering" in which every step in the process has a definite relation to the building up of the future embryo? These questions have been raised from time to time and have been variously answered. Upon this historical aspect of the question it is not my purpose to enter at present. But that each step of cleavage has some definite significance in relation to the organization of the adult or of the larva, at least in certain forms which have been most carefully studied, there can be no question. Thus in a certain animal, it has been observed that the nuclear substance of the ovum is divided, during the first cleavage, in such a manner that one of the new nuclei by its division gives rise to the right, and the other to the left side of the adult organism. In another case, it has been maintained, the first division of the nucleus distributes the nuclear substance into future ectoderm and entoderm. And again, the formation of a certain organ, or of a system of tissues, has been traced in a most definite manner to a particular cell or group of cells in an early stage of cleavage. The more carefully the phenomena are studied, the more astonishing is the regularity and the precision with which the cleavage process is conducted and the differentiation of tissues is accomplished.

The occurrence of variations or irregularities in the mode of cleavage in a certain animal — irregularities as judged by the arrangement of the superficial cytoplasmic furrows — does not invalidate the importance of the conclusion which can be derived from the study of forms where absolute regularity prevails. For the essential feature of the cleavage process is the division and distribution of the nuclear substance of the ovum, and in so far as the nuclear substance is distributed in such a manner as to produce a symmetry of growth in the developing organism, it is immaterial whether its total quantity be divided exactly in two equal halves and distributed into right and left at the first cleavage, or whether it be divided into dissimilar portions and the equilibrium of growth be gradually secured during the subsequent stages of cleavage. The distribution of the nuclear substance may have been just as accurate and precise in one case as in the other.

A comparative study of cleavage of different ova affords another example illustrating this point. For instance, as my friend Dr. C. Ishikawa tells me, the summer and winter eggs of a certain species of *Daphnia* undergo different "types" of cleavage, one being holoblastic and the other being meroblastic, the difference being produced probably by the conditions of the cytoplasm and its deutoplasmic contents. The same may be said in regard to the cleavages in different species of *Peripatus*, as the studies of Sedgwick and others have shown. The same is true in the case of *Renilla* as was shown by Wilson. In short, if we classify animals by the "types" of cleavage or differences of cleavage, rather than with reference to the potential qualities of the nuclear substance, we fall into an error of placing nearly related species of organisms in different categories, nay, we even fall into the absurdity of separating the individuals of one and the same species into different groups.

That the argument based on the arrangement of superficial furrows alone is not entitled to any weight, is further shown by their total absence in several forms of ova, which nevertheless develop into perfect organisms. It has been shown that in a certain plant, the cytoplasm becomes divided without a corresponding division of its nucleus. Such facts seem to point to the conclusion that the division of the cytoplasm and that of the nucleus are two independent phenomena, and that one process can occur without the other, and that when they do occur in close succession, as in ordinary cell-division, it is to be looked upon as a case of coincidence. At any rate, the following conclusion seems to be a valid one, viz. that the division of the nucleus and that of the cytoplasm are due to different causes.

It is now quite generally conceded that the nucleus of the fertilized ovum contains all the hereditary characteristics of the parent organisms. It is this substance in the ovum which stamps the particular characteristics upon an organism of a given species. The study of fertilization has clearly demonstrated the metamorphosis of the sperm-nucleus into a constituent part of the cleavage-nucleus, and thence it is distributed to all nuclei formed in the subsequent cleavages. Morphologically, all the hereditary characteristics which the infant organisms inherit from the parents, must be traced back to a certain number of chromosomes which come from the sperm and egg-nuclei of the fertilized ovum. By cleavage, the potential characteristics become gradually analyzed into their special attributes — the attributes which we assign to different tissues of the larval or the adult organism. If, therefore, I may use one word to characterize the whole process of cleavage of the ovum, the term *Analysis* will perhaps best express our interpretation of the phenomenon. It is true, that we know very little as to the essential respects in which the nuclear substance in the entodermic cleavage sphere differs from the similar substance in the ectodermic sphere. In the present state of our knowledge on this subject, we can only infer a structural difference of the protoplasm from the careful study of the fate of the respective segments. If, for instance, one cell gives rise to a sense-organ, the fundamental molecular structure of that cell must be different from another which contains all the germs of an excretory organ, just as we are forced to conclude that the ova of different organisms are of necessity different, even if they appear identical by the means of observation at our disposal. Thus, instead of inferring function from structure, we infer structure from function and conclude that whereever we detect a difference in function the protoplasmic structure must be different also. When, therefore, we speak of the analysis of nuclear substances we do not speak from actual knowledge of the substances thus analyzed, but from purely scientific reasoning.

It is probable that during cleavage, the original nuclear substance may undergo a series of molecular changes, and split up into a number of protoplasmic substances each of a different molecular structure, and that as a final result of this chain of metamorphoses different kinds of tissue cells come into existence. In short, different morphological stages of the developing ovum may be considered as so many different molecular conditions of the protoplasm. And perhaps, the molecular constitution of a dividing ovum in its earlier stage may differ more from that of the later larval stage than two organisms belonging to different species would differ from each other in their adult condition. Professor Weismann's phrase — "ontogenetic stages of idioplasm" — aptly expresses our meaning on this subject. For the metamorphoses of structures and of embryonic tissues must of necessity correspond to the change in the constituent protoplasm. Without change in the nuclear substance, development is impossible; the egg must remain an egg forever.

If all the determining elements of future tissues are contained in the nucleus of the ovum, and if cleavage is the process by which these elements are analyzed into more tangible tissues, the question naturally arises as to the method of analysis employed in such a process.

Such a *method* we find in *Caryokinesis.*

I will, therefore, describe the process which may be termed the mechanics of nuclear division, as based on my observation on Cephalopods and Echinoderms.

It is now agreed by many foremost investigators of the subject that the essential feature of caryokinesis lies in the division of the chromatic substance of the nucleus among the daughter cells, and the complicated system of spindle-rays is the mechanism to effect such a division. The development of a spindle clearly shows this, and the following is an attempt towards a further confirmation of the current view on the subject, as held especially by E. van Beneden and T. Boveri. In one important respect my view is entirely different from that of these authors, but this difference lies more in the interpretation of phenomena than in the facts themselves.

First of all, I will endeavor to describe the anatomy of a well-developed caryokinetic figure in the Cephalopod egg, upon which my observations have been chiefly carried on. The question of nomenclature presents some difficulty. I will use here a set of terms of a simple descriptive character, descriptive of either of function, of origin, or of topographic relationship of different parts. Since scientific nomenclature embodies marks of the progress of our knowledge on the subject, I will use, wherever convenient, such terms as have been introduced quite recently, and represent, in a measure, the latest phase of our information on the subject.

The accompanying illustration (Fig. 1) shows a caryokinetic figure in the blastoderm of the squid.

Figure 2 shows the same in a more advanced condition as seen in the developing ovum of a starfish.

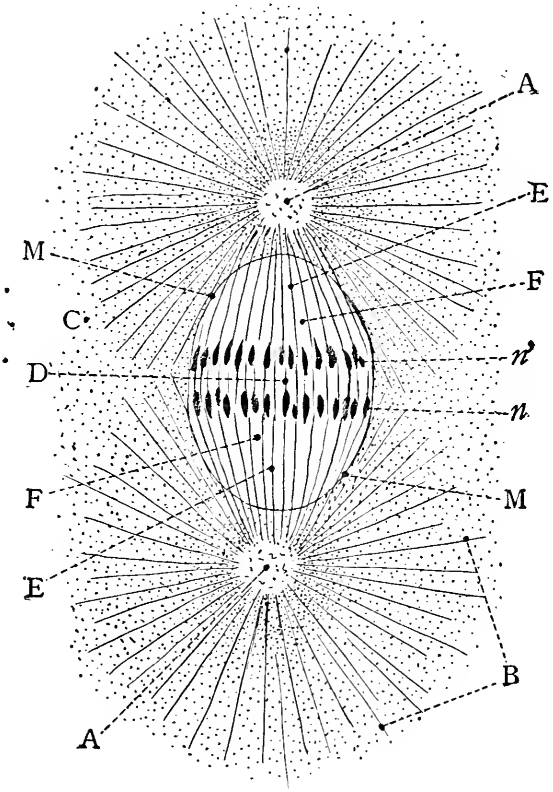

FIG. 1. — Loligo.[1]

A	Centre of Archoplasm.
B	Extra-nuclear archoplasmic filaments.
C	Cytoplasm.
D	Interzonal archoplasmic filaments.
E	Intra-nuclear archoplasmic filaments.
F	Remnant of nuclear cavity filled with nuclear fluid.
M	Limit of the original nuclear cavity, sharply separated from the surrounding cytoplasm.
n, *n'*	Two daughter chromosome bands.

The figure consists of two essential anatomical features, (1) the central, elliptical body, and (2) the two star-

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[1] Letters on other figures have the same significance.

like, radiating structures. The former corresponds to the outline of the original nucleus, as will be shown later, and the latter constitute the *asters* of Fol, *spheres attractive* of van Beneden, or, to use a more recent nomenclature, the *archoplasmic spheres* of Boveri. The central area of archoplasm (*A*), is situated in the substance of

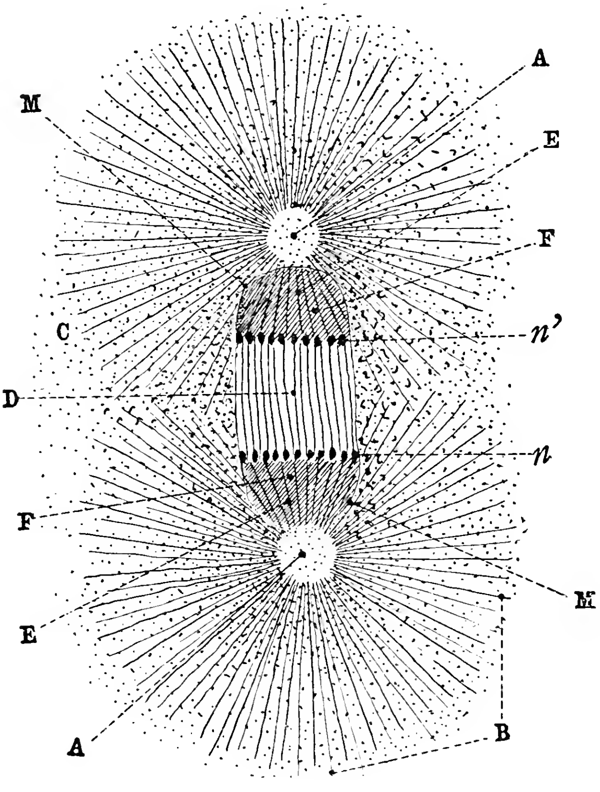

FIG. 2. — Asterias.

the *cytoplasm* (*C*). From the granular archoplasmic substance as a centre, there radiate out in all directions a large number of fibre-like rays, the *archoplasmic filaments* (*B* and *E*). A portion of these ray-fibres penetrate into the elliptical part of the figure, and constitute the *intra-nuclear archoplasmic filaments* (*E*); while those lying outside of the elliptical body are the *extra-nuclear archoplasmic filaments* (*B*).

The elliptical portion of the figure consists of three parts, two terminal and one intermediate. The terminal portion, which presents different optical properties from the intermediate part, consists of a hemispherical mass of a slightly stainable, semi-liquid substance, which I believe to be the nuclear-sap of the original nucleus. Into this part the archoplasmic rays extend, as has already been mentioned. The two terminal masses of stainable substance are separated from the intermediate non-stainable bundle of filaments by parallel chromatic "plates" (*n'*), (*n*), — the *chromosomes* (Waldeyer) of the original nucleus. The non-stainable intermediate filaments above referred to are the *interzonal archoplasmic filaments* (*D*), — "interzonal filaments" of Mark, "filaments réunissants" of van Beneden, "gubernaculum" of Maupas, "Verbindungschlauch" of Strasburger, "connective filaments," "Verbindungsfäden," etc., of authors.

One plate of chromosomes goes to one daughter nucleus, and the other to another. The cytoplasm accumulates around each, and there follows a separation into two cells, each with its distinct nucleus.

If one examine a nucleus at a tolerably early stage of caryokinesis, one will see a phenomenon such as is shown in Fig. 3. The nucleus with a network of chromosomes is intercepted between two archoplasmic spheres. More than this, however. That portion of the archoplasmic rays which falls on the surface of the nucleus presses that part inward and so flattens that side of the nucleus. This polar flattening of the nucleus goes on until the nucleus presents the appearance shown in Fig. 4.

Space only forbids the illustration of the further changes, but it may be easily imagined that when this flattening of the nucleus is continued, the whole solid contents of the nucleus are reduced to a single flat sheet as it were, as shown in Fig. 5, forming the equatorial chromatic "plate." The spindle then, as its history clearly indicates, consists of two cones with their bases turned toward each other, and with their apices in the archoplasmic centres, as was first pointed out by van Beneden.

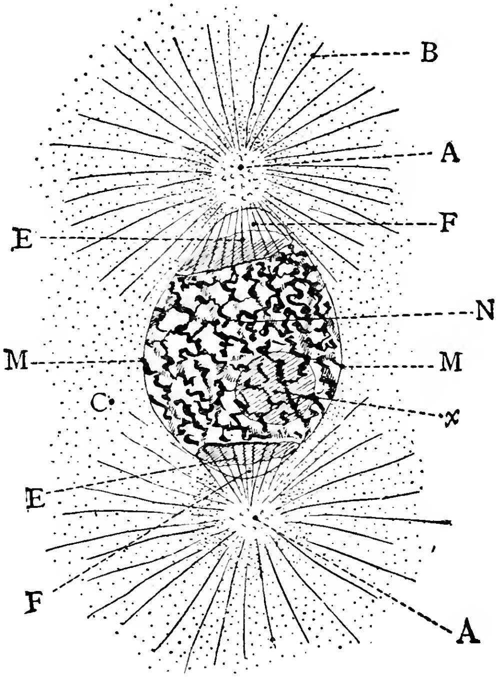

FIG. 3. — Loligo.

N Nucleus. *x* Nucleolus (?)

This stage of caryokinesis with its single chromatic "plate" leads to another with two daughter "plates,"—a phase which has been called by Flemming, metakinesis.

The question naturally arises, How is this separation of a single "plate" into two "plates" effected? With the separation of the two daughter "plates" of chromosomes, there comes into existence a series of parallel interzonal filaments which lie between the two separating "plates." The separation of the daughter "plates" of chromosomes, and the formation of the interzonal filaments, are so intimately connected with one another that we naturally look for a causal connection which underlies the parallel series of phenomena. Any theory which explains the one must also explain the other.

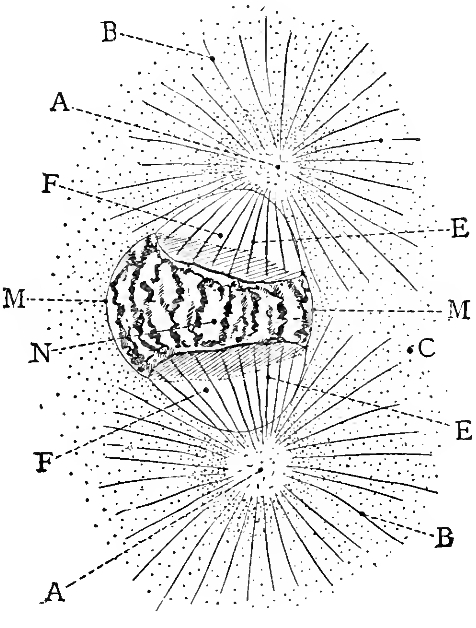

FIG. 4.—Loligo.

Boveri meets this difficulty by denying the filamentous nature of the interzonal substance, holding that what appears as filamentous is the optical expression of the longitudinal folds produced by the contraction of the two antagonistic groups of archoplasmic fibrils, whose distal extremities are fastened to the chromosomes. Strasburger ascribes to the substance the function of a wedge which grows in size by the absorption of the cytoplasmic fluid, and pushes apart the parallel "plates" of chromosomes. Platner explains the filamentous appearance of the interzonal substance as the optical expression of a protoplasmic stream. The existence of such a stream in a living dividing cell has, however, been denied by Strasburger.

As to the filamentous nature of the interzonal substance, there can be no question, as several observers have abundantly shown. My own studies on Cephalopods and Echinoderms have convinced me of the truth of this conclusion. Further, no optical difference could be observed between the archoplasmic fibrils at the poles of the spindle and the filamentous bodies in the intermediate zone, which fact has already been pointed out by several investigators.

Observing, then, that the interzonal portion of the caryokinetic figure consists of the bundle of filamentous substance, that this filamentous substance is essentially the same as the archoplasmic filaments of the spindle, that the length of these filaments is exactly the same as the space between the parallel bands of chromosomes in all stages, that the archoplasmic filaments have been growing in length from the poles toward the equator of the nucleus, and, further, that the interzonal filaments came into existence exactly at the moment when the single equatorial "plate" was dividing into two parallel daughter "plates," the following view becomes probable, viz. that after the archoplasmic filaments from the two centres have reduced the chromatic contents of the nucleus into a flat "plate" by gradual lengthening, they continue to grow in the same manner, and push through between each other, just as two brushes would do if their ends were pushed together. Their free ends will dovetail with each other. The distal extremity of each archoplasmic filament being fastened to the chromosome,

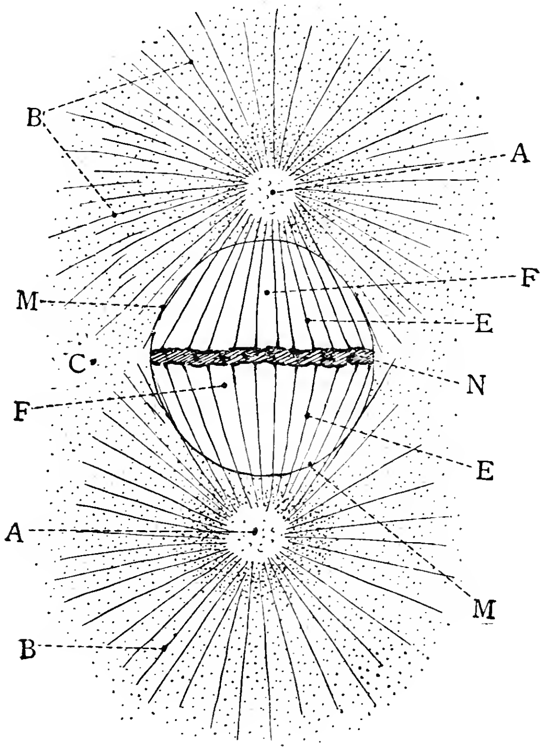

FIG. 5.

the latter will be carried by the former at its tip, and will be pushed forward as long as the filament continues to grow. Two opposing systems of the archoplasmic filaments behaving in a similar way, and lengthening in a contrary direction, would reduce the spherical nucleus first to a bi-concave disc, then to a flat "plate," and finally, into two parallel "plates," each "plate" travelling in an opposite direction. The interzonal filaments, then, according to this view, are the actual continuations of the archoplasmic filaments; but, instead of consisting of a single system, as at either end of the spindle, they are composed of two systems each dovetailing with the other, and growing in contrary directions. *Interzonal filaments* are, therefore, the prolongations of the *intranuclear filaments.* I am further inclined to believe that a certain optical peculiarity of the interzonal region, as, for instance, its aversion to take stains, is due to the existence in it of a proportionally large number of non-stainable archoplasmic filaments.

Having briefly sketched the general outline of the process by which the characteristic shape of a caryokinetic figure originates, it would be appropriate to devote a few words to the obscure point as to the origin and movement of the archoplasm itself. But as a matter of fact, we know as yet very little in regard to the origin of the archoplasm, sometimes with a definite body in its centre — the *centrosome.* A great authority like van Beneden looks upon it as a permanent organ of the cell, equal in value to the nucleus itself; but the whole question of its origin and its apparent homologues, which pass by different names in different cells, is too complicated and obscure to be discussed in this place.

The later history of the archoplasm is, however, better known. When we examine a cell at the close of caryokinetic division, we see a small nucleus with the archoplasmic sphere at one side of it, appearing somewhat like a satellite of a planet. This small nucleus is one of the daughter nuclei of the previous generation, and is destined to become the mother nucleus of the next. Just as new nuclei arise by the division of the old one, so the new archoplasmic spheres also arise by the division of the previous one. In the Cephalopod blastoderm, the division of the mother archoplasmic sphere into two daughter spheres could be observed with sufficient clearness. In *Ascaris*, its division has been

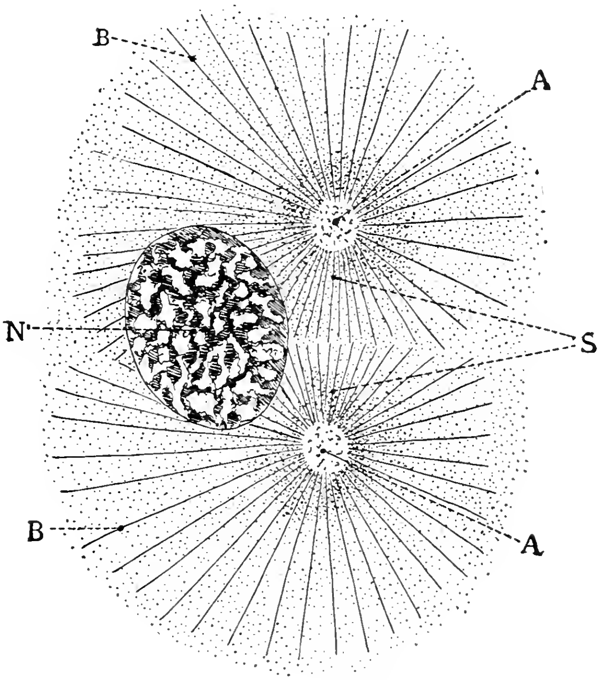

FIG. 6. — Loligo.

most carefully studied by several investigators. At first the two daughter spheres lie in close opposition, later they separate more and more widely. As each sphere has a system of radiating filaments, there is formed a little spindle (Fig. 6, *S*) where they come into contact. This spindle lies outside of the nucleus, and has nothing to do with the larger one which has been described already. The daughter archoplasmic spheres migrate further apart, and finally settle themselves on the opposite sides of the nucleus. Their effect on the latter is soon seen. That surface of the nucleus upon which the archoplasm rests soon shows signs of flattening, as was shown in Fig. 3. This polar flattening of the nucleus has been interpreted as due to the pressure exerted by the growing archoplasmic filaments. The growth of the filaments continues, and the effects it produces upon the nucleus, in the arrangement and distribution of the chromosomes have already been described. Compare in this connection the series of stages shown in Figs. 3, 4, 5, and 1.

The above is a sketch of the mechanics involved in the distribution of the nuclear substance in the dividing cell. The history of the formation of the spindle has been briefly given, and the mode of its activity has been suggested. The spindle, however, plays only a part in the production of the caryokinetic phenomena. The whole behavior of the chromosomes preparatory to division, such as the transformation from a resting condition to a coil stage, followed by the longitudinal splitting of each filament, — phenomena which take place independently of the influence of the spindle, — has received no consideration, and, so far as I can see, has no causal connection with the behavior of the archoplasm, although both tend to accomplish the same end, viz. the formation of two nuclei out of one. It is conceivable that one mother coil may sometimes split into two different kinds of substances, and the archoplasmic filaments play simply the part of a distributing agent in carrying these into opposite halves of the dividing cell. In view of the general theoretical conclusion regarding the intimate correlation between form and matter, and mechanism and function, such a view does not appear improbable; for, as has already been stated, the differences of two cells lie in their structure, and the structure being the expression of the chemical substance of the protoplasm which compose them, wherever we find the difference of structure we find difference of substance or substances, and wherever we find difference in the substance, we find difference in property or function. It is probable, as has been mentioned already, that the nuclear substance, by its constant metamorphoses, gives rise to a series of substances to isolate and distribute which is the function of the spindle, and thus give rise to a number of differently constituted cells.

In the study of caryokinesis, then, Cytology and Morphology may properly be said to meet; and the relation which it bears to the broad field of Embryology may not be unlike that which the latter bears to Anatomy.

If, in conclusion, I recapitulate what has been said in a few words, the cleavage of the ovum may be characterized as *Analysis* of tissues, caryokinesis as the *Method,* and the archoplasmic spindle as the *Instrument.*

NINTH LECTURE.[1]

THE EAR OF MAN:

ITS PAST, PRESENT AND FUTURE.

By HOWARD AYERS.

THE study of the human ear, its structure and its functions, is not alone a *modern* endeavor on the part of man to "know" himself; for history tells us, that the Greek philosophers and anatomists sought, both by dissection and physiological experimentation, to ascertain the anatomy of the organ, and how it is that we hear by the ear. The extent of their knowledge we do not know, for most of their anatomical treatises are lost to us.

Empedocles, 473 years B.C., referred the perception of sound to the cochlea; and Aristotle (384 B.C.) was acquainted not only with the internal ear of the higher vertebrates, but with that of fishes as well.

The Egyptian school of anatomists does not seem to have progressed beyond the knowledge borrowed from the Greeks.

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[1] The memoir, of which this lecture is an abstract, will be issued in the *Journal of Morphology*, Vol. IV., No. 3.

At the present day we owe our knowledge of audition and its apparatus mainly to the French, German and Swedish anatomists of the past half-century. For notwithstanding the fact that the earlier Italian school had paid much attention to the auditory organ, they did not make any noteworthy contributions to our knowledge.

With all honor to the large number of workers in this field who have added facts from this side and that, and without whose labors it would have been far more difficult for the more recent writers to have accomplished their comparative studies and to have formed their generalizations, there are a few names among them which stand out in greater prominence than the rest, and to whose investigations we owe the facts which, when properly combined, furnish us with a solution of the problems of the origin of the ear and of its existing condition. They further allow us to predict with reasonable certainty the course which it will pursue in its further development. In other words, their investigations of the ear enable us to understand its past, its present and its future.

First among these names are those of C. Hasse of Germany and Gustav Retzius of Sweden, John Beard of England and E. P. Allis of our own country.

The two first mentioned have, by extended investigations into the structure of the adult condition of the internal ear of a large number of species, representing every important group of vertebrates, built up a comparative anatomy of the internal ear upon an anatomical basis alone. They have also given accurate descriptions and figures of the forms thus studied, which render possible the comparison of the embryonic conditions with the adult, and the establishing of important phylogenetic conclusions based on these relations.

John Beard first clearly saw the relation existing between the sense-organs on the surface of the body and the organ enclosed within the head by the formation of the auditory vesicle (the auditory labyrinth of the adult), but he failed to apprehend the *nature* of the involution and the relation of the sense organ to its walls.

E. P. Allis, by giving us the first thorough investigation of the relations of the sense-organs of the lateral line system to the surface of the body, in the account of which he describes the method of their enclosure within canals, the laws of their increase, and of the fusion and division of canals, the process of their sinking below the surface of the body, and of their enclosure within the cartilage (or the bone) of the skeleton,—made known the developmental plan according to which not only the superficial canal sense-organs grow and reach their adult relations, but also, as it is now discovered, the plan according to which the *ear sense-organ* divides and forms its canals and other parts. This latter fact is demonstrated by the published results of numerous embryological investigations on animals from the several classes of vertebrates.

In order that we may fully recognize the influence these investigations have had on the solution of the problems concerning the phylogenetic history of the human internal ear, it will be necessary first of all to understand the anatomy of the ear in some type form. For this reason I ask your forbearance while I briefly describe the internal ear of one of our American Torpedoes or Electric Rays (*Torpedo occidentalis*), and bring into comparison with it, part by part, the homologous structures of the ears of *Myxine*, or the Hag-fish, and Petromyzon, or the Lamprey Eel, as two representatives of the Cyclostome type; the Alligator as a representative of the reptilian type, the Thrush (*Mimus*) to illustrate the avian condition, and the ear of Man as typical for the mammalian group.

You will find the vertebrate internal ear described, in the text-books and special memoirs dealing with this organ, as a paired sense-organ, occupying a position on either side of the head behind the eye. It resembles in the general features of its relations to the head and nervous system the other organs of special sense. One prominent feature is its constant position between the roots of the fifth and tenth cranial nerves, which in the higher vertebrates especially, may be said to be pushed cephalad and caudad respectively by the growth of the ear.

The first trace of the ear seen in the embryo is, as shown in Fig. 7, a simple saucer-shaped depression of the ectodermic epithelium on the dorso-lateral region of the head, not far removed from the gills. This thickened saucer sinks into the head, and divides into two parts, a superior and an inferior, or an utriculus and a sacculus as they are called. From the former the semicircular canals are differentiated, while the latter portion gives off the aqueductus vestibuli, or the endolymphatic duct, and the cochlear canal. These parts by further growth are converted into the *auditory labyrinth* of the adult.

Leaving out of consideration all other developmental processes connected with the completion of the auditory organ, such as its enclosure in mesodermic tissue which solidifies to form the ear-capsule (the bony labyrinth of the adult ear of higher forms), I wish to call your attention to two points of great importance for the correct understanding of the morphology of the ear.

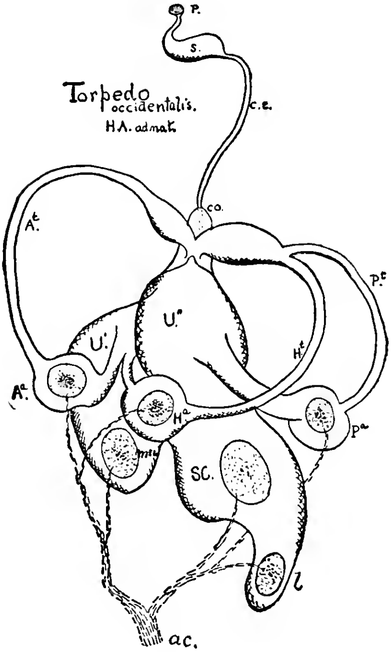

FIG. 1.—The left internal ear of *Torpedo occidentalis* dissected out of its cartilaginous capsule, and viewed from the outside. The somewhat diagrammatic figure represents the ear about twice its natural size, as found in a fish five feet in length.

A^a	Anterior ampulla.
A^t	Anterior canal.
ac	Auditory nerve.
c.e	Endolymphatic canal.
co	Utriculo-saccular cone.
H^1	External ampulla.
H^t	External canal.
mu	Macula utriculi duct.
l	Lagena and papilla lagenæ.
P	Surface pore of endolymph canal; *s* its sac.
P^a	Posterior ampulla.
P^t	Posterior canal.
SC	Sacculus and its macula sacculi.
U' and *U''*	Utriculus and utriculo-saccular chamber.

1st. The ear vesicle does not divide, as previous investigators have supposed, into superior and inferior portions, *but into an anterior and a posterior chamber.*

2d. The semicircular canals are not given off from the utriculus alone, but from the *sacculus as well.* With these two misconceptions corrected, the way is clear which leads to the really simple-as-the-truth account of the morphology of the vertebrate ear, and we shall never again encounter an *auditory labyrinth.*

An inspection of the Torpedo ear (Fig. 1) shows it to be composed of a number of more or less curved tubes, three of which approach a semicircular form, and have been on this account, since their discovery by Fallopius in 1561, called the semicircular canals. These three canals project from the central sac of the ear in three directions, and they lie approximately in the three planes of space. These planes do not coincide with the sagittal, horizontal and transverse planes of the body respectively, nor do the planes of any of the canals of the right side form continuations of the planes of the canals of the left side, or *vice versa*. The importance of these spacial relations will appear when we come to consider the physiology of the organ.

One of the canals projects forwards and outwards, and is known as the anterior vertical canal (the terms superior and sagittal canal have also been applied to it), another projects backwards and outwards, and is called the posterior vertical canal (the terms inferior and frontal have been given to it), while the third canal projects outwards and downwards nearly in the horizontal plane, and is called the external or the horizontal canal. Although it is usually stated in the text-books, that these canals occupy the three planes of space, and although, if not stated directly, it is none the less implied, that the canals also coincide with the three planes of the vertebrate body, — the sagittal, frontal, and horizontal respectively, — yet, we find that the very considerable and universal deviation from this hypothetical condition has been recognized by several investigators and the important bearing of the facts on auditory physiology at least in part recognized. I shall return to this further on.

Each of these canals opens into the main sac of the ear by its two ends, though this usual relation is not adhered to by all vertebrates, since some of the cartilaginous fishes show the posterior canal separated almost completely from the main sac, communicating with it only by a small, much reduced canal, the two ends of the semicircular canal having been brought together and its two terminal openings fused into one.

In Torpedo the proximal (superior) ends of the canals (Fig. 1, near *co*), are brought together and empty into a common but very short tube, which serves to maintain the communication with the main sac. Before uniting, however, the external and posterior canals unite by communicating with a common ama,[1] while the anterior canal swells out into an ama of its own. There is no constancy in the relation of the ends of the canals to each other or to the main sac, and, as we shall see later on, the matter has no great morphological or physiological importance. The enlargements at the proximal ends of the canals are found among most of the lower forms and occur in the *development* of the higher groups, usually disappearing before maturity is reached. The distal (inferior) ends of the canals are swollen into globular bodies, the ampullæ, which are usually flattened on one side by the entrance of the nerve branch, which breaks up into a brush of fine fibrils as it enters the ampullar wall. The nerve fibrils are distributed to the sensory cells of the crista acustica or transverse ridge, which

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[1] I shall call the superior terminal enlargements of the semicircular canals amæ, from the Greek *ama*, — a water-vessel, — since, unlike the ampullæ or the inferior terminal enlargements, they contain no nerve end organs and are mere fluid-holders. Their significance is unknown to us.

projects from the bottom of the ampulla into its cavity and bears on its free surface the hair-bearing sensory cells constituting the percipient elements of the nerve end-organs of the ear.

Each ampulla is connected with the main sac by a shorter or longer tube (Figs. 1–6), the length of the tubes varying with the canal, and in greater degree with the animal species under consideration.

In the Torpedo the ampullar tubes of the anterior and the external canals join before opening into the utriculus (Fig. 1, near *U'*), while the posterior canal has a separate and very large tube which opens into the saccular division of the main sac (Fig. 1, near *U''*).

So far as the main sac of the Torpedo ear is concerned, it appears when viewed from the side (Fig. 1) to be composed of three large communicating chambers,—*U*,' *U*,'' and *SC*. When, however, it is seen from the inside, the chamber *U''* appears as a median vesicle from which are given off cephalad the utricular recess *U*,' and caudad the saccular recess *SC*, and the lagena. This central portion, then, is the connecting chamber of the primitive ear-sac, and is composed in part of the original sacculus and in part of the original utriculus. This chamber, as you see, is produced into a conical body, *co*, which is continued outward to the surface of the body by the long and slender canal *c.e.* Shortly before the slender tube or endolymphatic duct reaches the surface it presents an enlargement in the form of a broad sac which lies just below the skin of the dorsal region of the head. The duct is continued beyond the sac where it pierces the skin, and thereby places the cavity of the ear in communication with the surrounding medium. This duct communicates with some of the sense-organ canals lying in the skin, and is innervated by one of their nerves.

The sense-organs, six in number, with perhaps a trace of a seventh, are placed, three in the ampullæ of the semicircular canals, as already described, these being designated the cristæ, while the other three are known as the maculæ and papillæ acusticæ; the one in the recessus utriculi, *U,'* being the utricular macula *mu,* while the one in the saccular recess *SC* is called the macula acustica sacculi. It has budded off the lagenar spot, or papilla acustica lagenæ, *l.*

These organs are derived from the division of a single parent organ, as we shall see later, and hence their differences of form are secondary. The trunk of the auditory nerve (Fig. 1, *ac.*) is composed of two branches, each of which gives off three branchlets to the anterior and posterior divisions of the ear respectively. We may thus speak of an utricular and a saccular branch, each supplying the structures belonging to (*i.e.* developed from) its part of the ear. In Torpedo the anterior branch or the ramus utriculi gives off one branchlet to the crista of the anterior ampulla, another branchlet to the crista of the external ampulla, and a third to the macula utriculi. This latter branchlet is in reality composed of several branchlets; for the macula utriculi is a compound sense-organ, as the sequel will show.

The posterior or saccular branch gives off one branchlet to the crista of the posterior ampulla, a second branchlet to the macula sacculi, and a third to the papilla lagenæ, while there is possibly a fourth given off from the ampullar branch to an abortive ampullar organ for which Retzius proposed the name of *macula neglecta*. In the figure of the Torpedo ear this organ would lie in the ampullar tube of the posterior canal about where the horizontal canal crosses it, and its nerve would be in the figure entirely hidden from view.

Both Hasse and Retzius, after many years spent in the comparative study of the internal ear, have decided that between the ears of the *Cyclostomata* and the vertebrates of the *gnathostome* type there was no discernible basis of homology. The gulf separating the two types prevented the recognition of such genetic relationships as might exist. Since my studies lead to a very different conclusion, a short account of the salient features of the Cyclostome ear, introduced here, may serve as a preliminary to the consideration of the morphological laws governing the development of the vertebrate ear, alike in its ontogeny and its phylogeny.

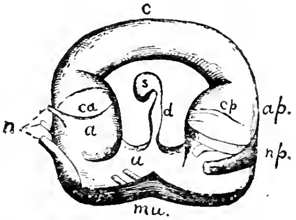

FIG. 2. — The right internal ear of the Hagfish (*Myxine glutinosa*), seen from the inside or cerebral face. Figure after G. Retzius. The figure represents the ear somewhat enlarged, and does not show the shape or exact positions of the contained sense-organs.

a	Anterior ampulla.	*d*	Ductus endolymphaticus.
ap	Posterior ampulla.	*mu*	Macula utriculi et sacculi.
c	Anterior and posterior canals.	*n*	Nerve branchlets.
ca *cp*	Ampullar ends of the same.	*u*	Utriculo-sacculus.
		s	Sacculus endolymphaticus.

The internal ear of *Myxine* (Fig. 2) is the simplest known among vertebrates. It is divided by a vertical line passing through the letter *c*, the sac of the endolymphatic duct (*s*), and the duct itself into two quite symmetrical portions. The anterior corresponds to the anterior part of the Torpedo ear, and there is a similar correspondence between the posterior halves of these two ears. The main points of difference are, 1st, The sense-organs of the Myxine ear are only three in number, or at most four. 2d, The canals, only two in number, and they do not communicate by their amal ends with the main sac of the ear, or the utriculo-sacculus, for here the chambers are not separated though distinctly marked off. 3d, The endolymphatic duct does not communicate in the adult with the surface of the body.

The auditory nerve, however, has the same number of divisions, — two, — and they supply the utriculus with its anterior ampulla, and sacculus with its posterior ampulla, respectively, the same as in the Torpedo ear.

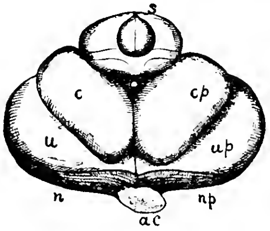

FIG. 3. — The right internal ear of a Lamper-eel (*Petromyzon fluviatilis*), viewed from its inner or cerebral face. The figure after Retzius.

ac	Auditory nerve.	*u*	Utriculus.
c	Anterior canal.	*up*	Sacculus.
cp	Posterior canal.	*s*	Ductus et sacculus endolymphaticus.
n	Ramus utricularis.		
np	Ramus saccularis.		

In *Petromyzon* the ear is much more compact than in any other known form; the canals, though two in number and well developed, do not rise above the surface of the utriculo-sacculus; and although they fuse together at their proximal ends as in *Myxine*, they also open into the main sac by a short, small tube. The whole structure is divisible by a vertical passing through the apex and the middle of its base into anterior and posterior divisions, and the parts thus separated are very much the same as in *Myxine*, showing but slight modifications of the floor of the sac in the direction of a differentiation of the sense-organs contained, and in the formation of chambers for the reception of the new organs thus budded off. Though slight, this change

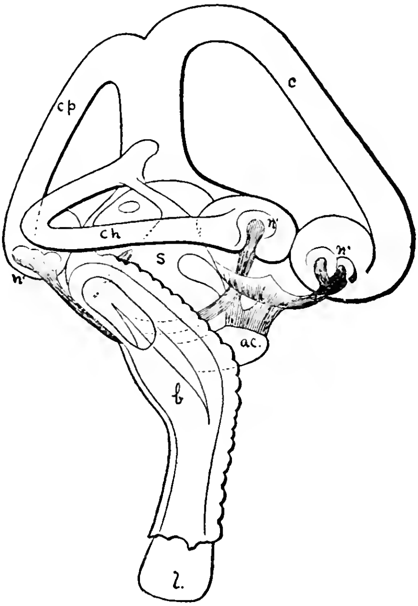

FIG. 4.—The right internal ear of *Alligator mississippiensis*, seen from the outer face. Figure after G. Retzius. The figure outlines do not bring out the relations of the parts distinctly, and only the more important parts are lettered.

ac	Auditory nerve.
b	Pars basilaris cochleæ auct.
c	Anterior canal.
ch	External canal.
cp	Posterior canal.
l	Lagena.
n'	Cristæ acusticæ of the ampullæ.
s	Sacculus.

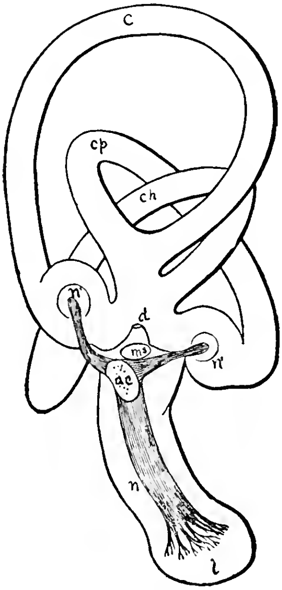

FIG. 5.—The right internal ear of *Turdus musica*, seen from the inner or neural face. Figure after G. Retzius. The letters are placed only on those parts of the organ plainly visible in the figure.

ac	Acoustic nerve.
c	Anterior canal.
ch	External canal.
cp	Posterior canal.
d	Ductus endolymphaticus.
l	Lagena.
ms	Macula sacculi.
n	Lagenar nerve.
n'	Cristæ acusticæ of the ampullæ.

is very important, for it introduces us to a series of changes which have led to the production of the gnathostome type of ear.

The reptile, bird, and mammal ears furnish us with a progressive series in which the parts already present in the Torpedo are carried to successively higher degrees of perfection. The most noticeable change from the Torpedo condition is the much elongated lagenar region, or, as it is called in the mammalia, the cochlea, which by means of the high differentiation of its contained sense-organ has risen to first rank among the auditory sense-organs.

The utricular and saccular regions are relatively much reduced. The semicircular canals have undergone a similar reduction, and among the birds and mammals appear more nearly semicircular or more evenly curved than in either the reptiles or the fishes.

All of these ears retain traces of the primitive division into anterior and posterior chambers, and the relation of the nerves described for the *Cyclostome* and the Torpedo obtains throughout the group, except, of course, where a given sense-organ has divided, when, as is frequently the case among the higher types, two or more nerve branchlets are present where only one existed in the lower type.

In Fig. 6, which is a figure of the developing human ear seen from the outside, the anterior and external ampullæ are intimately related to each other and to the utriculus *U*, while the posterior is given off from the sacculus. A line passed through the space between *U* and *S* of the figure, and continued so as to pass out just above the ampulla of the posterior canal, divides the ear into its anterior and posterior halves, which, owing to the distortion produced by the enormous growth of the cochlea, now appear as superior and inferior portions of the canal system of the ear.

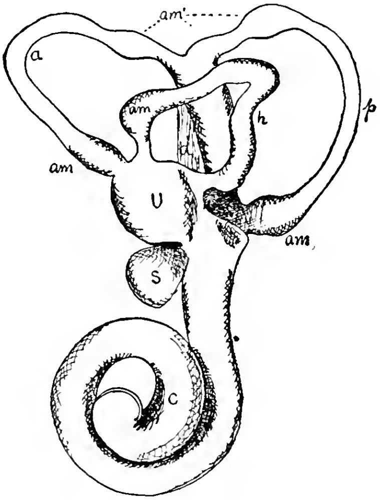

FIG. 6.—The left internal ear of a human embryo, 22 mm. in length, seen from without and below. Figure after W. His., Jr. The figure is from a model constructed from serial sections, and represents the ear much magnified.

a	Anterior canal.
am	Ampulla.
am'	Amæ. The middle reference line is superfluous.
c	Cochlea.
d	Ductus endolymphaticus.
h	External canal.
s	Sacculus in the restricted sense; really only the recessus sacculi.
u	Utriculus.

The development of the special sense-organs of the lateral line in *Amia* or the ganoid Dog-fish, as made known by Allis, gives us the key to the solution of the problem of the homologies of the parts of the internal ear. In this fish the inclosure of the canals and the formation of the pores and tubes, while it is undoubtedly the primitive process, is essentially a simple and regular process, and when it is fully carried out *the canals arise in separate sections, each of which contains a single sense-organ.*

In the young Dog-fish, in which the canals have not begun their development, the sense-organs lie below the surface and may be traced as more or less continuous whitish lines. "These lines mark general and extensive surface depressions." From the bottom of these general surface depressions the sense-organs sink down forming, as they do so, small pits, at the bottom of which the organ lies. The lips of the pit grow upward and inward, and meeting above arch over the pit forming the beginning of a canal. This arch grows away from the pit in two directions until it meets another canal, with which it fuses, or until its energy is spent, when it comes to a standstill and remains a longer or shorter canal open at both ends, possessing somewhere near the middle of its course the canal sense-organ which gave the first impulse to the development of the canal. The sense-organ lies in a pit which represents what we know in the ear canals as the ampulla. The lateral line sense-organs are then supplied with, or lie in, ampullæ.

The canals being formed in short sections, one to each sense-organ, and fusing as they do to make longer canals, we should expect the compound canal at the point of fusion of its two components would retain a pore connection with the surface from which the canals were formed. Such is the case.

Again, in the division of a canal organ and its canal, we should expect to find the canal retaining its surface communication by means of a single pore, if the division did not progress to completion, and we find this occurs regularly in the development of canals. The reverse of this process also occurs, in which the pore divides first, while the parent canal may remain undivided.

We shall see later on that the ear canals fuse and retain their communication with the surface by means of a single pore, and that in one instance a canal organ divides, bringing about an incomplete division of the original canal, so that both canal organs communicate with the mother surface by means of a single pore. This is true in the case of the anterior and external ear canals of Torpedo (Fig. 1, *U'*). We shall also find that the division of a canal organ may be barren of result so far as the production of a separate canal is concerned, and that in this case the offspring may retain its position in the parent canal. As an instance of this condition in the ear we have the macula neglecta (Fig. 7, *ma*), which has arisen by the division of the parent organ, the primitive sense-organ of the posterior ampulla.

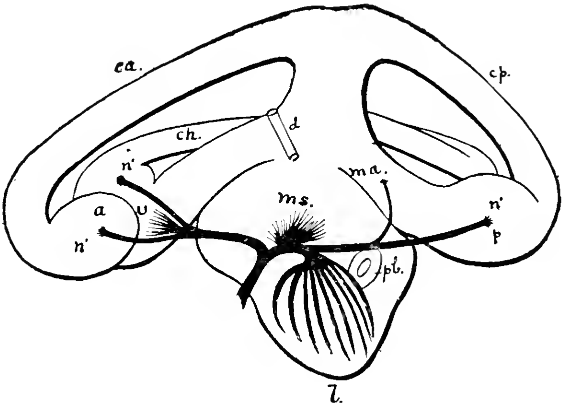

FIG. 7.—The right internal ear of the European Adder (*Tropidonotus natrix*), seen from the inside. Figure after Dr. Kuhn. This ear shows very distinctly the division into anterior and posterior chambers, especially in the arrangement of its sense-organs.

a	Anterior ampulla.	*ma*	Macula acustica neglecta of Retzius.
ca	Anterior canal.	*ms*	Macula acustica sacculi.
ch	External canal.	*n'*	Crista acustica ampullarum.
cp	Posterior canal.	*p*	Ampulla posterior.
d	Ductus endolymphaticus.	*pb*	Pars basilaris cochlear auct.
l	Lagena.	*u*	Utriculus.

The early history of the Elasmobranch auditory capsule does not differ materially from that of other forms except in the rate of growth.

In this respect it is a much more favorable object for the study of the development of the internal ear than any vertebrate with which I am acquainted. Fig. 8 shows the auditory involution after it has assumed the saucer-shape already alluded to. This condition is the result of a concomitant thickening and sinking of the ectoderm, which over the area of the saucer represents one of the canal sense-organs of the lateral line system, and the whole process from the beginning on is but a repetition of the formation of the canal organ and its canal, as seen in *Amia*. As the saucer-shaped thickening sinks below the surface, the opening on the surface grows smaller, the bottom of the saucer increases in size, and the resulting structure is an auditory vesicle distinctly flask-shaped (Fig. 9, *a. v*). The neck of the flask grows longer, and finally appears bent backwards and inwards, owing to the increase in size of the head in this region, which causes a transla-

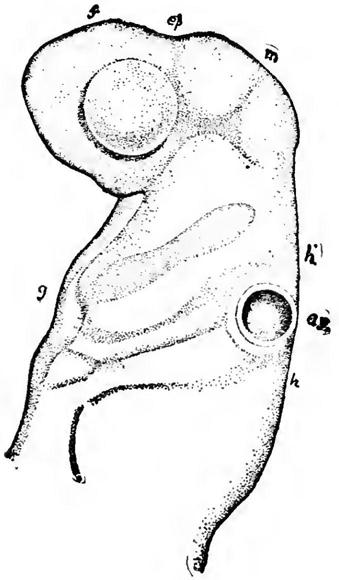

FIG. 8.—The head of an embryo Shark (*Acanthias vulgaris*), from nature, magnified 20 times. The figure shows the saucer-shaped depression containing the insinking sense-organ which is to be converted into the auditory sense-organs of the Shark.

a.v	Auditory saucer (vesicle).
ep	Epiphysis.
f	Fore-brain.
g	Gill region.
h *h'*	Upper and lower hind-brain region.
m	Mid-brain.

tion of the auditory capsule forwards and outwards (Fig. 10, *d*).

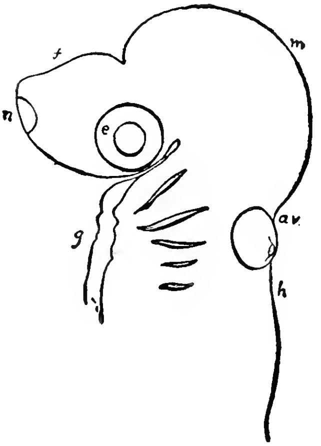

FIG. 9.—The head of the embryo smooth Dog-fish (*Galeus canis*), seen from the left side. Figure drawn from nature, magnified about 20 times. The flask-shaped auditory vesicle is shown prominently placed above the gill region. Letters as in the preceding figure.

a.v	Auditory flask.
e	Eye.
f	Fore-brain.
g	Gill region.
h	Hind-brain.
m	Mid-brain.
n	Nose.

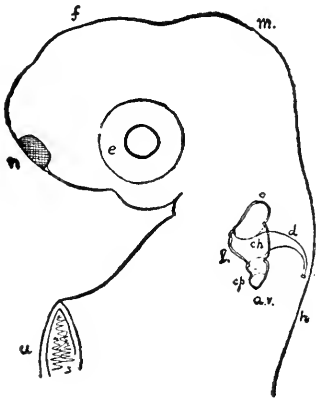

FIG. 10.—The head of an older Shark of the same species, viewed from the left side. The figure, which was drawn from the living fish, shows the internal ear well advanced in its development. The rudiments of the semicircular canals and lagena are seen pushing out from the auditory sack (respectively the utriculo-sacculus, which has sunk far below the surface, with which it is, however, still connected by its sickle-shaped ductus endolymphaticus).

a.v	Auditory vesicle.	*cp*	Posterior canal.
c	Anterior canal.	*l*	Lagena.
d	Ductus endolymphaticus.	*m*	Mid-brain.
		h	Hind-brain.
e	Eye.	*n*	Nose.
f	Fore-brain.	*u*	Umbilical cord.
ch	External canal.		

During this lengthening of the neck of the flask, which becomes the surface canal of the adult ear, the body of the flask is much changed in shape.

First of all, it becomes compressed laterally, and is then drawn out in an antero-posterior direction. During this process the anterior end comes to point outward, while the posterior end is directed inwards toward the median line. There may now be seen several changes in the shape of the vesicle which, while not conspicuous, are very important, since they usher in a succession of transformations which ultimately produce the three semicircular canals and the rudiment of the cochlea. These changes are visible on the outer and upper faces of the vesicle as slight ridge-like elevations of the surface, and on the posterior ventral end of the vesicle as a knob-like prominence (Fig. 10, *c*, *ch*, and *a.v*). Of the former there are two, of the latter a single one. The

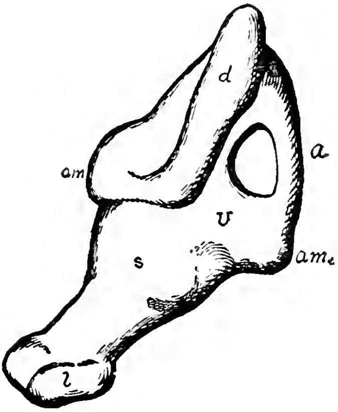

FIG. 11.—The ear of a very young Rabbit embryo, 11 mm. long. Figure after Krause.

a	Anterior canal.
am	Ampulla.
d	Ductus endolymphaticus.
l	Lagena.
s	Sacculus.
u	Utriculus.

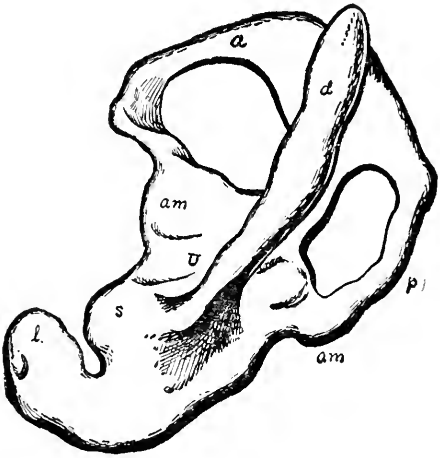

FIG. 12.—The internal ear of a somewhat older Pig embryo, 33 mm. long. Figure after Krause.

a	Anterior canal.
am	Ampulla.
d	Ductus endolymphaticus.
l	Lagena.
p	Posterior canal.
s	Sacculus.
u	Utriculus.

former structures seen from inside the vesicle are merely depressed grooves in the wall of the vesicle, and the latter a sunken but broadly open pit. These grooves grow deeper, their edges grow together, first, along the middle part of their course, thereby producing canals.

The lips of the pit fuse by reaching across the middle of the opening, and thus produce the beginning of the posterior canal, which, by its continued growth upward, soon reaches and fuses with the anterior canal. The terminal pores of these two canals, at what proves from later events to be their amal ends, fuse and open into the vesicle by a single pore.

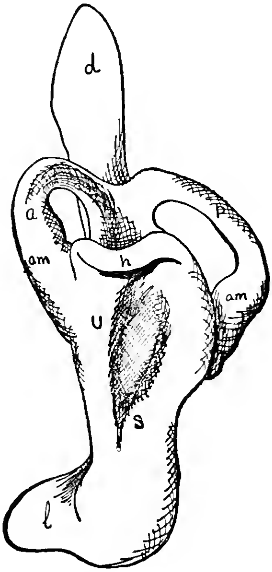

FIG. 13.—The left internal ear from a human embryo, 13 mm. long, about the fifth week of development.

a	Anterior canal.
am	Ampulla.
d	Ductus endolymphaticus.
h	External canal.
l	Lagena.
p	Posterior canal.
s	Sacculus.
u	Utriculus.

The introductory stages in the development of the human ear are but a repetition, as regards essentials, of the process as I have described it in the shark.

When fully cut off from the exterior, the auditory vesicle forms a compressed sac having an irregular quadrangular shape. This condition is found in embryos of three and a half to four weeks. The utricular and saccular divisions are readily distinguished, and even now the semicircular canals have begun to differentiate by the formation of two shallow depressions in the walls of the utriculus. Both the pocket common to the vertical canals and the pocket for the external canal are present. Below the latter is seen the larger and deeper evagination for the cochlea. When the embryo has reached the length of 8 mm., the cochlea has so far developed as to stand out distinctly from the sacculus, and is at the same time bent (Fig. 11, *l*). At both ends of the common pocket of the verticals, and at one end (anterior) of the external depressions, are slight enlargements — the future ampullæ. From now on, the parts rapidly acquire individuality. The anterior canal is completed first. Then the posterior becomes cut off, and soon after the external is perfected.

The whole vesicle undergoes a marked change in form during this period, for, owing to the growth of the ductus endolymphaticus from the apex of the primitive vesicle, and the great elongation of the cochlear tube from the bottom of the saccular region, the canal complex now appears drawn out in a dorso-ventral direction. The cochlear canal has now, about the fifth week, one half a spiral turn, and a long groove has appeared on the inside of its wall (fold on the outside), from which the nerve end-organ — Corti's organ — arises. In the embryo of 30 mm. (Fig. 6) length the canals are well formed, and the ampullæ are quite prominent. The two verticals which from *their mode of development have up to this time occupied the same plane*, now begin to diverge, and the planes of the canals now meet in the middle of the common tube which unites them. Their angle at this time is 150°.

This method of origin is most interesting and important in its bearings on the spacial relations of the adult ear canals. The cochlea has now made nearly a whole spiral turn. About the second month the internal ear has assumed the fœtal conditions, and its development from this point on consists in the perfection of the parts already marked out. The canals and ampullæ have acquired their adult characters, and the cristæ are distinctly formed, although the sensory cells have not acquired their mature structure. Each canal has at this stage a noticeable swelling at the opposite end from the ampullæ. In these you will recognize the amæ which I described in the fish ear as an adult characteristic. In the human ear the ama of the external canal is the only one usually persisting beyond the fœtal condition.

The cochlea has continued its development, and is readily seen in the greater number of spiral turns it has acquired, and the row of sense-organs, formed by the budding of the original cochlear sense-organ or papilla lagenæ, has now several hundred discreet sense-organs which are so closely related in structure and function as to pass as one organ, the organ of Corti.

One very important matter belonging with the anatomical facts I intentionally neglected, for, until we had gained a knowledge of the course of development of the ear as a whole, and of the details of canal formation in particular, we were not likely to fully appreciate its bearings on the problem of the inter-relation of the sense-organs of the auditory complex and of their canals. It is the morphological value of that sense-organ which, ever since its discovery by Retzius, has been such a source of discussion and investigation; viz. the macula acustica neglecta, supposed by some to belong to the utriculus; by others, to the sacculus in the older sense.

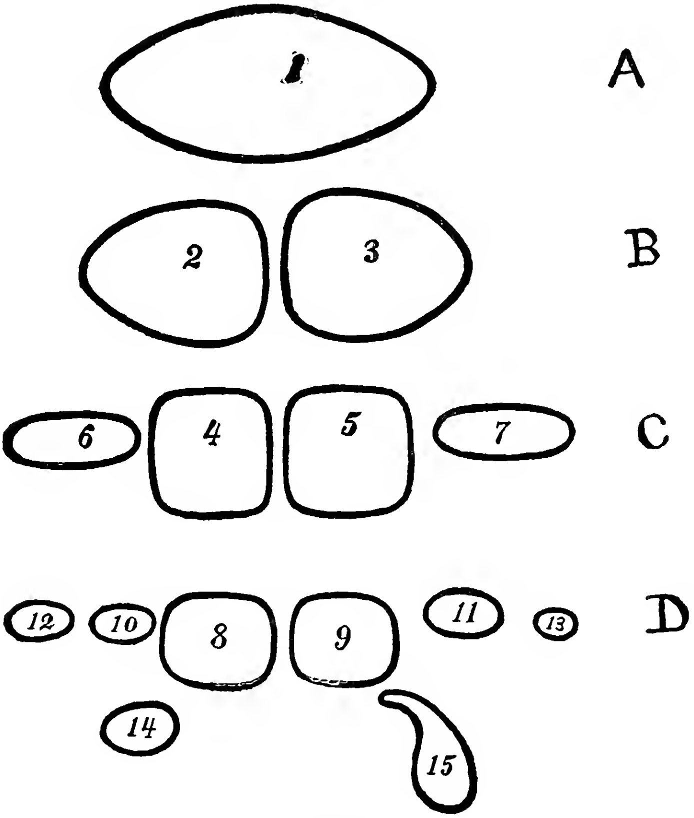

FIG. 14.

A Auditory vesicle.
B Utriculo-sacculus.
C Utriculo-sacculus + two ampullary canals.
D Utriculo-sacculus + two ampullary canals and lagenar canal.

Stage A represents the undivided superficial sense-organ of the vertebrate ancestor, as it is invaginated from the surface and enclosed within the auditory vesicle to function as the macula acustica vesiculi; the only auditory sense-organ of this stage. It is but little removed from the canal organs as they exist in, *e.g.*, *Amia*, and differs from it mainly in size. This condition is not represented in the adult of living vertebrates.

Stage B represents the first division of the macula vesiculi, into its two offspring the maculæ acusticæ utriculi et sacculi. This stage is likewise not represented among living forms.

Stage C is so characteristic of the *Cyclostomata*, so far as we know them, that we will call it the Cyclostome stage. Here the cristæ acusticæ anterior et posterior have made their appearance.

Stage D shows the condition of the organs in the *Gnathostomata*, hence its name the Gnathostome stage. The cristæ acusticæ anteriores, horizontales, posteriores and abortivæ are all developed by the division of the two parent ampullary organs of the Cyclostome ancestral stage, while the maculæ utriculi et sacculi undergo division, giving rise to the parents of the utricular and saccular complexes of sense-organs. These latter reach their highest differentiation in some rodentia and porcine species.

Retzius finally came to the conclusion that this nerve-end organ had arisen from the posterior, ampullar sense-organ, and that among the higher forms, especially the mammalia, it was no longer produced, or, as he expressed it, the macula neglecta in these forms had disappeared in the crista acustica posterior.

After an examination of all the evidence bearing on this question, both from the embryological and the anatomical sides, I have solved the problem of the morphological value of the parts of the internal ear and their inter-relationships, by the discovery of the very simple law which governs their origin and succession. Let me give you the whole problem in a nutshell, even at the risk of some slight repetition.

The primitive auditory sense-organ is invaginated from the surface of the body, and may be said at this time to be in the vesicular stage (Fig. 14, *A*). So far as we know, this condition is not retained by any adult living vertebrate. And it is quite possible that the auditory saucer may contain the rudiments of the two primary sense-organs of the Cyclostome ear. The parent sense-organ soon divides transversely into two nearly equal parts, which are the anterior and posterior sense-organs respectively. The auditory vesicle is at the same time partly separated into two chambers (incomplete canals) to accommodate them. These chambers are the utriculus and sacculus.

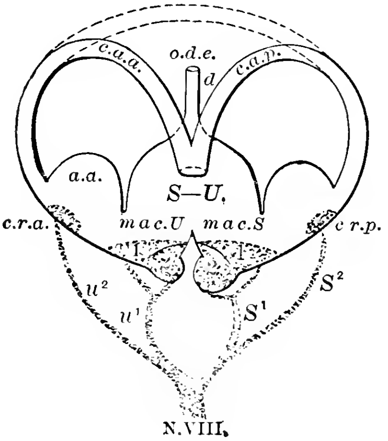

Fig. 15.— The Cyclostome type ear shown here is a very simple structure as compared with the complicated organ found among the *Gnathostomata*, but compared with its ancestral condition, *i.e.* the auditory vesicle, it is seen to have gone through many changes, and stands to-day midway between its earliest condition and the highest differentiation known. This diagram is constructed on the basis of the anatomy of the only two known forms of this group, *Myxine* and *Petromyzon*. The canals and their organs retain a very primitive condition of structure.

caa	Anterior canal.
cap	Posterior canal.
cr. a	Crista acustica anterior.
cr. p	Crista acustica posterior.
d	Endolymphatic duct.
u.s	The utriculo-sacculus.
u 1 and 2	Branchlets of the utricular branch of the auditory nerve.
s 1 and 2	The saccular branches of the same.
ode	Terminal portion of the endolymphatic duct, which in neither of these Cyclostomes opens on the surface of the body in adult life.
mac. u	Macula acustica utriculi.
mac. s	Macula acustica sacculi.
1 and 2	The portions (1) of the sense-organs that remain in the parent cavity and the portion (2) which migrate into the recessus utriculi and lagena respectively.

Each of the two sense-organs of the second generation after a while divides into two unequal parts in such a manner that the smaller sense-organ appears as a bud from the parent. There are thus formed within the two chambers of the ear four canal sense-organs belonging to the third generation. The two external organs are soon enclosed within the ampulla of two complete and relatively large canals, which are now formed about them. An anterior vertical and a posterior vertical formed in the manner already fully described. Up to this time the organs have retained the primitive relations to each other — a serial arrangement along a line running in an antero-posterior direction. Now, there begins a distortion of the structure as a whole, which continues ever after, and reaches its greatest development in the mammals — viz. a process of sinking and drawing out ventrally of the posterior chamber of the ear, so that hereafter we might speak of a superior and an inferior portions or chambers. The sense-organs of the third generation play the leading *role* in these changes, and by means of four sets of divisions, viz. by the bipartition of each sense-organ present in the Cyclostome stage nearly simultaneously there is produced a fourth generation of canal sense-organs.

To this fourth generation belong all the sense-organs of the internal ear of the higher vertebrates which in the diagram are numbered eight to fifteen consecutively.

During this process of sense-organ differentiation, the canals have been variously modified, and to show the relationship of the third generation to the fourth let us examine the diagram shown in Fig. 15, in the construction of which I have ignored the ventral distortion spoken of.

The sense-organ numbered six in the Cyclostome stage (the crista acustica anterior, or anterior canal organ, of *Myxine* and *Petromyzon*) has divided to produce sense-organs ten and twelve of the Gnathostome stage, *i.e.* the cristæ acusticæ anterior et horizontalis, of the human ear.

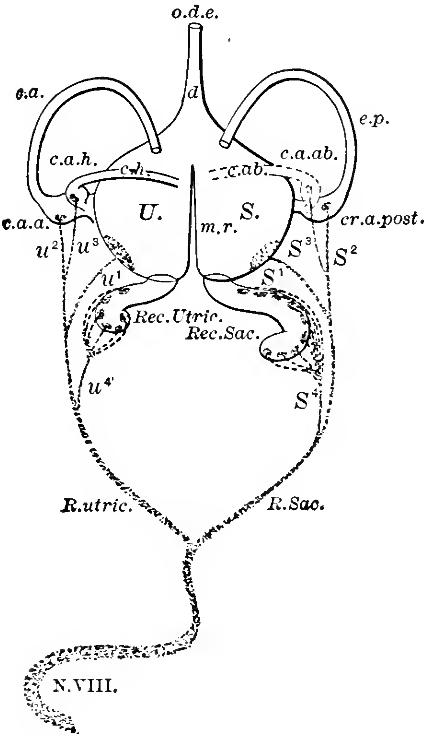

FIG. 16. — The Gnathostome type ear shown here illustrates the method and the extent of the modifications which the Cyclostome ear has suffered in its descent to this group. The anterior and posterior canal organs have each budded off an organ which, in the case of the anterior canal, produces a well-formed canal, the external, present in all the members of this group, while the posterior bud never produces a well-formed canal. The utricular recess, which contains a number of sense-organs derived from the division of the macula utriculi, is represented as forming a tubular prolongation of the utricular cavity, in order to more clearly show the parallelism of this group of organs with the lagenar group. In no known form does the production of the canal proceed to the extent shown in the diagram. The sense-organs of the lagenar group are represented as separated from each other by an interval, whereas the actual relation in nature is much more intimate.

ca	Anterior canal.	*rec. utric*	Recessus utriculi.
cp	Posterior canal.	*rec. sac*	Recessus sacculi.
ch	External canal.	*d*	Ductus endolymphaticus.
c. ab	Abortive canal.	*s*	Sacculus.
u	Utriculus.	*o. de*	Orifice of the same.

The sense-organ numbered four of the Cyclostome stage (the macula utriculi of *Myxine* and *Petromyzon*) divides into the sense-organ eight and sense-organ complex fourteen of the Gnathostome stage, the macula utriculi of the human ear, which is, as I stated when describing the Torpedo ear, a compound organ composed of the parent organ and its numerous progeny, all of which remain close together.

The sense-organ numbered seven of the Cyclostome stage is the sense-organ of the posterior canal of *Myxine* and *Petromyzon*, and has divided to produce sense-organs, eleven and thirteen, of the Gnathostome stage, or the crista acustica posterior, or the canal sense-organ of the posterior canal of the human ear, and the so-called *macula acustica neglecta* of Retzius, which is the abortive second horizontal canal organ of the internal ear of man.

Sense-organ five of the Cyclostome stage has divided to produce the sense-organ nine, and the sense-organ complex fifteen of the Gnathostome stage, or the macula sacculi and the lagenar organ respectively, the organ of Corti of the human ear.

With the exception of the generalization that the vertebrate internal ear is derived from branchial sense-organs — *i.e.* organs of the lateral line system — a generalization which we owe to Beard, but which he did not attempt to establish by any detailed anatomical or embryological investigations, the phylogenesis of the vertebrate ear has been studied only on the basis of the adult structure. Such structures as the semicircular canals and the divisions of the body of the auditory vesicle have been used alone as the basis for proofs of the genetic connection of the types of internal ear — even the nerve supply has been excluded from its just share in forming the conclusions.

These canal structures had no special phylogenetic significance for investigators in this field; for although it was known that the auditory vesicle was invaginated from the surface of the body, the connection of the sensory part of the invagination with the superficial canal organs was not understood. Now that we know that there is a genetic connection, many of the intricate problems receive their solutions, and the genetic relationships appear clear and certain for all the types. The demonstration of these facts deals another blow, and a fatal one, at the degeneration hypothesis which has been so persistently applied to the elucidation of Cyclostome anatomy and development, with such pernicious morphological results. (This will apply equally to Amphioxus, though only indirectly in this particular instance.) This solution relieves us from the necessity of explaining away the vertebrate ear on every occasion, when we seek to establish a relationship between the vertebrate and the invertebrate types; for we are led to see the value of very simple, superficial, sense-organs in an undifferentiated group of animals, for the building up of structures of great complexity, and of intricate relations to other parts of the animal body in the members of higher forms, and also to recognize the manner in which the structure and functions of organs may be profoundly changed in the course of time.

Now, while it is not known that Amphioxus is provided with an organ of hearing, the next higher forms do possess an internal ear of such structure that not only does it help us to understand the more complex

Gnathostome type, but proves conclusively that, so far as the ear is concerned, the Cyclostomes have not suffered degradation of structure.

Against the view that the completely closed or perfect canal is the primitive condition of this system, *so far as existing vertebrates are concerned,* one may raise the very plausible objection that since all the Holocephala and some Teleosts have the canal incompletely developed, as a more or less open groove on the surface of the body, and since the Cyclostomes do not retain the superficial canals except in very imperfect form during adult life, and further, since the closed canal is produced in ontogeny, and may have appeared in phylogenetic history by the action of the same process,[1] it is only reasonable to suppose that the open groove is the primitive condition, and constitutes a phylogenetic stage passed through in the development of the *higher* (?) types of closed canal.

When, however, we consider that the internal ear is a very ancient structure, and that in all known cases the sense-organs developed in it become enclosed in *complete* canals, by a process exactly similar to that known for the formation of the superficial canal organs and their canals in the admittedly primitive ganoid type, we are compelled to admit that such a process could hardly have arisen independently within the closed capsule after its separation from the surface and its removal away from the external influences which originally caused their development, and that consequently *there*

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[1] *e.g.* the grooves present on the surface of the head and body of *Chimæra* and *Tetrodons,* could readily be converted into tubes by the fusion of their edges.

must be a genetic relationship between the canal organs of the internal ear and the superficial canal organs; and since there is not the slightest doubt that the superficial canal organs are the original or parent organs, we are brought to the unavoidable conclusion that *the vertebrate internal ear is a transformed canal organ.*

It follows from what I have said that the system of canal sense-organs must be a *very* ancient one, since it must have antedated the origin of the internal ear of the Cyclostomes.

Although *ontogenetic* evidence seems to lead to the conclusion that the auditory organ arose by the invagination of *a single superficial sense-organ,* it is by no means certain that this is true; for there are certain facts of comparative anatomy and certain phylogenetic considerations which point to the conclusion that the auditory organ has arisen by the bringing together of two originally distinct sense-organs which were together sunk below the surface. The main facts at present in favor of this view are these:—

1. In all eared vertebrates the auditory organ is supplied from two distinct brain centres, one lying in close connection with the facial nuclei, the other intimately related with the glossopharyngeal nucleus.

2. In all eared vertebrates the so-called auditory nerve is composed of two distinct roots—an anterior and a posterior—which supply the anterior and posterior chambers respectively.

3. In all these forms the anterior root is external to the brain, united with the facial nerve.

4. In some fishes the nerve to the posterior ampulla is derived from the glossopharyngeal nerve, between

which nerve and the posterior root of the auditory there exists, however, a more proximal connection.

5. The auditory vesicle is always developed between the facial and glossopharyngeal nerve roots.

6. The ductus endolymphaticus is supplied on its anterior face by a branch of the utricular nerve, while its distal end, in some fishes, opens into a canal containing sense-organs innervated by the glossopharyngeal nerve.

7. The so-called eighth cranial or the auditory nerve must have arisen from branches of two distinct cranial nerves, and is not homodynamous with such cranial nerves as the fifth or tenth, as we now understand them. This is true (*a*) because the auditory sense-organs thus supplied were primarily only a portion of the canal sense-organs innervated by the original nerves of the preauditory condition of these sense-organs; (*b*) because the auditory nerve is clearly not a complete nerve, and is not even equivalent to a dorsal root of a cranial nerve, for its two divisions are probably merely branches of the dorsal roots of the seventh and ninth nerves, since they draw off only a portion of the sensory fibres from these two nerves.

The primitive division of the auditory chamber and its nerve supply into two so sharply marked portions is thus phylogenetically accounted for, and at the same time the early ontogenetic changes in the auditory vesicle receive their explanation.

The two sense-organs, the maculæ acusticæ of the utriculus and sacculus, are thus derived from two organs terminating two separate canal systems which had, as they may still be seen in *Amia*, become confluent on the surface of the body midway between the roots of the facial and glossopharyngeal nerves as they issue from the brain. At the point of junction the two half-pores united into a single pore, which in some fish forms (*e.g.* Torpedo) persists as the outer opening of the endolymphatic duct, and the only persisting indication of the separate origin of these organs and their canals is their nerve supply. It is a necessary consequence of the great functional differentiation which the ear organs have suffered that their nerves should also become much increased in size, and instead of appearing now as *nerve branches* they have become really larger than the parent nerves from which they arose.

As a prelude to the little I have to say on the physiology of the internal ear, I wish to emphasize the following considerations: We have very slender foundation indeed for correctly judging of the functional relations of the integral parts of the internal ear, and what we have is largely speculative, based on our knowledge of the structure of the parts.

What we need at the present time is physiological experimentation. First of all, an extended series of varied, careful, and unbiassed experiments on the sense-organs of the lateral line system of the lower vertebrates, to determine their functions, and then more experiments on the internal ear of the least differentiated representatives of our type, to determine what functional modifications have arisen during the transformation processes. Finally, the combination of the knowledge thus gained, with the results of experiments upon the human subject.

If proof were needed for the statement that most of the speculation and experimentation on the auditory function, especially as regards its different phases, has led mostly to negative results, it is easily forthcoming; for there is not a single investigator who, during the last half-century has written on this subject, but regrets the paucity of facts and the depressing insufficiency of the prevailing theories.

The amount of experimental knowledge of the functions of the lateral line organs is very limited indeed. Of the many theories which have been proposed Merkel's is by far the most satisfactory. According to this investigator, the function of these organs is in all probability that of receiving and transforming the *mechanical* stimuli occurring in the surrounding medium, and it cannot be in any way connected with the perception of *chemical* changes in the water.

Mayser and Emery consider the organs of the lateral line system as forming an accessory auditory organ, and Mayser has proved that these organs find their central brain connections in the immediate neighborhood of the auditory nuclei.

The functions of the ear are usually separated into two classes by physiologists. The first and most prominent of which is AUDITION, with its several subdivisions; the second, though less prominent, not for that reason, however, less important, viz. equilibration. The function of audition certainly belongs to the ear; not so, however the equilibrious function; for it can be conclusively shown that equilibration is not necessarily affected by the removal of the ear, and that injury to other organs is not unfrequently followed by loss of the ability to equilibrate the body.

An extended presentation of the arguments for and against the equilibration theory of the semicircular canals would be too long and unprofitable to justify introducing it here, especially so now that there is no longer the slightest evidence in favor of the theory, since the results of experiments by the physiologist Steiner have been published. It is commonly stated that the auditory nerve, besides possessing the function of transmitting auditory impressions, also transmits stimuli to the equilibrious centre, and that the ampullæ of the semicircular canals contain the sense-organs which subserve this function.

The ampullar sense-organs may, however, be completely severed from their respective nerves without producing any disturbance in the equipoise of the body. The section of the ampullar nerves, even though the greatest care be taken to prevent damage to the connecting nerves, must produce an intense stimulation of the central end cells, and it is wholly unexplained why the ampullar nerves may be thus cut without producing any visible effect if the equilibration theory were true.

Experiments carried out in Hermann's laboratory in 1877, by Fraulein Tomaszewicz, showed that in bony fishes the semicircular canals and their ampullary sense-organs could be entirely removed without in the least influencing the equilibration of the body. Another set of experiments, even more decisive, were performed by Professor Steiner in 1888, in the physiological department of the Naples zoological station, on the common Dog-fish of the Bay of Naples. Steiner's experiments proved that so long as the fibres of the acoustic nerve were neither pulled so as to disturb their central relations, nor displaced in a manner injurious to their peripheral terminations, disturbances in the equilibrium of the body did not make their appearance. While observing these conditions it was possible for him to cut out one, several, or *all six of the semicircular canals without destroying or in the least disturbing the fish's power to equilibrate its body*, though the operation evidently caused the fish very painful sensations, *i.e.* very intense irritation of central end cells.

Now under the old hypothesis of the equilibration functions of the semicircular canals, these removals without equilibrative disturbances would be impossible. Experiments of a similar nature performed on warm-blooded animals were formerly used as evidence in proof of the theory. In all of these experiments disturbances of the power of equilibration never failed to make their appearance. These disturbances, however, were due to the conditions under which the experiments on warm-blooded animals are necessarily performed, and are not directly related to the injury to the nerve from simple cutting. In Pigeons whose semicircular canals have been more or less injured[1] or destroyed, the loss of coördinating power is certainly to be connected with the injury done to the richly nervous structures; but it does not follow that this loss of coördination is due solely to the disturbance of the function of the canals,

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[1] As in the experiments by Elourens, Cyon, and others.

for it can be clearly shown that during the wounded state the bird is still able to equilibrate itself under certain conditions, and those conditions involve calling into use the tactile sense. The sensation of giddiness produced by injury to or destruction of the canals is due not to the injury of the ampullar sense-organs, but either to a disturbance of the centre of equilibration in the brain by mechanical injury to the cells of this centre, or to the cessation of the perceptions arising in part from the functional activity of the auditory mechanism. It has been observed that a pigeon operated on by canal section or destruction can, and usually does, steady itself and properly direct and execute coördinated movements, the moment its sense of sight is aided by the tactile sense sufficiently to enable it to form a correct judgment of its position in space and its relation to surrounding objects.

Now, barring nausea or other nervous disturbance accompanying section among the warm-blooded animals, it is plainly true that the animal's failure to coördinate its movements lies in the fact that it forms false judgments of its spacial relations on an insufficient basis sense-perception, the constant stream of auditory impressions having been cut off, even in the milder experiments, by the disturbance of the pressure equilibrium of the endolymphatic fluid.

On the basis of the evidence which had been produced by the advocates of this doctrine, Milne-Edwards disposed of the kinetic and statical theories of the equilibration functions of the semicircular canals in the following words: "Mais les hypotheses proposées à ce sujet ne reposent pas sur des bases suffisantes pour que nous y arrêtions ici."

Audition is the resultant of all the wave motions, transformed and transmitted to the auditory centre in the brain by the fibres of the auditory nerve.

There are several kinds or conditions of auditory stimuli, depending, first, on the *intensity* or force of sound (*i.e.* the amplitude of vibration); second, on the pitch of sound (*i.e.* the number of vibrations in a given unit of time); and third, the quality or timbre (*i.e.* the result of the form of the sound wave). Upon the combination of these conditions, in varying proportions as they occur, depend the character of the auditory impressions.

The variability in the powers of auditory perception among animals is much greater than is commonly supposed. As instances of increased sensitiveness above that of the human ear one may mention mice, cats, and other nocturnal animals. Galton found that the house cat among domestic animals possessed a wonderful capacity to perceive shrill tones, and it is a common experience that the cat's ear is super-sensitive to auditory stimuli.

All vertebrates above the fishes are provided, like man, with a tympanic membrane and a chain of bones, or its functional equivalent, which serve to transmit vibrations to the internal ear; but while we are accustomed to look upon this arrangement of the parts as presenting us with a greater perfection of the auditory apparatus than is present in the lower forms, it is not by any means proven that such is the case, for this accessory apparatus is a ponderous mass, which only relatively powerful vibrations can set in motion. All vibrations of the air which do not succeed in moving this conducting apparatus are lost to us. It is for the purpose of making up this great loss that the external ear has been developed. Traces of accessory apparatus to place the internal ear in more favorable communication with the exterior, begin to make their appearance among the cartilaginous fishes, whose ears still retain their direct connection with the sea-water by means of an endolymphatic duct. This tendency is due to

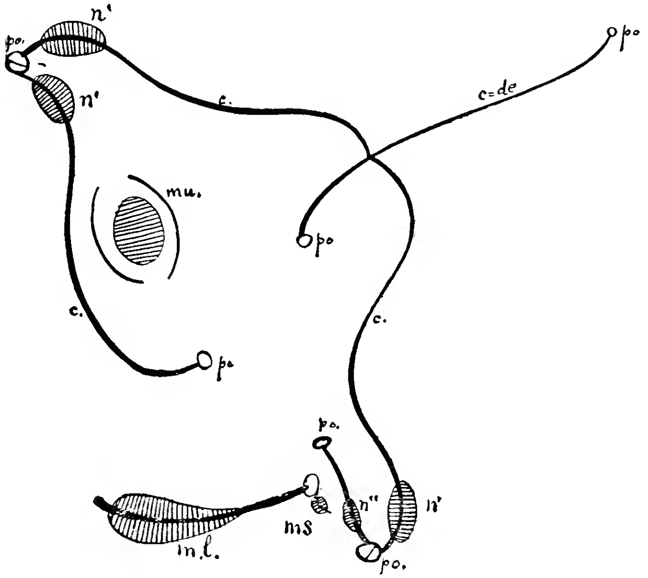

FIG. 17. — A projection of the internal ear on a flat surface, to illustrate the relations of the sense-organs and canals of the Torpedo ear, when the auditory chamber is brought to the surface and spread out flat.

c	Canal.	*n''*	Macula neglecta.
po	Canal pore.	*ml*	Papilla lagenæ.
n'	Crista acustica.	*ms*	Macula sacculi.
mu	Macula utriculi.	*c. de*	Endolymphatic duct.

the removal of the ear from the surface of the body, and is greatly increased as soon as the forms emerge into the poorer conducting medium of the aërial ocean.

When the structure of the internal ear of the higher vertebrate has been analyzed with reference to determining its functions, we find that it is easily reduced to the type of the canal organ on the surface of the body, and we should expect an essential harmony between the functions of these two groups of organs, although in the case of the ear the functions would necessarily be in some degree modified to correspond with its modifications of structure. These latter, we know, have not been extensive, except in the case of the cochlea, and, strange as it may seem, we are not able to assign to the cochlea any function at all in keeping with the great complication of structure which it has undergone during its evolution from the lagena.

The Helmholtz piano-string theory is entirely inadequate to account for perception of musical tones by vertebrate animals, in that it can be applied only to the higher mammalian forms, and leaves us to seek another explanation for the equal, if not greater, powers of musical perception possessed by some birds. Whatever explanation future investigation may disclose to us, it is safe to say that it will prove equally applicable to all vertebrate forms capable of musical perception, while being in perfect harmony with the then perfected knowledge of sound (tone) perception by means of lateral line organs.

In closing, allow me to recapitulate the more important features of oto-phylogeny, past, present, and to come.

In the PAST the ear of man was a canal organ of the lateral line system of sense-organs. A system which has disappeared from the surface of the adult human body; but which still occurs in a reduced condition during embryonic development. All its organs regularly produced protective canals, and the auditory organ came to differ from the neighboring organs merely in size and the greater depth of its ampullar pit. At first its functions were identical with those organs of the same system, having the same nerve supply; but as it was more and more removed from the surface of the body, it acquired greater protection against injuries and concomitantly greater sensitiveness. It increased in size and began the process of division, which has resulted in the organ as it exists at the present day.

These changes required untold millions of years for their perfection; for, since palæontological science tells us that this same Amia or ganoid Dog-fish which has retained its surface organs in such a primitive condition, existed in its present form, at the very least, twelve millions of years ago, you will readily conclude that the human mind can form no adequate conception of the period of time which elapsed since the ancestors of the Dog-fish were like the Cyclostome fishes in the structure of their ears.

For we know that at the present time Amia has an internal ear of greater complication than the Torpedo, which I briefly described to you at the beginning of the hour. The auditory organ has played a long and very important rôle in the phylogenetic history of man. The auditory organ of man has no genetic connection with any of the invertebrate auditory structures.

At the PRESENT time the human ear is a canal organ complexus, constructed according to a simple and symmetrical plan, whose ontogenetic history is a recapitulation of many of the stages of its phylogeny. During its development it is badly distorted, and the simplicity and symmetry of the plan of its construction is thus in a measure concealed. In its adult condition it is not the most highly differentiated ear known to us, for some other mammals are far more fortunate in this respect. It is an organ about whose functions we know little, since most of what is written in the text-books is pure speculation, much of which is proven to be without foundation, if, indeed, it is not directly controverted by recent experiments.

It subserves the auditory function, and has no more to do with the equilibration of the body than many other organs, especially those of the higher senses. Its canals are not organs of equilibration.

The FUTURE of the human ear can only be foreseen in terms of its past and present. It will probably develop functionally much more than structurally. Its semicircular canals will gradually undergo reduction, while its utricular and saccular complexes of sense-organs will increase in size and perfection of structural detail, in response to the increasing demands for tonal differentiation; it will, nevertheless, remain in the human descendants of the distant future, whatever their form may be, however keen or diversified their auditory function may become, merely A TRANSFORMED CANAL ORGAN.

TENTH LECTURE.

THE STUDY OF OCEAN TEMPERATURES AND CURRENTS.

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Professor Whitman has been kind enough to ask me to speak to you this evening upon the physical work of the U. S. Fish Commission. As this work is so intimately connected with the study of the Gulf Stream, a few statements concerning ocean currents in general and their causes will not be out of place.

I do not know whether it is generally known that the word "ocean," as applied to the waters of the globe by the ancients, seems to have been intended to convey some idea of currents. It is derived from two Greek words *ὠκέως* and *νάειν* which mean "fast flowing." This has sometimes been thought to refer to the onward motion of the waves toward the shore. This may be its meaning, but when we remember the great number of references to the "river ocean" in the classics, and the inscriptions upon the older maps giving the direction of the currents, as for example the "Periplus maris erythraei" flowing along the Somali coast, we cannot help thinking that the ancients not only knew of these currents but supposed them to be the essential features of the oceans.

While speaking of these older maps, I might add that there are many curious graphic attempts to explain the ocean currents. Among them the attempt of Vossius is noteworthy. His currents start from the interior of the globe, and after running their course, are taken back to mid-ocean (a safe place perhaps at that time because it was not likely to be investigated), and then they disappeared in a most remarkable series of mysterious whirlpools.

Twenty years after the discovery of America, Ponce de Leon, who had been Governor of Porto Rico, was replaced by Diego Colon. He set sail in 1513, with three vessels, to cross the straits between the Bahamas and Florida. While sailing south along the coast of Florida, they kept off shore to avoid shallows, and found themselves in a current against which they could not make headway even with a favorable wind. Their journals are very interesting at this point, because in them we have the first recorded descriptions of the Gulf Stream. Two of the vessels came to anchor, their cables "vibrating like musical strings," while it is recorded as a remarkable fact that the third vessel, being further off shore than the other two, failed to obtain an anchorage and "drifted out of sight in a clear day, with a fair wind."

The pilot of this expedition was Francisco de Alaminos, later on the pilot of Cortez. In his actions we have a fine example of the hardy character and practical nature of those early explorers. When the "Gold-land" of Mexico was discovered, you will remember he utilized the information obtained on this trip, took advantage of this current, and boldly put out over an untried portion of the Atlantic to carry the news home, and made a very fast trip.

This current was known from this time on, and for two hundred and fifty years was utilized or avoided, before any attempt was made to study it. Benjamin Franklin was the first to study all the records he could collect concerning it, and in 1772, supposing the current to arise in the Gulf of Mexico, gave it the name which has clung to it ever since, largely through his influence. It was known and shown upon the maps as the Florida current before this time, receiving its name from the same fact that gave the name to the peninsula, viz. that they were both discovered on Easter Sunday (Pascua Florida). Since that time it has been most carefully studied. About fifty years ago Maury collected all the observations to be had, and gave a most substantial basis for future work in his careful summary of the results. Then came the Challenger trip which is so famous for the new epoch made in the study of the oceans. Their success was largely due to the new methods instituted. This expedition has been followed by many others, to the several oceans of the globe. In the Atlantic there have been two great systematic attacks upon these problems. First, that of the Norwegian expedition in the North Sea, under Professor Mohn, and then the studies, carried out by the Coast Survey under that brilliant series of investigators, Sigsbee, Bartlett, and Pillsbury, upon the temperatures and currents off our own coast. The work of the Fish Commission steamer

Albatross deserves an honorable place in connection with this work. There is, however, room for the more careful study of the relations of these currents, their changes under various meteorological conditions, and their effect upon the distribution of marine life. This has been the problem upon which we have been working for the past two seasons.

Let me now give a short outline of the course of a part of the North Atlantic currents. About two or three hundred miles west of the coast of Africa we find the first indications of the Equatorial current; this passes westward to the neighborhood of Cape St. Roque, where it divides, the portion in which we are interested passing northward. When this branch reaches the Windward Islands, it again divides, a part known as the Antilles current passing up to the eastward of these Islands; the main portion, however, under the name of the Carib current, passes westward between them. At this point Bartlett speaks of it not as a mere stream but a sea in motion. When this body of water reaches the straits between Yucatan and Cuba, its width is decreased to one-seventh of its former size, and its velocity doubled. At this point a small arm passes into the Gulf of Mexico, but the main current is deflected to the eastward by the banks to the north of Yucatan and passes out between Florida and Cuba as the Gulf Stream or Florida current.

The following table will give a more concise view of the character of the stream from this place onward and serve to give point to our discussion of it: —

	Temp. F.	Breadth.	Velocity.
Gulf of Mexico . . .	78°	—	—
Straits of Florida . .	80°	30 miles.	3 –5 miles.
Off Charleston . . .	78°	120–150 "	2½–4 "
Off Hatteras	75°	200–250 "	1½–3 "
Off Nantucket	71°	300 "	1 –2 "

Taking up the velocity, first let us compare it with that of some of our best known rivers. Three to five miles per hour means about 5 to 10 ft. per second. The flow of the Rhine at Manheim is about 5 ft. per second, that of the Danube at Vienna is about 6 ft. per second, and the same is true for the Mississippi between the Ohio and the Arkansas. Such contrasts give a much clearer idea of its velocity than a mere statement of the figures.

We notice next that the velocity decreases. This "river in the ocean" is subject to the same laws of friction which control the flow of all rivers, and consequently is slowly retarded in its onward progress by contact with the water at the sides and on the bottom of the current. This frictional element becomes greater from the fact that, as the current proceeds, the warm water has a tendency to rise to the surface in spite of its velocity, and as it spreads out, the frictional surfaces are naturally increased. When the velocity has considerably decreased, this friction seems to break up the stream into numerous bands which separate and pass over the various portions of the North Atlantic. A simple illustration of the way in which this effect is produced is obtained by placing the hand with the fingers together upon the table, and then forcibly moving it forward, when it will be found almost impossible to keep the fingers together; contact with opposing currents, also, tends to reduce the velocity and breaks the main band up into smaller bands.

I would call attention to the fact that this widening of the stream takes place upon its eastern side, the western edge being much sharper and better defined than the eastern. This is probably due to the position of the Labrador current between it and the coast. The line of contact between these two currents is so sharp that it can often be seen in the surface water from the deck of a vessel. During one of the late trips of the *Grampus*, I had a curious illustration of the fact, that under proper conditions the line of contact could be noticed in the dark. We were about forty miles south of Nantucket, and had just completed a set of observations upon one of our stations. We had a strong southwesterly tide, the air was so nearly quiet that we could just get headway enough to hold our course, and the temperature of the surface water was 67° F. We had scarcely gotten under way, when I noticed a distinct noise similar to that of a tide rip, about a mile ahead of us. I watched our approach to this noise with great interest, as I knew there were no tide rips in this portion of the ocean. We soon passed into the troubled water, which was producing this noise. Upon taking the temperature at this point I found it to be 72° F. We had passed from water flowing southwest to water moving to the northeast, and were, undoubtedly, in one of the smaller outlying bands of the Gulf Stream.

You will also notice from the table that the temperature of the water decreases, as the water moves onward. Distance from the source of heat, contact with the colder air and water, and radiation to the air are without doubt the main factors in this decrease. Notwithstanding this decrease, the stream still has a wonderful amount of power left to modify climate. According to Croll, this current removes from the equator each day an amount of heat equivalent to 154,959,300,000,000 foot pounds. This is equal to 325,000 horse power per second. Now, if we should wish to produce the same effect by burning coal, we should have to use 336,000,000 tons of coal per day, and when we remember that the total output of the mines of America is but about 100,000,000 tons in a year, we will see that we have here a very abundant supply of heat at work, modifying our climate to an extent utterly beyond our imagination's power to grasp.

Let me now speak a few words upon the subject of the modification of the course of these currents. They are the great means of exchange between the waters of the equator and those of the poles. How are these circuits established, and why should they have this orbit-like course in each of the oceans, irrespective of the size or shape of the ocean? At first, it was supposed that elevations upon the bed of the oceans controlled their course, but the soundings of modern times have done away with this idea completely. We must have recourse to the law of inertia to explain this phenomenon. As the warm water of the equator starts from the equator to go towards the pole, it passes from a region of great velocity of rotation to one where a lesser velocity is found, and consequently gradually drops back to the right or left, as the case may be. So, too, the water of the pole, as it moves towards the equator, is constantly advancing from a region of small velocity to a greater one, and consequently gains in longitude as it goes on.

Upon examination of any good map of the currents of the oceans, it will be found that they follow this law in their circuits without regard to the coast lines, though the coasts materially change their directions in many instances. This is particularly true of the southern portions of the Atlantic, Pacific, and Indian Oceans, where the courses of the currents are not interfered with by the land masses of the globe, and are perfectly free to move according to the law which controls them.

We shall now consider some of the causes of these currents, and the various theories which have been held concerning them. Magnetism and the moon have been a great source of comfort to people perplexed over the difficulties presented by some of the phenomena of nature. It was only recently that I saw an attempt to explain the currents by the use of the laws of magnetism.

Among the earliest explanations we have of these currents are those given by Kepler and Leonardo da Vinci. Kepler believed they were due to the rotation of the earth, while da Vinci thought they were caused by a disturbance of the thermal equilibrium at the equator. I will only take time to allude to one of the many curious explanations given by the older geographers of these currents. Vossius, whose map I have already referred to, explains them as follows. If we watch a ship passing along through the water, we will notice that it seems to depress the water at its bows, thereby causing currents to set in from the higher water on both sides of these depressions on either side of the ship. In like manner the sun in passing around the globe compresses the waters around the equator, and hence starts a current from the higher waters of the northern and southern regions. This was in the age when perpetual motion was the "craze," and he found his source of perpetual motion in the tropics. It is certainly very strange that men allow their imaginations to run away with them to such an extent.

Up to the year 1700, we find no satisfactory explanation of these currents. At that time it was believed that the strong evaporation of water at the equator produced them. It can be easily shown, however, that such variations will only produce local currents, and that the effects produced by the heat of the sun in this way are not sufficiently far-reaching in their power to account for our great ocean currents. Then came Franklin with his proposition that they were initiated in their course by the constant action of the trade winds, which reasoning we shall see, later, has considerable force. Later on, in this century, we find Maury advocating the differences in specific gravity of the waters as the main cause. He believed that the cold waters at the poles sank, and then moved towards the equator, being replaced by the warm waters which came from the tropics, and were in turn cooled off. There is a kernel of truth in this idea, but it does not in any way explain the origin of the motion. The sinking of cold water and the rising of warm water is simply an exchange brought about within narrow limits, and involves no other motion than that of conduction in a fluid. Besides, later observations by Forschhammer and Buchanan have shown us that these variations are not as important as they were supposed to be.

About the same time V. Schilling, a Russian, advanced a tidal wave theory. It is interesting only from the fact that it is exactly the reverse of the theory of Vossius. As the tidal wave passes around the equator, it produces a flood tide at that point, and consequently an ebb tide must be formed at the higher latitudes. Existing facts and the theory cannot be harmonized without straining both, and so it must be rejected.

There are two modern schools of theorists with regard to the causes of ocean currents.

I. Those who advocate a *thermic circulation* in explanation. This idea is defended by Schmid, Mubry, Carpenter, and Krummel. It is believed by this school that the differences in temperature between the tropics and the poles are sufficient to account for the currents. This belief is based largely upon an experiment of Carpenter's, in which the water at one end of a trough was cooled, whereas that at the other end was warmed. Small objects, such as pigment granules which floated and colored the water as they advanced, show a motion of a character tending to support this view. Mubry adds to this the idea that the motion is aided by the rotation of the earth.

The difficulties in the way of this theory are: first, that centrifugal motion does not do what it is supposed to, *i.e.* start a rotary current. I have already shown its true effect upon the currents. Secondly, neither are the temperature differences able to do what is ascribed to them. It is very clearly shown by Croll that their effective power has been overestimated. He finds an unexpectedly small value for the velocity of the current induced in this way. Further, the theory demands much larger and more extensive currents than we know to exist.

II. Those who advocate the *friction* of the *winds* as a cause. This side has been taken by Herschel, Franklin, Croll, Zöppritz, and Haughton. Its best defence is in the mathematical work of Zöppritz. This school claims that the force of the wind applied to the surface of the water constantly for a given period will transmit some of its velocity by means of the motion of the molecules upon one another. Taking the coefficient of the friction of water as 0.0144, it would take about 240 years for this velocity to be transmitted to a depth of 400 feet; of course, if the velocity varies on the surface, this time will vary, but we have ages to draw upon.

Professor Ferrel has raised the only objection to this theory which seems valid at first sight, namely, that the moment of velocity of the sea current is greater than that of the wind, and hence we are trying to prove the greater by the less. He has apparently not considered the constancy of the winds and the time element involved. Many instances could be given of the effect of the wind upon the water, such as the massing of the waters of some of the Swiss lakes at one end of their basins, after the winds have blown constantly in that direction for several days. The most marked example of their power, however, is found in the temporary reversal of the regular current of the North Indian Ocean during the period of the southwest monsoon.

It is not to be wondered at, then, that such a difficult problem as that of the ocean currents presents many dark and unsolved points. If I might suggest a theory, I would say that the winds are the prime mover, setting the current in motion, and all the other factors produce variations or aid this motion and quite likely retard it under the varying conditions in which they are found. The words of Humboldt are almost prophetic in this connection, but I very much doubt whether he had any definite conception of the fulness and completeness of his statement, when he said: "They (the currents) cannot be explained by any *one* assignable cause; the phenomena are complicated by the ebb and flow of the tides, the duration and force of the predominating winds, the density and specific gravity of the water, as modified by temperature in different latitudes, seasons, and depths of water."

Whatever may be their cause, we cannot help but wonder at some of the efforts produced by the constancy and power of these currents. I sometimes think a good way of seeing the benefit of any given order of things is to suppose them reversed. Suppose, for instance, that instead of having this continual circulation in the oceans, keeping every portion in a normal and proper condition for life, and blotting out all dangerous variations, our oceans were stagnant bodies of water. You will instantly recognize the effect which would be produced upon the life of the globe. These great currents have been aptly compared to the veins and arteries in the body, and it is certain that we owe a great deal to them in the daily economy of nature.

Upon the organization of the United States Fish Commission, the essential problems to be studied were properly believed to be largely biological in character. Some attention was paid to the physical conditions under which marine life existed, but the bearing of these conditions upon the successful propagation of fish, or the uses which could be made of a careful study of these conditions under given states of the air or sea, was not deemed an important item in the problem placed before the Commission for their consideration. The result was that the early work of the Commission was devoted to the collection of specimens of fish and other forms of marine life, the study of their distribution, and the discussion of their embryological development. After this, the examination of the food of these fishes and their physical surroundings attracted attention.

When the attempt was made, however, to compare the isolated observations upon the temperature and specific gravity of the waters, it was found that sufficient data of a proper character were not at hand to give a complete and satisfactory basis for an explanation of the phenomena which were known to exist. The necessity then presented itself of making a more systematic survey of some specific coast region, with the view of obtaining the law of the changes which take place under given conditions.

If the changes which take place in the temperature and specific gravity of the waters influence the movements of the schools of fish, then the various movements of the currents, tides, winds, etc., all affect the changes which occur to such an extent, that they must be studied simultaneously and over a considerable area, and also during the various seasonal changes before any adequate idea can be obtained of even the limits of the problem.

The physical, mechanical, and chemical changes which take place are all the result of the operation of laws, which are so complicated in their action and interaction that their study in combination becomes an interesting as well as profitable occupation.

If some relation could be found to exist between the meteorological conditions upon the land (which are being constantly observed and discussed) and the changes which occur in the bodies of water, the information would be of the greatest service to our fishermen. It would prevent many fruitless searches for schools of fish in regions unfitted by the temperature of the water for the distribution of the food of these fishes, and consequently of the fish themselves. As the temperature of the water, doubtless, controls this distribution, a systematic study of the various causes of its changes, and the means by which they are brought about, becomes an eminently proper subject for investigation.

Thus a definite object has been kept in view in the prosecution of the physical inquiries of the Commission. This became necessary as the work of the Commission developed. At first it was quite right that the investigations should be experimental and tentative, and only as the problems assumed shape could some positive object be given to each research along definite lines, with the view of uniting the results into a studied system which should represent the policy or plan of action of the Commission.

Such has been my understanding of the work in hand. Professor Baird was an organizer of great power, and doubtless knew well that the only chance of success in this important work was to gather facts broadly, before attempting to particularize. Later, when, in their turn, the biological and embryological work took such shape that the practical work of the Commission (which was being carried on in a limited way) could be benefited by the aid of facts obtained by specialists in these departments, the results attained in the practical work showed the advantage gained by this greater knowledge of the life-laws of each species. The work of the biologist thus came to the aid of the practical fish culturist, enabling him to avoid mistakes, which in many instances would have blocked his way to success, by showing him the periods at which especial attention should be given to the developing fish, and the best methods of raising them.

In all these matters, Colonel McDonald, the head of the practical work of the Commission under Professor Baird, followed in his predecessor's steps, when he became Commissioner.

It was soon evident that the study of the conditions involved was incomplete, as it did not include a knowledge of the physical conditions under which marine life exists. Attempts were made to stock localities in a hit-or-miss fashion, which were sometimes successful, and in other instances resulted in failure. Conditions once favorable were changed, partly by man's interference and partly through natural causes. Thus it became necessary to study these changes and ascertain their law, if possible, in addition to the careful study of the biological problems otherwise involved.

Two such investigations are now being carried out by the Commission, one upon the ocean, and the other in Long Island Sound. A description of these will suffice to give an idea of the character of the physical work which is now being carried on, and its importance as an element in the study of this problem of making good a deficiency in such an essential food product, caused by the increased demands of our times, and intensified in its effect by the carelessness or thoughtlessness of our fishermen through ignorance and in some instances wilfulness in the pursuit of a merely temporary gain.

In order to give a practical and positive character to the investigation upon the ocean, the region between Nantucket Island on the east and Block Island on the west was taken, since it lies in the track of the schools of fish. After consideration, it was decided that a preliminary survey should be made to obtain some definite ideas upon the relations of the cold and warm currents, the changes which take place in their relations, the influence of the winds and other meteorological phenomena in producing these changes, and to notice any effect produced by the tides. The Fish Commission schooner *Grampus* was placed at my disposal, and outfitted with the proper apparatus and instruments, to carry out this work as an experiment, to see whether any results of interest could be obtained.

A series of lines 130 miles in length and at ten-mile (ten minutes of longitude) intervals from one another, were laid out between the two above-mentioned islands.

Along these lines at ten-mile intervals, observations were made upon the temperature of the water at various depths. These depths were determined experimentally in order to ascertain the best position for the instruments, and this involved considerable preliminary work because of the vagueness of the information at hand. The intervals finally adopted were 5, 10, 15, 20, 25, 30, 40, 50, 75, 100, 150, 200, 300, 400, and 500 fathoms. After these lines had been run out, some of them were repeated under different meteorological conditions in order to note any changes which had taken place. The above observations were accompanied by an hourly set of meteorological records, which were compared with the regular series of the Signal Service offices of New York and Boston. The work was limited to about two months, in which time 136 such stations were studied, 1600 water temperature observations were taken, 300 observations were made upon the specific gravity of the water, both at the surface, the bottom, and at intermediate depths; and in addition over 10,000 general meteorological observations were recorded. These observations have all been reduced and plotted, and a report, embodying the results and comparisons, is now in process of publication.

The report shows, in brief, that an important influence is exerted by the winds, forcing the warm surface water of the Gulf Stream to a considerable distance northward towards the coast, when blowing from the south, and that this warm body of water swings back again, when the wind blows from the opposite direction. This warm water, which affords the proper temperature conditions for the development of the forms of marine life upon which the fish feed, is crossed and followed by the schools of fish. In this way the cold coast current is bridged over, so to speak, and the fish brought within reach of the fishing fleet. As the warm water approaches the coast, it seems to be broken up into bands, which lose their velocity by coming into contact with a current flowing in the opposite direction to that in which they originally moved, and their course is again modified to such an extent that they are found flowing in the opposite direction of the Gulf Stream. We have further gained concise ideas of the relations of the cold coast current and the warm waters of the Gulf Stream; and know something of the changes which take place in these relations through the mechanical influence of the winds. The outline of the problem has thus been obtained. The results were interesting enough to induce Professor Mendenhall, the superintendent of the Coast Survey, to coöperate with the commission in the study of these temperature problems; and this summer a still more extended investigation is in hand, in which the Coast Survey steamer *Blake* and the schooner *Grampus* are engaged. The work has progressed to such a point that I may say that we shall have over 375 stations to study, giving us over 4000 serial temperatures, 1000 specific gravity observations, and over 14,000 general meteorological records.

Last year the only means of comparison for our meteorological observations were the records made in New York and Boston; but this year we shall have in addition for this purpose a station upon the Nantucket New South Shoal light-ship, through the courtesy of the Light-house Board. Here a series of observations have been made upon the atmospheric conditions, attention paid to wind velocity, tidal movements, and also to the direction and velocity of the currents. This lightship occupies the most exposed position upon our coast, being twenty-one miles southeast of the island of Nantucket, and affords a fine opportunity for the study of these phenomena.

Many interesting results are expected from this investigation, which, while they will be of scientific value in other directions, will be welcome sources of information to aid in the solution of the problems of the Fish Commission.

The physical investigations in Long Island Sound can be described in a few words.

For several years a decrease has been noticed in the oyster crop from that body of water. At first it was believed that the natural enemies of the oyster, such as the star fish, the drills, etc., were the main cause of the evil. After investigation it was seen that where the oyster beds were properly cared for, their enemies did not exist in sufficient numbers to cause the trouble, though the oysters continued to disappear from these beds, masses of empty shells being brought up in the dredges. While the Fish Commission steamer *Fish Hawk* was investigating this matter last year, they occasionally brought up in their dredge great quantities of decomposing matter, which was so offensive that it had to be instantly washed back into the water. It should be remembered that for several years past the river mouths and harbors along the Sound have been dredged, and the matter obtained dumped into the deeper portions of the Sound; and further, that the action of the tides in that body of water do not carry any substance placed in it out to sea, but keep it moving back and forth until it is decomposed. This fact suggested the idea that possibly the oxygen in the water could not take care of any such excessive charge of poisonous nitrates and nitrites as would be developed by these decomposing substances.

The waters of the Sound are therefore being investigated this season with reference to their chemical condition at various depths. The currents are at the same time being carefully studied by a member of the Coast Survey, and it is hoped in this way to obtain a complete view of the physical conditions under which the oyster has been evidently forced to live.