THE
EVOLUTION
OF THE
VERTEBRATES
AND
THEIR KIN

PATTEN

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INTRODUCTION.

It is many years since a sustained attempt has been made to unite the various branches of the animal kingdom into a natural, coherent system, or genealogical tree, that would indicate the rise and decline of the important functions and organs, map out the highways of organic evolution, and assign in geological terms the approximate dates and surroundings for the critical events in structural innovation and readjustment that have marked its progress.

The most important problem involved in such an undertaking is to discover which one, if any, of the many existing invertebrate phyla forms the trunk line of descent from the lowest vertebrates to the cœlenterates, and through them to the protozoa.

The vertebrates abruptly make their appearance as fully formed fishes, at the close of the Silurian or the beginning of the Devonian. They were evidently more highly organized than any of the invertebrate types that had appeared up to that time, and they must have arisen, either by a marked transformation of some of the known, preexisting types, or from some extinct and totally unknown ones. On either supposition, the apparent absence of transitional forms is surprising, since the relatively large size, distinctive form, and well developed skeleton of primitive vertebrates, under the known conditions, should leave behind some recognizable traces of their predecessors in the form of fossils.

The real missing links in the graded series of animal forms that most concern the morphologist belong, therefore, to the Silurian period. There the main trunk of the animal kingdom, upon which the whole vertebrate stock rests, is lost, leaving without reason or warning a vast unknown abyss beside which the gap between man and his immediate predecessors sinks into microscopic insignificance.

On the one side are the vertebrates, including a long series of animals, from the lowest fishes to man. All of them agree in their fundamental plan of structure and mode of development; the principal organs of any member of the series may be surely identified in the others, and the general trend of evolution in the phylum is clearly indicated. The fishes, for example, are the lowest members of the series, and they are followed by the amphibia, reptiles, and mammals. Comparative anatomy shows the gradual evolution of form and structure in this series as a whole, and its evidence is corroborated, in the main, by the embryonic development of any member of the series, while the geologic, or historic record harmonizes with, and confirms the testimony of the other two. In fact, the vertebrates clearly constitute a common stock, a single phylum of the animal kingdom. It has many side branches, it is true, but comparative anatomy, embryology, and paleontology are in substantial agreement as to what kind of animals and what organs and functions came first in time, what were the most highly developed, and what was the general trend of evolution.

Even the simplest vertebrates, that stand at the beginning of this long series, were very highly organized animals, for all the fundamental systems of organs well known to us in man, such as the sensory, nervous, skeletal, circulatory, and excretory, were there fully established and highly efficient. But there is little in the structure or development of these organs that gives us any positive information as to their previous history, condition, or origin, the very information essential to a true understanding of their meaning.

On the other hand, when we look below the vertebrates for the main highway of evolution, we are bewildered by the multiplicity of doubtful trails that appear to have neither beginning nor end, that lead as readily in one direction as another. Each invites us onward; but if followed, suspicion soon grows to conviction that we have been deceived, that some other road is after all the right one.

The familiar cry, "This way," "I have it," that rose when an enthusiastic pioneer struck the annelid, tunicate, balanoglossus, or some other promising trail, would for a time rouse great expectations; but it always ended in disappointment, and gradually created an attitude of indifference, and the feeling that the solution of this great problem was forever beyond our reach. The conviction grew that one or more large classes of animals that once constituted the living trunk of the genealogical tree during Silurian, or pre-Silurian times, were entirely extinct, and had left no traces whatever behind.

With the historic record of the most important period in the evolution of the higher animals completely destroyed, the problem did indeed appear hopeless. What was lacking in actual records was supplied by the speculative biologists, and they did their work so well, and reiterated it so often, that it finally passed for the truth, and its central idea, that the vertebrates had their origin in the annelids, in some more or less roundabout way, became a dogma.

We then witnessed the interesting phenomenon, common enough but always profitable to contemplate, as lightning that strikes near by, that those who would not make the annelid theory a part of their creed, and who continued the search in other directions for a substantial body of facts to build upon, were branded as morphological heretics and speculators, or as the victims of a too vivid imagination; and it was always the most "orthodox" and persistent speculator that waved the hottest brand.

But when the annelid dogma passed the period of productivity without offspring, even the orthodox biologists lost all hope of solving the real problem of the origin of vertebrates, as well as many other large problems in invertebrate phylogeny, and turned their attention toward the Eldorado of cytology, heredity, and experimental evolution, where "results" were easy and promised to carry far.

Sterility has often turned devotion to contempt, and it is not suprising that the biologist, whose theories were unfruitful, wrecked his wrath on the temple of morphology and condemned its triune god to the consolation of his more credulous colleagues; "Paleontology," he cried, "is mute, Comparative Anatomy meaningless, and Embryology lies."

But perhaps the fault was ours. We did not understand, because of ignorance and over confidence. It is not fifty years since the doctrine of evolution has been generally recognized, and during the latter half of that period surprisingly little persistent, or concerted work has been done on the larger problems of phylogeny, and there is but little to justify the too common attitude that the possibilities of morphology are exhausted. Much disconnected fragmentary work has been done, but how little is known about the evolution of any one organ or system of organs; how very few animals, if indeed there are any, whose structure, development, and paleontological record are known with even approximate fullness or accuracy. What large class of animals is not separated from its next of kin by a gap too wide to be bridged by any known forms? Are these gaps due merely to a hiatus in the available records, or in our knowledge of them, or are they realities, representing periods of unusually rapid transformation due to sudden changes in the methods, or conditions of growth? If the gaps between the vertebrates and ostracoderms, and the ostracoderms and arachnids appear to be wide ones, are they really any wider than those between the fishes and amphibia, the reptiles and mammals, or the cœlenterates and arthropods? Are not the evidences of genetic relationship of the same nature and value in one case as in the other? Is not the paleontological record more precise and complete than we have supposed? Will not embryology be less enigmatic under a new interpretation? If the arachnids are indeed the next of kin to the ostracoderms, and through them to the vertebrates, is that after all so incredible? With this gigantic column in position, will not the remaining branches readily fall into their natural positions, and the entire genealogical tree of the animal kingdom take on the convincing symmetry and coherency of reality, of a living, growing organism that contains the story of its own creation?

* * * * * * * * *

These are some of the problems bound up in the evolution of the vertebrates. Clearly it is not merely a question of constructing a convenient and more or less satisfactory genealogy of the animal kingdom. The whole philosophy of creative evolution is involved in the answer. We must face these problems fairly, without prejudice and without arrogance (surely the record of past achievements affords no grounds for that attitude), and with a full recognition of their significance. Facts are stubborn things that will not be ignored, that call out for recognition, and for their proper location in a well ordered scheme, if not in one, then in some other that is better.

The problem is of the utmost importance to the biologist, for the answer should determine the location of several large classes of animals, now completely isolated; it will enable us to reconstruct the broad outlines of the genealogical tree of the animal kingdom where the main branches emerge from the darkness of the pre-Cambrian period; it will furnish us the only means by which we can hope to solve some of the most important problems in vertebrate morphology, such as the meaning of vertebrate cephalogenesis, of concrescence, germ layers, gastrulation, and the structure of the oldest fossil representatives of the vertebrate series. The answer to such problems cannot be found till after we have discovered the immediate ancestors of the vertebrates and the broad outlines of their structure, for when the point of departure is determined, and only then, can we determine which is the base and which is the summit of a series of changes, which the primitive, which the derived; in short, the direction in which evolution is moving.

The arachnid theory of the origin of vertebrates has made slow progress. This is not surprising since it has had to contend against the fixed ideas of the specialist working in some narrow field of vertebrate or invertebrate morphology, and who is unfamiliar with the multitude of facts and details, intricate in themselves and in their bearings, upon which the arachnid theory rests. It has also had to contend against the indifference of the newer school of biologists, who look on morphology as an exhausted field, and who attach an exaggerated importance to experimental, or statistical work, or to the minute structure of cells, or to the analysis of protoplasm.

This is largely due to a common misconception of the real aim of the morphologist; for it is evident that tracing the identity of structure under the disguise of new forms is only the beginning of the morphologist's work. His real problem is to measure the rate of these changes, and to seek out the underlying causes. Hence, a great morphological problem, such as the origin of vertebrates, is essentially a problem in experimental evolution, an experiment performed on the largest scale of any in the history of organic evolution. But here the problem presents itself in a different form from the ordinary laboratory experiment. There the experimenter fixes the conditions, as nearly as possible, and then records and measures the events as they appear. Here the morphologist records and measures the events, and from them tries to discover the conditions. I believe I have discovered the main events in this experiment of Nature, and I have recorded it, in terms of systematic zoology, in a genealogic tree of the great arthropod-vertebrate stock. This discovery enables us to see clearly some of the factors that have brought about the results. They are mainly internal factors, insignificant in themselves, but acquiring such immense transforming power by persistent and prolonged action that it is unnecessary to invoke the agency of such factors as external environment, natural selection, and heredity. At most, it seems to me, these factors can account only for the superficial details of the essentially completed body. Morphology teaches us that the foundations of anatomical structure are automatically created by the processes of growth and organic readjustment, and that they remain essentially unmoved by external conditons.

For almost a quarter of a century the problem of the evolution of the vertebrates has been to me a stimulus and a guide. What appears to be an approximate solution of it has been tested and tested again, and elaborated—in itself the severest test of all—by many methods and from many points of view, for it has seemed to me the one great problem that must be solved before the biologist can approach the problems of creative evolution on a reasonably secure footing. To gain this end, I have given the best I had; whether that is much or little is of no consequence, except in so far as it is a guarantee of serious endeavor and of good faith. That I am conscious of many difficulties and imperfections need not be emphasized. I would gladly make them less. But to be overconscious of the one, unsteadies the hand and draws the eye away from the open waters, and too long a delay over the inevitable defects means to be surprised by the night, and still unprepared.

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HISTORICAL SKETCH.

The resemblance between vertebrates and arthropods first attracted my attention in 1884. In my paper on the development of the phryganids, it was stated, page 594, that a wonderful analogy, if not homology, exists between the structure and mode of growth of the medullary plate, the neural and gastrular invaginations, and the neurenteric canal of insects and the corresponding structures in vertebrates.

Three years later, a resemblance between the minute structure of the compound eyes of arthropods and the retina of vertebrates was recognized.

In 1888, it was shown that the invagination of the procephalic lobes, supposed by writers of that period to give rise to a two-layered compound eye, in reality gave rise to the optic ganglion only, while the eye itself consisted of a single layer. Further study of the developing brain and eyes of Acilius, Buthus, and Limulus, showed that in many arthropods the procephalic lobes underwent a complex process of invagination, accompanied by the overgrowth of a neural crest, or palial fold, the result being the formation of a vesicular forebrain, and the transfer of the ocelli, located on the outer margin of the lobes, to the end of a tubular or epiphysial outgrowth of the membranous roof of the forebrain vesicle.

Here were revealed, for the first time, all the steps in the transformation of an invertebrate type of eye into the type of eye so characteristic of vertebrates. This apparently simple fact was in reality the result of very complex conditions, and it seemed incredible that they could be duplicated except in animals belonging to the same stock.

These discoveries, therefore, appeared so profoundly significant that I determined to follow the clue to the end, to see whether further analysis of the eyes, the brain, and other systems of organs would not confirm the obvious conclusion to be drawn from them. The results proved to be so surprisingly in accord with them, that in the following year, 1889, a definite theory was formulated, and a preliminary sketch, or outline, of it was published under the title "On the Origin of Vertebrates from Arachnids."

This theory has formed the basis of all my subsequent work, and as far as it went, is practically the same as the one presented here. In that paper it was maintained that the vertebrates are descended from the arachnid division of the arthropods, in which were included the typical arachnids, the trilobites, and merostomes. The ostracoderms were regarded as a separate class, uniting the arachnids with the true vertebrates. Limulus and the scorpion were the types most carefully studied, because they were the nearest and most available living representatives of the now extinct merostomes, or giant sea scorpions, that were regarded as the arachnids standing nearest to the ostracoderms.

Other evidence and conclusions were as follows: 1. In the arachnids a forebrain vesicle is formed by the same process of marginal overgrowth as in the vertebrates. From the floor of the vesicle arise the forebrain and optic ganglia; from the membranous roof, a tubular outgrowth is formed that contains a parietal, or pineal eye, similar in structure, mode of origin, and innervation to the pineal eye of vertebrates. 2. The kidney-shaped compound eye of arachnids has been transferred to the walls of the cerebral vesicle in vertebrates, giving rise to the retina, which still shows traces of ommatidia in the arrangement of the rod-and-cone cells. Its original shape is temporarily retained in vertebrates, but gives rise ultimately, by adaptive exaggeration, to the choroid fissure. 3. The arachnids have a cartilaginous endocranium similar in shape and location to the primordial cranium of vertebrates. 4. They have an axial, subneural rod comparable with the notochord. 5. In arachnids, the brain contains approximately the same number of neuromeres as in vertebrates. It is also divided into similar regions, each one having a similar number of neuromeres, a similar distribution of nerves, and a similar relation to cranial ganglia and sense organs, to those in vertebrates. 6. The segmental sense organs (median and lateral eyes, olfactory and auditory organs) are comparable with those in vertebrates. The coxal sense organs are associated with special sensory nerves and ganglia, comparable with the cranial dorsal-root nerves and ganglia (suprabranchial sense organs) of vertebrates. 7. The basal arches of the appendages are comparable with the oral and branchial visceral arches in vertebrates. 8. The tendency toward concentration of neuromeres has narrowed the passage way for the stomodeum and modified the mode of life in the arachnids. This ultimately led to its permanent closure, the infundibulum and adjacent nerve tissues in vertebrates representing the remnants of the old stomodæum with its nerves and ganglia. 10. The progressive degeneration of hæmal thoracic muscles, the fusion of thoracic metameres, the position of the oral, or neural surface, in swimming and crawling, were identified with corresponding conditions in vertebrates. 11. The eye muscles of vertebrates arose from a special group of hæmo-neural muscles belonging probably to the first two or three thoracic segments. 12. The process of gastrulation in vertebrates and arachnids is confined to the procephalic lobes, in the place where at a later period the primitive stomodæum appears. The so-called "gastrulation" of vertebrates and arachnids is an entirely different and independent process, that is, the process of adding by apical or teloblastic growth a segmented, bilaterally symmetrical body to a primitive radially symmetrical head. 13. The arachnids resemble the vertebrates in more general ways, as in the minute structure of cartilage, muscle, nerves, digestive, and sexual organs.

In the following paper, '93, the structure of the forebrain of Limulus, with its lobes and cavities was compared in detail with the brain of vertebrates. The coxal sense organs were described and shown to be gustatory organs comparable with the suprabranchial organs of vertebrates. The remarkable structure of the olfactory organs in Limulus was also described for the first time.

In 1894 it was shown that the exoskeleton consisted of a complicated, and for an invertebrate, a very remarkable system of chitenous trabeculæ resembling a primitive form of dermal bone.

In 1896 was published a paper on the "Variations in the Development of Limulus." It was undertaken in the hope that it might throw some light on the normal development, or give some indications of the kind of variations that have led to the higher types.

In 1899 and '00, in cooperation with Mr. Redenbaugh and Miss Hazen, a description of the peripheral nervous system, endocranium, and coxal glands was published. The work was begun with the purpose of furnishing a detailed account of the various systems of organs in arachnids as a basis for further comparisons with vertebrates.

In 1901 advantage was taken of a six months leave of absence from college duties to study the principal collections of ostracoderms in European museums. It was rarely possible to make use of such collections for anything more than a superficial examination. An effort was therefore made to obtain material that could be sectioned, or used in any manner that seemed desirable, in order to get at the anatomical structure. A valuable collection of Tremataspis and Thyestes was obtained in the island of Oesel in the Baltic Sea, and a few cephalaspids and pteraspids were obtained by gift and purchase in England. In the next four or five years an effort was made to obtain ostracoderms in the vicinity of Dalhousie, N. B., Canada, at first with little success. Finally, I obtained a very large number of specimens in a beautiful state of preservation, from which it was possible to work out the anatomy in great detail. The structure of the eyes, jaws, and internal organs afforded a striking confirmation of our conclusion that the ostracoderms form a new class of animals standing between the vertebrates and arachnids.

In 1888, '89, and '90, Gaskell published his first papers on the Origin of the Central Nervous System of Vertebrates. The basis of his theory was that "the central nervous system of a crustacean ancestor had grown round and enclosed the alimentary canal." "The ventricles of the brain were the old cephalic stomach and the canalis centralis of the spinal cord, the long straight intestine which led originally to the anus." The vertebrate develops a new heart, alimentary canal, and other organs to take the place of those enclosed in the central nervous system.

In its conception and mode of analysis of the conditions in the vertebrates and arthropods, this theory is entirely different from, and wholly irreconcilable with my own. In my judgment, the foundations on which it is built are totally wrong. The fundamental error, which is inextricably interwoven in all his conclusions, making a detailed criticism of them unnecessary, is the assumption that the neural surface of an arthropod is the same as the hæmal surface of a vertebrate. In this confusion of opposite surfaces, which is like starting on a voyage of discovery with the notion that north ~~is~~ south, and east is west, the nerve cords are transferred from one side of the body to the other, turning them literally upside down and inside out, annihilating the most fundamental systems of organs, such as the heart and entire alimentary canal, and necessitating the creation "de novo" of whole systems of organs to take their place. In this process the axes of growth and differentiation are reversed, or ignored, and no attempt is made to reconcile these assumptions with the actual conditions that are so familiar in the embryonic development of both vertebrates and arthropods.

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1907. On the Origin of Vertebrates. I. The Conditions Controlling the External Morphology of Primitive Vertebrates. Lantern Slides. Read before Section VII, General Zool, VII. International Zool. Congress, Boston, August.

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Exhibits. A. Collection of Bothriolepis from the Devonian rocks of New Brunswick.

B. Fifty Models Illustrating the Structure and Embryology of Primitive Vertebrates and Related Forms. Reviewed in Amer. Nat., Vol. XLI, No. 490.

THE
EVOLUTION OF THE VERTEBRATES AND THEIR KIN.

CHAPTER I.

OUTLINE OF THE ARACHNID THEORY.

In the two following chapters we shall present a brief outline of the arachnid theory, showing the broad foundations upon which it rests and the relation of the principal organs in the arachnids to those in the vertebrates.

I. Its Scope and Relation to Other Theories.

The arachnid theory, like every other large problem in descent, should be based on comparative physiology, anatomy, embryology, and paleontology, and should be constructed in accordance with the established principles of these sciences. This particular theory has the additional task of reconciling, eliminating, or absorbing the claims of strongly entrenched rival theories, some of which contain certain elements of truth, It is important, therefore, to at once determine which supplies the greatest volume of evidence; which draws its evidence from the widest fields; which can eliminate the others, or include the others within itself.

We shall show that in these respects the arachnid theory stands in a class by itself, for it is the only one that is securely built on the natural science trinity of structure, function, and historic sequence. It not only has its own distinctive merits upon which it claims recognition, but it is the only theory that can either eliminate the others, or incorporate them within itself, where they become reinforced and revitalized.

The essential features of the annelid theory, for example, are included in the arachnid theory, because both arachnids and annelids agree in the fundamental nature of their metameric structure. But when standing alone, the annelid theory ceases to be of value as a working hypothesis, or as a touchstone to solve the problems of vertebrate morphology, because we find no traces in the annelids of those illuminating modifications of metamerism so characteristic of the arachnids, and that afford us the required data for filling in, and explaining, the enormous gap between the unspecialized metameres of an annelid and the groups of highly specialized metameres in the head of a vertebrate. The annelid theory, therefore, in the form in which it is generally understood, could be incorporated into the arthropod theory, but it is evident that the conditions could not be reversed, for no resemblance of annelids to vertebrates could either eliminate, or account for, the resemblance of arthropods to vertebrates.

The tunicate, echinoderm, balanoglossus, amphioxus, etc., theories have similar inherent weaknesses, indicating that they must be subordinated to some larger view. The baffling resemblances between the embryonic stages of these forms and vertebrates do not help us to explain vertebrate cephalogenesis, or to account for the origin of the most characteristic vertebrate structures; and so long as their own origin is unknown, and they have no fixed location in a general system of classification, they can throw no light on the origin of vertebrates, or on the still broader problems of the origin and inter-relations of the other great subdivisions of the animal kingdom.

All this is changed, however, as soon as we recognize that the echinoderms tunicates, balanoglossus, and cephalodiscus are degenerate offshoots of a common arthropod-vertebrate stock. In the light of this interpretation, the arachnid theory not only recognizes and explains the resemblance of the echinoderms, tunicates, and other acraniates to the vertebrates, but it fixes approximately their position in the animal kingdom, and elucidates the salient features of their morphology. It supplies, in the evolution of the arthropod cephalothorax, the key to the analysis of the vertebrate head. It unites the apex of the arthropod stock with the base of the vertebrate stock, and welds the entire series of segmented animals into one homogeneous group. It shows that the great vertebrate-ostracoderm-arthropod phylum forms the main trunk of the genealogical tree of the animal kingdom; that, emerging from unsegmented, cœlenterate-like animals, as though driven by some mysterious internal power, moves with astonishing precision, through broad, predetermined channels—from which neither habit, nor environment, nor heredity, can cause it to diverge—toward its goal. And finally it lays before us in their historic order the critical events of these age-long periods, the succession of structural and functional changes that have followed them, and that have in turn given rise to still other changes of form and new conditions of growth. It thus reveals to us, as only the true science of morphology can reveal, the important agents that have directed the course of evolution, and that have determined the organic forms, or shapes, in which it is expressed.

The arachnid theory thus not only unites and harmonizes these apparently conflicting views as no other interpretation can, but it will, in my judgment, go a long way toward restoring morphology to its former dominant position as the expounder and prophet of the biological sciences. Morphology reduced to a barnyard science, without its vast resources in comparative anatomy, its perspective in geological time, and its world-wide laboratory of Nature, is robbed of its chief glory and power.

One naturally looks on the arthropods as the probable ancestors of the vertebrates, because they are the most highly organized of segmented invertebrates and because the histological structure of their muscles, nerves, sense organs, cartilages, etc., closely resembles that of the vertebrates. This view was, therefore, the first to be entertained by the older anatomists (Leydig and Dohrn); but in more recent years it has not been regarded with favor.

So far as I have been able to determine, most zoologists of to-day, who make any attempt to justify their deep rooted prejudice against the arthropod theory, base their objections on the a priori ground that the arthropods, being highly specialized animals, cannot have given rise to the vertebrates, because the vertebrates must have come from some generalized type. This objection clearly has but little weight, for the general application of such a law would exclude the possibility of any evolution. Every animal is a specialized one when compared with its ancestors, and at the same time a generalized one when compared with its descendants. Even the most primitive vertebrate is a highly specialized animal, and its immediate ancestors were also highly specialized. It is clear, therefore, that in order to solve our problem we must discover not some generalized ancestor but a specialized one, and the only evidence of value in determining whether we have found the right one or not, is the degree to which its particular kind of specialization agrees with that of a vertebrate.

II. NATURE OF THE EVIDENCE TO BE PRESENTED.

Our problem then is a perfectly simple one in principle, although it is one that involves an enormous amount of detail in its application. We have merely to strip off the superficial disguise of our hypothetical arachnid ancestors and see whether either their underlying structure, their mode of growth, the general direction and historic sequence of their evolution, does or does not harmonize with the assumption that they are the ancestors of the vertebrates. We venture to state at the outset, that in our judgment they do harmonize with this assumption, and so fully and in such detail as to leave no other conclusion open than that the vertebrates arose from arachnid-like arthropods.

A. Cephalogenesis in Arthropods.—We shall show, with the aid of comparative anatomy, that the process of cephalizing the anterior part of the body, that is, the transformation of a large number of independent metameres into a compact, organized group of unlike structures that may be called a "head," is the dominant process in the evolution of arthropods, and that this process has already definitely established in the higher forms the more characteristic features of the vertebrate head. The process is initiated in primitive arthropods either by the division of the anterior part of the body into regions, or by the addition from time to time of distinct groups of like metameres, or tagmata. The successive appearance of new groups of metameres at the tail end of the body marks distinct epochs in the evolution of the arthropods, and they constitute the underlying basis for the characteristic subdivision of the body into pre-oral, oral, thoracic, vagus, abdominal, and caudal regions. We shall call them the procephalon, dicephalon, mesocephalon, metacephalon, and branchiocephalon. Each region usually consists of a certain number of metameres, modified, or specialized, in a very constant and definite manner in respect to its sense organs, nerves, and other characters. In the higher arachnids they unite in various ways to form larger aggregates, such as the cephalo-thoracic-branchial region. In the vertebrates they have become still more compactly united to form the head, the subdivisions of which still consist, as nearly as may be determined, of the same number of metameres, modified in the same characteristic manner as the corresponding subdivisions of the arthropod trunk and cephalothorax. (Figs. 1, 3 and 5.)

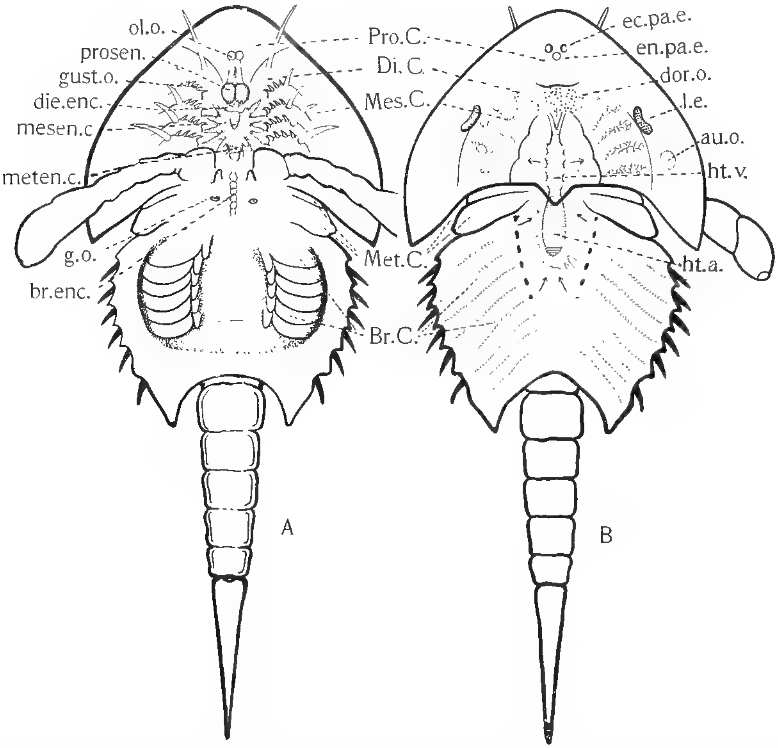


FIG. 1.—Plan of a marine arachnid, based in part on Limulus. Designed to show the principal body regions and their characteristic organs. *A*, Neural, or oral surface; *B*, hæmal, or cardiac surface.

B. Embryology.—We shall show that arachnid and vertebrate embryos, from the very beginning of their development, are fundamentally alike in structure and mode of growth, and that this likeness is continued through successive, parallel stages, up to a point where the arachnid stages cease; then the vertebrate embryo, entering on its particular phases of development, carries them to completion. We shall show that the similarity between them consists: *a.* in the origin of the germ layers; *b.* in the general form and segmentation of the neural plate, its flexures, mode of enclosure, and the location of its principal parts; *c.*

in the serial location and subsequent migrations of the primary cephalic sense organs (median and lateral eyes, olfactory, and auditory organs); *d.* in the degree of development of the cephalic mesoblast, and in the direction and extent of its growth in the several regions; *e.* in the development of the heart; *f.* in the concrescence of the so-called "lips of the blastopore," and in the growth of the margins of the embryonic area ("germ wall"); *g.* in the formation of the head fold.

C. Arachnid Cephalogenesis Prophetic of the Vertebrate Head.—We shall show that the continuation, or the exaggeration, of the processes already initiated in the arachnids inevitably leads to the establishment of the conditions now seen in the vertebrates. For example: *a.* The further withdrawal of the principal alimentary and urogenital organs of the arachnids into the postcephalic regions, would produce the condition in vertebrates. *b.* The continued enlargement and closer union of the thoracic neuromeres, and their more precocious development during embryonic periods, aided possibly by the further overgrowth of the labrum and optic ganglia, would lead to a further narrowing, and overgrowth of the passage for the esophagus, and ultimately to the permanent closure of the old mouth, as in vertebrates. *c.* The continued increase in the size of the yolk sphere, the absence of mesodermic structures on the hæmal side of the tho-

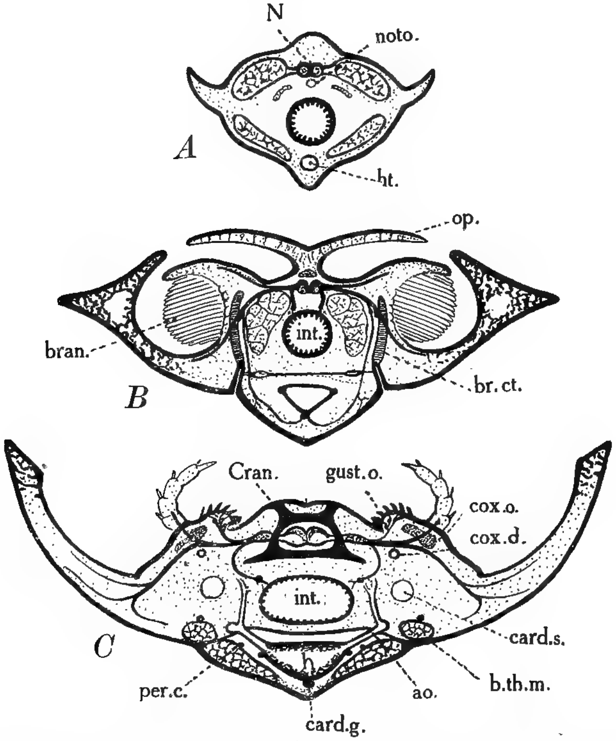


FIG. 2.—Semi-schematic cross-sections of a marine arachnid, showing location of principal organs. *A*, abdominal region; *B*, branchial region; *C*, mesocephalic, or thoracic region.

racic and cephalic region, and the increasingly precocious development of the forebrain, would inevitably lead to the formation of a more pronounced head fold, with a disproportionately shortened or diminished hæmal surface, and would force the bases of the more anterior oral appendages forward and hæmally till they meet on the opposite side of the head, thus giving rise to the premaxillary, maxillary, and mandibular arches of the vertebrate head. *d.* This shortening of the anterior hæmal surface of the head inevitably draws the heart, with its neighboring muscles and nerves derived from the vagal and branchial segments, farther forward into the head region, thus producing that remarkable forward dislocation of the heart, hypobranchial muscles and nerves so familiar in vertebrates. (Figs. 17, 19, 33, 77.) *e.* Finally the readjustment of the whole head, in response to these changes, leads to that new condition of architectural stability that marks the true vertebrates.

The preliminary stages that lead up to these readjustments were, no doubt, gradual and more or less tentative, for they did not in themselves create sufficiently altered conditions to upset the balance of organic power. But the later stages of the readjustment, especially the final stages in the transfer of the oral arches to the hæmal side, appear to have been rapidly accelerated for a period and then checked by their approaching reunion on the hæmal side of the head and by the creation there of a new condition of organic stability.

The closing of the old mouth, the formation of a new one, the transfer of the oral arches to the hæmal side, and the appearance of true gill clefts must have taken place during the embryonic, or larval period, the increasing volume of the yolk sphere making such a cataclysmic metamorphosis possible. Hence it is probable that the transition from the arthropod to the vertebrate type will never be completely bridged by the discovery of new animals. The gap between the two classes is a real one, representing a comparatively short period of rapid transformation from the old condition in the arthropods to a new, approximately stable condition in the vertebrates.

D. Paleontology.—Nevertheless, we shall show that the wide gulf which now separates the arachnids and vertebrates, in some important respects, was bridged in early paleozoic times by a large and varied class of animals known as the ostracoderms. They constitute the only great class of animals that have flourished for a comparatively short period and then become totally extinct; a fact that in itself testifies to the unstable, transitory character of their anatomical structure.

Heretofore it has been assumed that the ostracoderms were highly specialized vertebrates, in spite of the fact that they possessed a very simple and primitive structure, and were the first vertebrate-like animals to appear on the geological horizon. They were contemporaneous with the highest and most dominant type of arthropods then in existence, the marine arachnids, or sea scorpions, of the Silurian period. There is a striking resemblance between these early vertebrates and the contemporaneous arachnids, not only in their form and general appearance, but in the minute structure of their exoskeleton, the character of their appendages, the arrangement of their median ocelli, and in the structure of their jaws. (Figs. 232 to 265.) For a long time the ostracoderms were supposed to be jawless fishes, but a special investigation of this point was made and it was demonstrated that Bothriolepis, the best known member of the class, possesses well developed maxillæ and mandibles, quite unlike those of typical vertebrates, but precisely like those demanded by the arachnid theory.

Thus, in the light of the arachnid theory, these ancient and remarkable animals, that have been repeatedly mistaken for arthropods and for vertebrates, but which are neither wholly; which have withstood the keen scrutiny of Agassiz, Huxley, Ray Lankester, and Smith Woodward, take on a new meaning. We can now clearly see that they belong neither to the vertebrates nor to the invertebrates, but form a class by themselves, intermediate between the two; presenting on the one hand, in their appendages, jaws, eyes, skeleton and gills, affinities with the marine arachnids, and on the other, in their tail, dermal skeleton, and dorsal fins, affinities with true vertebrates.

III. The Process of Cephalization in the Arthropods.

If we trace the evolution of cephalization in the arthropods and analyze the causes that have brought it about, we shall see that it reaches its highest expression in the arachnids and that it was brought about by the same kind of changes that have taken place in the vertebrates.

* * * * * * * * *

A. The Grouping and the Increase in Number of Metameres.—The dominant process in the evolution of the arthropods is the spasmodic generation of new groups of terminal metameres, the gradual specialization of each group, and its more intimate union with the older, more anterior members of the series. The increase in the total number of metameres, from the first three that are characteristic of the nauplius, to the seven found in the ostracods, eleven in the cladocera, and the twenty-one or -two so commonly present in the higher forms, goes hand and hand with the specialization and union of the more anterior groups into an increasingly complex organic unit that in the vertebrate sense may be properly called a "head."

While this process, in a variable degree, occurs in all arthropods, it is only in the arachnids that it takes place in the particular manner that is characteristic of vertebrates. In the more typical representatives of that class, the first fifteen or sixteen metameres are divided into unlike groups that have a similar sequence, consist of a similar number of metameres, and present a similar morphological and physiological specialization of organs to that seen in the corresponding regions of the vertebrate head.

It is evident, therefore, that the ancestral history of the vertebrate head is contained in the first fifteen or sixteen arachnid metameres, and that in the arachnids we may study this process of cephalization in detail. At one end of the body we may observe the birth of new, independent metameres, and at the other the gradual

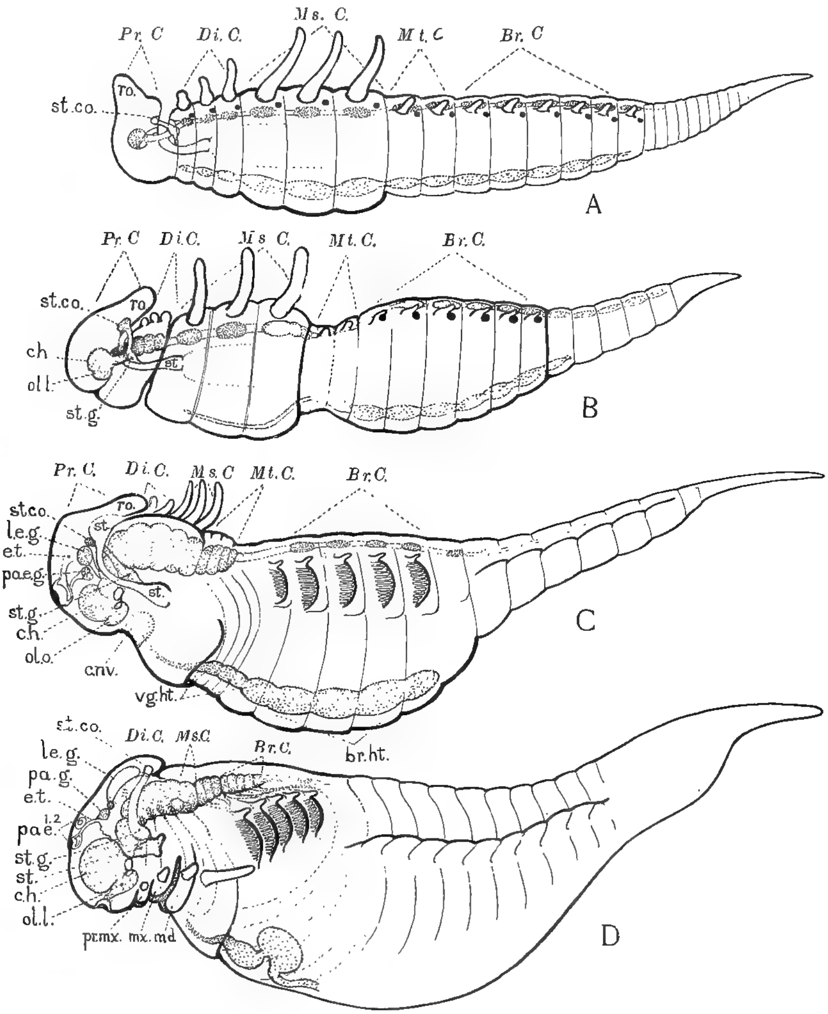


FIG. 3.—Diagrams showing the five characteristic body regions of arthropods, and their progressive concentration to form the head of a vertebrate. The principal points illustrated are: *a*, The early location of the principal functions; *b*, the concentration of the cardiomeres in the branchial region; *c*, the enlargement and concentration of the anterior cephalic neuromeres; *d*, the change in position of the optic ganglia and oral arches; *e*, the closure of the old mouth and the formation of the new one; *f*, the transfer of locomotor organs from the mesocephalon to the postbranchial metameres. *A* and *B*, Insect; *C*, arachnid; *D*, vertebrate.

decline of metamerism, and the incorporation of the old metameres, as specialized subordinate parts, into a new and more highly organized unit.

* * * * * * * * *

B. Origin of the Linear Arrangement of Unlike Cephalic Functions.—It is frequently assumed that the primitive vertebrate head consisted of a considerable number of like metameres, each one complete in itself, that is, having all the organs of an ideal metamere. This assumption is untenable. A considerable number of cephalic, or anterior metameres, even approximately complete or perfect, rarely, if ever, occur in any animal outside those pictured in text-book diagrams. It is certain that no such condition occurs in the arachnids. While it may be assumed that metameric growth tends to produce a linear series of like parts, it is clear that it does not do so in reality. The first products of apical growth must necessarily differ from the last, because different conditions are created by apical growth at each successive stage of its progress. The actual result, therefore, is a linear sequence of *unlike* structures and functions for a given number or generation of metameres. This particular sequence becomes unbalanced and remodelled with the appearance of the next generation. But on the whole a definite linear succession of unlike organs becomes established at a very early period in the evolution of segmented animals; and it follows a logical, inherently necessary order, that is never completely lost or disguised.

With the elongation and increase in size of the primitive trunk the ingestive, gustatory, locomotor, cardiac, and respiratory functions become more localized, their position being determined, in part, by the necessary conditions for their activities, and in part by the historic order in which they became established; for the location of any new function is limited to the territory that is not already pre-empted by other organs. For that reason we find that the most essential organs are the first to develop, and they arise from the oldest parts of the body, that is, from the more anterior and median neural surface; the organs of more recent origin arise on the hæmal and caudal sides of the older ones.

The primary sense organs, *i.e.*, the parietal and lateral eyes, the olfactory organs, and the coordinating centers (forebrain) are already definitely located in the procephalon of the nauplius, which probably represents, in part, the remnants of a trochosphere. These organs are, therefore, of very great antiquity. They retain their original position throughout the entire range of the arthropod-vertebrate phylum, and by the root-like extension of their nerve fibers establish relations with the new metameres as fast as they are formed.

Hence the primary sense organs and the primary coordinating centers are located at the anterior end of the body, not, as is frequently asserted, because the body moves head first, or because of any necessary correlation between the location of the brain and sense organs (Parker), but because the head is the oldest part of the animal, and because these particular sense organs and nerve centers were, in a historic sense, the first ones to be definitely established, taking their origin back to a period when the primitive head was the whole body.

With the appearance of the first postcephalic metameres, arose the first gustatory organs, and the first swimming, grasping, crushing, and chewing appendages. They were necessarily located immediately behind the primitive head, in the oral region. With the addition of another generation of metameres, the body became heavier and larger, and the appendages on the new metameres were used as supplementary swimming, or respiratory appendages, or for crawling or walking, and the circulatory organs appeared in the hæmal region. (Fig. 308.)

The internal organs, such as the stomach, digestive glands, gut pouches, organs of excretion and generation, establish their relations to the rest of the body, if at all, through the circulation. They are less dependent on location, or on specialization in form, for effective action, hence they are eventually crowded into the more posterior metameres, or they atrophy and new ones arise farther back to take their places. (Figs. 307, 308.)

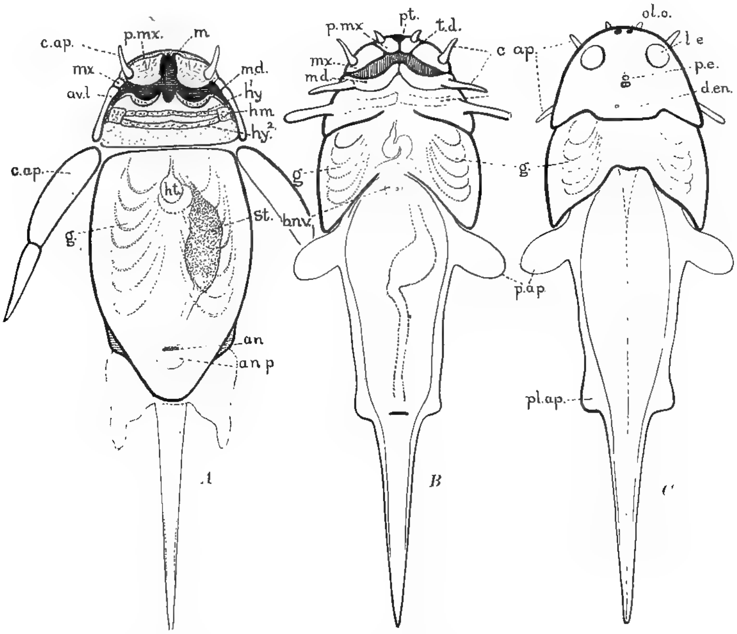


FIG. 4.—Diagrams showing location of principal organs in Bothriolepis and a primitive vertebrate. *A*, *B*, Hæmal; view; *C*, neural view. *A*, Bothriolepis; *B*, *C*, primitive vertebrate.

In the typical arachnids, a definite linear arrangement of unlike functions, in accordance with the above principles, is established at an early period. The order is essentially the same as that in the vertebrate head, and is as follows: olfactory, coordinating, visual, swallowing, gustatory, auditory, locomotor, equilibratory, cardiac, and respiratory. (Figs. 5, 57 and 114.)

In the posterior cephalic regions, the digestive, excretory, and genital organs are closely associated with, or overlap, the branchial and cardiac organs, this arrangement forming a conspicuous feature in the arachnids. It appears to be retained, to a large extent, in Bothriolepis and other ostracoderms. (Fig. 5.) In the vertebrates, this arrangement is further modified by the atrophy of the prebranchial locomotor appendages, by the formation of new ones behind the gills, and by the gradual transfer of the digestive and urinogenital system still farther back into the newly developing trunk.

We need not follow in detail the further progress of these changes in the higher vertebrates; the atrophy of the gills and the development of the lungs behind them; the atrophy of head kidneys, and the development of new ones farther, and then again farther back; and the final shifting of locomotor functions to the pelvic appendages, are all familiar manifestations of the same process.

Thus the evolution of the arthropod-vertebrate stock consists: 1. in the successive generation of groups of like metameres, each group being from the beginning somewhat different from the preceding one; 2. in the subsequent enlargement, diminution, or elimination of segmental organs and the consequent readjustments that follow these changes; the result always leading toward a more successful linear coordination of unlike organs, the process attaining its highest expression in man. Hence, broadly speaking, the progress of organic evolution in segmented animals may be measured by the extent to which the linear coordination of unlike organs replaces the linear succession of like metameres.

IV. The Subdivisions of The Incipient Vertebrate Head in The Arachnids.

The five main divisions of the anterior part of the body in the arachnids are as follows: (Figs. 3, 5, 14–21.) 1. The *procephalon*, or primitive head, consists of three pre-oral segments, the principal organs contained in it being the rostrum, olfactory lobes, cerebral hemispheres, the visual and the olfactory organs. 2. The *dicephalon* consists of two or three metameres immediately surrounding the mouth, and includes the stomodæum with its appropriate nerve centers, the leg-jaws, principal gustatory organs, and the anterior part of the endocranium. 3. The *mesocephalon* consists of three or four posterior thoracic metameres and includes the principal locomotor appendages, auditory and excretory organs, and the posterior part of the endocranium. 4. The *metacephalon*, or vagus region, consists of from two to four greatly modified metameres, the appendages being either very small and standing close to the median line, or absent, or converted into sense organs. The neuromeres and their ganglia are large, but very compact. Other components of the metameres are absent, or small and degenerate. The whole region forms a highly specialized, constricted intermediate zone lying between the mesocephalon and the next following division. 5. The *branchiocephalon* consists of four or five metameres, in which are located the principal respiratory organs, branchial cartilages, and the heart.

The Brain.—The structure and grouping of the neuromeres reflect the conditions characteristic of these subdivisions of the body, thus laying the foundations for the subdivisions of the brain in vertebrates. In the latter, the original appearance of the arachnid brain is modified by the closure of the old mouth, and by the location of the optic ganglia over the diencephalic and mesencephalic neuromeres, instead of over the prosencephalic ones, to which they really belong. (Figs. 46, 47, 57 and 58.)

The Mesoderm. (Fig. 138, *A* and *B*).—The procephalic mesoderm is scanty and in the early embryonic stages forms a single, thin-walled cœlomic chamber. In the dicephalon and mesocephalon, six pairs of cœlomic chambers are formed, constituting true somites, or head cavities; but segmented lateral plates are conspicuously absent. In the metacephalon and branchiocephalon, distinct somites and lateral plates are developed in each metamere.

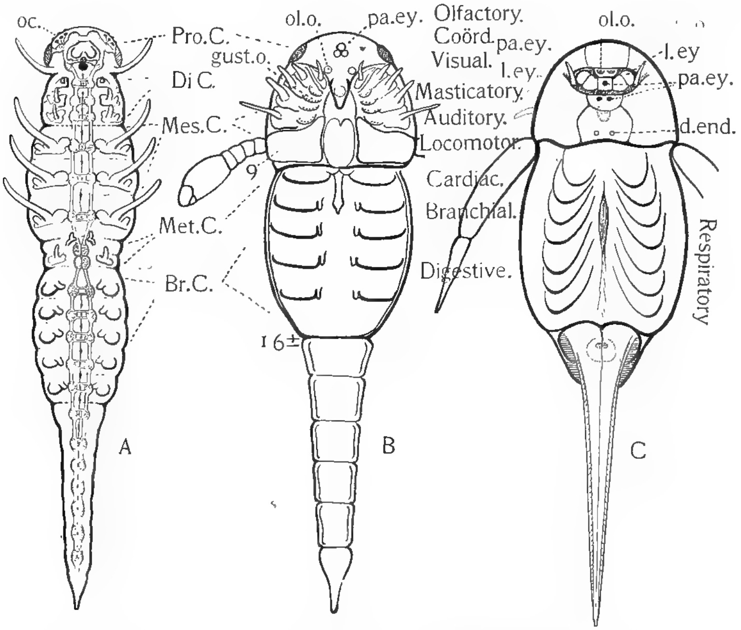


FIG. 5.—Diagrams showing the probable relations between the subdivisions of the head and trunk, and the location of the principal organs in an insect, merostome and ostracoderm (Bothriolepis) seen from the neural side.

The Middlecord, or *lemmatochord* (notochord of vertebrates), extends through the posterior sections of the head. In the older stages it may terminate in an enlargement in the mesocephalon, but it never extends beyond the dicephalon, ending abruptly just behind the stomodæum (infundibulum).

Let us examine these subdivisions of the future head more carefully.

1. The Procephalon.

The procephalon is the primitive head. In the adult arachnids, it is, externally, an irregular, ill defined area of ectoderm within which lie the rostrum, and the primitive visual and olfactory organs. (Figs. 149–155, *p.c.*) In the early embryonic stages, it is represented by the procephalic lobes, from which the forebrain with its olfactory lobes, hemispheres, and its appropriate sense organs are derived. (Figs. 14–21.) The structure of the procephalic lobes, their main divisions, and the relations of the three sets of primary sense organs to them, are practically identical throughout the arthropod series. In the higher arachnids, their structure and mode of development, and that of their associated sense organs, resembles that of the vertebrates.

In Insects (Acilius), the procephalic lobes consist of three segments, each one containing a neuromere, an optic ganglion, a segment of the marginal plate, and two pairs of segmental sense organs, or ocelli. (Fig. 14.) Three infoldings occur on the margins of the lobes, between the optic plate and the optic ganglia, iv$^{1-3}$, but they soon close without involving the marginal sense organs, and without forming a common cerebral vesicle.

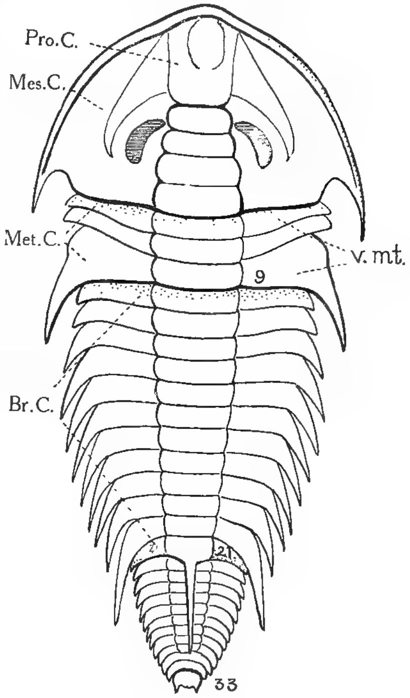


FIG. 6.—Mesonacis (Olenellus) vermontana (Hall!). Lower Cambrian, showing body regions, and groups of like metameres, or tagmata.

In the Arachnids (scorpion), the lobes are at first similar to those of Acilius; later they are depressed, and a thin marginal fold, or neural crest, advances over them, converting the entire forebrain into a hollow vesicle that for a long time opens to the exterior through an anterior neuropore. (Figs. 15, 16, 18, 46, 47, *an.p.* and *eph.*)

Sense Organs.—Meantime the anterior pair of marginal sense organs move forward and unite in the median line to form the anlage of the olfactory organ (Limulus). (Figs. 38, 39, 141, 142, 153, *ol.o.*) The two pairs of sense organs on the second segment (ocellar placodes, parietal eyes) are ingulfed in the palial overgrowth and carried to the middle of the roof of the forebrain vesicle. Here a tubular outgrowth is formed, on the end of which the ocellar placodes are located, after the manner of a typical parietal eye. (Figs. 46, 47, 57, 141, 142, *pa.e.*) In the arachnids, the sense organs of the third segment (lateral eye) lie for a time on the outer margin of the neural crests, but later they move away from them, so they are not ingulfed in the palial overgrowth. (Fig. 16, *A.l. e.*) The lateral eyes of insects, crustaceans, and arachnids appear to belong to the fourth neuromere (antennal or cheliceral), that is, to the first metamere of the next division of the head.

Olfactory Lobes, Hemispheres and Optic Ganglia.—During the formation of the palial overgrowth, the first forebrain segment becomes deeply infolded to form the olfactory lobes. The cerebral hemispheres arise from the median part of the second segment, the optic ganglia of the parietal eye (ganglion habenula), from the lateral margin of the second segment, and the ganglion of the lateral eyes (tectum opticum), from the lateral lobes of the third or fourth segment. (Figs. 15, 46, 47, *ol.l.*)

The Rostrum (labrum) in insects arises as a pair of small cephalic appendages, on the very anterior median margin of the cephalic lobes. (Fig. 14.) In the arachnids it forms an unpaired, immovable process, which in the later stages lies on the anterior margin of the mouth. (Figs. 15, 17, 18, 43, 47.) It differs from all other arthropod appendages, in that it receives its nerves from ganglia situated on the *median* side of each nerve cord, that is, from the stomodæal ganglia and commissure, which are situated near the fourth, or first post-oral, segment. (Figs. 38 and 39, *st.g.*)

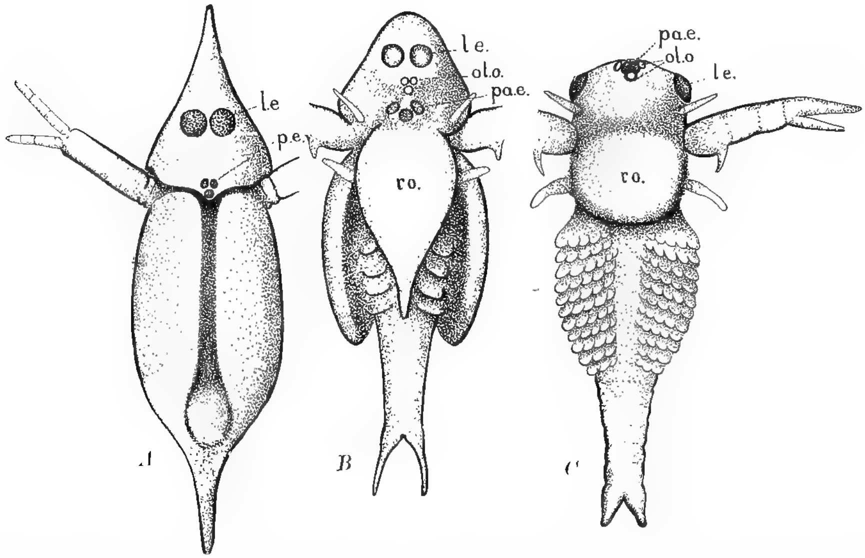


FIG. 7.—Primitive crustacea seen from the neural surface, showing various arrangements of the procephalic sense organs. *A*, Sida; *B*, Limnadia larva; *C*, Branchipus larva.

External Boundaries of the Procephalon in the Adult.—The margins of the ectodermic area covering the outer surface of the forebrain, after the palial overgrowth is formed, mark the boundaries of the primitive head. The latter becomes greatly distorted by the forebrain flexure, which carries the anterior part of the forebrain round the end of the egg onto the future hæmal surface, while the posterior part is drawn a long way backward by the caudad migration of the mouth and rostrum. (Figs. 3, 17, 43, 44, 46.) It thus happens that the neural surface of the procephalon is the only one that is actually developed. The hæmal surface is not formed from procephalic tissue, but by the extension of the lateral and anterior margins of the procephalic lobes around the anterior end of the ovum, and by their union there with the hæmal end of the first thoracic metameres. (Fig. 17.)

In this way the original area of the procephalic ectoderm has been greatly extended. In the adult Limulus, it is divided into two isolated parts: that which has been carried onto the hæmal surface of the carapace, and that which remains on the neural surface. (Figs. 141–155.) The latter portion may be approximately defined as an elongated area, with the olfactory organ at its anterior end and the apex of the rostrum at its posterior end; it is drawn out laterally by the migration of the lateral eyes toward the posterior hæmal surface. (Fig. 153, *pr.c.*)

In the scorpion, there is a neural and hæmal section of the procephalon, as in Limulus. (Comp. Figs. 16, 17, 18, 43.) The original neural surface of the embryonic procephalon has been doubled over in the adult so that its anterior edge lies on the hæmal surface, directed backward instead of forward. (Figs. 17, 22.)

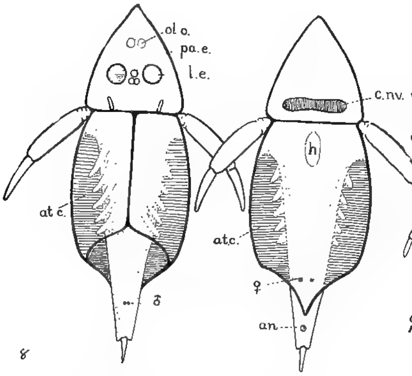


FIG. 8.—Primitive crustaceans (Cladocera). *A*, Neural surface; *B*, hæmal.

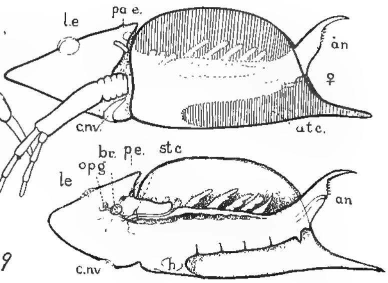


FIG. 9.—Same in side view and in median section.

It is important to bear these facts in mind, since where these changes have taken place, the linear arrangement of the segmental sense organs appears to be the reverse of what it is when the procephalon remains largely on the neural surface, as it does in many phyllopods and vertebrates. (Figs. 7, 8, 9, 34.)

2–3. The Dicephalon and the Mesocephalon.

The dicephalon and the mesocephalon include the first six or seven post-oral metameres, frequently spoken of as the thorax. It is generally divided into two regions. The anterior one, the dicephalon, consists of two or three circum-oral metameres whose appendages may be smaller than the others, and specially modified to serve as leg-jaws for testing, holding, tearing, or crushing food, and conveying it to the mouth. It includes the stomodæum and the stomodæal ganglia, the latter being intimately associated with the gustatory and swallowing reflexes. The posterior division, or mesocephalon, comprises three or four well-developed metameres whose appendages serve for walking or swimming.

In the insects, the first four metameres fuse with each other, and with the procephalon, to form the so-called "head," the last three metameres usually remaining separate. (Figs. 3,*A*, 5,*A*.)

In phyllopods (Branchipus) the first two metameres, and possibly an evanescent third, or premandibular, fuse with each other and with the procephalon. The remaining three metameres, the mandibular and two maxillary, fuse with each other, forming a group by themselves distinct from the anterior division.

In arachnids, such as the scorpions, spiders, trilobites, and merostomes, all six thoracic metameres unite with one another and with the procephalon to form the cephalothorax, leaving on the hæmal side little or no indication of the larger divisions, or of the more primitive division into metameres.

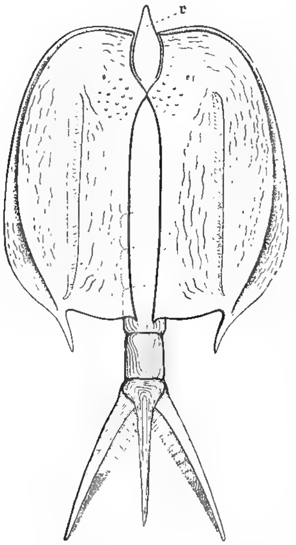


FIG. 10.—Mesothyra (after Hall and Clark). Upper Devonian.

On the neural side, the metameric structure is always retained. The reduction in size, and the modification of the first two or three pairs of appendages for feeding purposes, are usually clearly indicated, the last three or four pairs serving mainly for locomotion.

In Limulus, the subdivision of the thorax into an anterior and a posterior division at first sight does not appear to exist; but I have shown that in abnormal embryos the first two or three thoracic metameres act as a unit, in that they frequently separate from the posterior ones opposite the large thoracic sense organs, or they fuse with each other, or disappear entirely, or otherwise manifest a distinct independence in their development. The large thoracic placodes, the forerunners of the auditory placodes of vertebrates, mark this latent cleavage line between the group of oral metameres of the diacephalon, and those belonging to the mesocephalon. (Figs. 141, 142, 184–188.)

The endocranium arose primarily in association with the dicephalic metameres, but in the higher forms takes its origin from the mesocephalic metameres also. With the concentration of all the cranial neuromeres, the endocranium embraces, or underlies all of them except the more posterior ones of the branchiocephalon.

* * * * * * * * *

Oral Arches.—The basal joints of the thoracic appendages, especially in the arachnids, are greatly expanded where they join the body, forming oblong arches to which the slender, more movable part of the appendage is attached. In the arachnids, these basal arches may be located some distance from the median line, on the lateral wall of the head. At least four or five of these anterior thoracic arches persist as the circumoral, visceral arches of vertebrates, that is, as the pre-maxillary, maxillary, mandibular, and hyoid arches, and possibly the first gill arch. (Figs. 32–34, 160–172.)

* * * * * * * * *

Taste Buds, Slime Buds, and Cranial Ganglia.—In the typical appendicular arches of arachnids, there is a lobe on the median or neural side that forms the mandibular or coxal spurs, and in which are located important groups of sense organs, *i.e.*, gustatory buds and slime buds. They are the forerunners of the "epibranchial organs," "lateral line organs," and "gustatory organs" of vertebrates. At an early embryonic period, in the wide zone between the nerve cord and the coxal and gustatory spurs, and in close connection with the latter, immense oblong ganglia (pedal ganglia) are developed from thickenings of the overlying ectoderm. (Figs. 36–39, 134–137.) These ganglia arise independently of the medullary plates. Later, they unite the proximal end of the pedal nerve with the corresponding neuromere. They are the forerunners of the cranial ganglia of vertebrates.

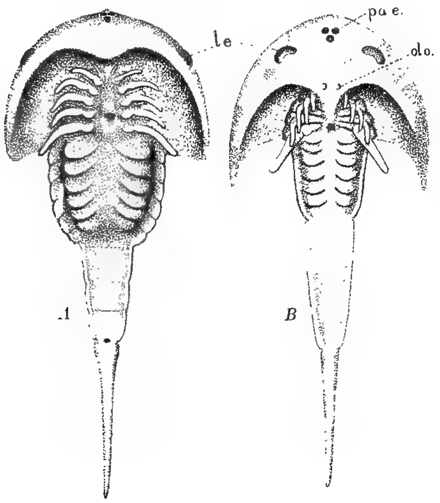


FIG. 11.

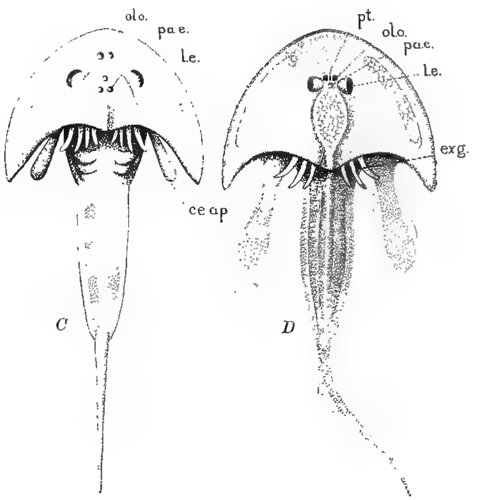


FIG. 12.

FIG. 11.—Diagrams of marine arachnids, to illustrate the relations of their organs to those in the ostracoderms.

FIG. 12.—*C*, hypothetical form, intermediate between a merostome and an ostracoderm (Cephalaspis); *D*, is an accurate restoration of a small cephalaspid (sp. nov. ?) from Scaumenac Bay, P. Q., except the external gill, *ex. g.* which are hypothetical.

Segmental Sense Organs.—In the scorpion, each appendicular arch, except the first, has, on its lateral margin, close to the base of the coxa, two sensory cups, in form and in minute structure very similar to the conspicuous pits on the outer surface of the neuromeres. (Figs. 15–16, 74, *s.so.*) All these pits quickly lose their sensory character and later apparently disappear or are converted into ganglion cells.

Similar segmental sense organs are seen in Limulus, but farther removed from the bases of the appendages. The one that develops into the so-called "dorsal organ" (auditory pit of vertebrates) lies opposite the fourth appendage. (Figs. 140–153, *s.o.*^{4}) Later it becomes greatly enlarged and is a conspicuous feature on the hæmal margin of the thorax till after the last moult of the trilobite stage. At the height of its development, it is a disc-shaped thickening, slightly pigmented and sensory in appearance. (Fig. 131.) The four remaining pits (Fig. 140) are very faint and transitory, although in the corresponding regions of the adult, there are patches, or knobs of skin that are highly sensitive and richly supplied with nerves. The thoracic segmental sense organs of Limulus and the scorpion lie nearly in line with the cephalic sense organs, and are probably serially homologous with them.

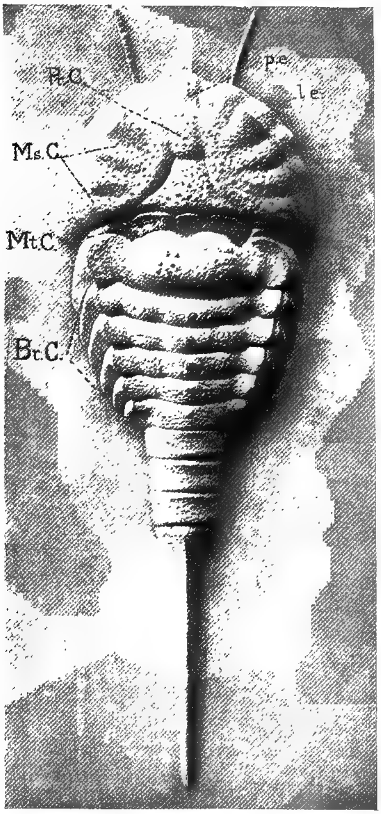


Fig. 13.—Bunodes lunula. Restoration from numerous specimen in the author's collection obtained from the island of Oesel, Russia. Photograph of enlarged plaster model by the author. × about 2.

* * * * *

The Diencephalon and the Mesencephalon.—We may recognize two groups of thoracic neuromeres, the diencephalon and mesencephalon, approximately corresponding with the external divisions of the thorax.

The diencephalon, or tween-brain, consists of the first one, or two or three, neuromeres that surround the oesophagus.

It includes the large, lateral stomodæal ganglia that are attached to the median wall of the cheliceral neuromere, but which arise as thickenings, or evaginations, from the side walls of the œsophagus. These neuromeres contain the swallowing center and an important center for all the taste organs of the more posterior thoracic appendages. (Fig. 114.)

The enlargement and closer union of the thoracic neuromeres, and the backward overgrowth of the rostrum and the optic ganglia, ultimately lead to the closure of the mouth. After it closes, the inner end of the stomodæum persists in vertebrates as the epithelium of the saccus vasculosus, the passageway between the circum-oesophageal neuromeres becomes the infundibulum, and the stomodæal ganglia, arising from its deeper side walls, the lobi inferiori. (Figs. 43 and 44.) The last position occupied by the arachnid mouth may be identified in vertebrates, as the opening behind the cerebellum, now closed by the choroid plexus of the fourth ventricle. (Figs. 3, 43, 44, 46, 58.)

The mesencephalon consists of the last three or four thoracic neuromeres; they are usually conspicuous for their distinctness, great breadth and volume, and for the large size of their ganglia. In the vertebrates, they form the posterior portion of the crura cerebri, and are still further accentuated as one of the principal divisions of the brain, by the migration of the optic ganglia of the lateral eyes backward and upward till they come to overlie them as the tectum opticum. The parietal eye ganglia overlie the diencephalon as the ganglia habenulæ. (Figs. 43, 44, 57, 58.)

The Suprastomodæal Commissure and the Cerebellum.—In all arthropods, the lateral stomodæal ganglia are united by a large commissure that forms a prominent arch over the anterior or neural surface of the stomodæum. This commissure is one of the most conspicuous and constant landmarks in the arthropod brain. (Fig. 3, *st.co.*) In the insects, it contains a large, median mass of ganglion cells, arising as an evagination, or as a thickening, in the anterior, median wall of the stomodæum, close to its external opening. (Fig. 3, *a.*) The projecting arch of the commissure becomes crowded backward by the backward migration of the mouth and rostrum, and by the increasing size of the lateral eye ganglia, forming in vertebrates the rudiment of the cerebellum. (Figs. 3, *D*, and 46.)

Thus the median stomodæal ganglion of arthropods and the cerebellum of vertebrates are the only brain structures that may be said to arise originally in the median line above the neural surface of the brain; the parietal eyes, the ganglia habenulæ, and the optic lobes being originally paired structures arising from the lateral margins of the medullary plate.

4. The Metacephalon, or Vagus Region.

The metacephalon, or vagus region, forms a remarkable intermediate zone between the mesocephalon and the branchiocephalon. It consists of from one to four metameres that usually atrophy, or fuse with one another at an early period, leaving little or no external trace of their existence in the adult. Their feeble development is the principal cause of the sharp constriction which, in many insects and arachnids, separates the thorax from the abdomen. (Figs. 3, 6, 14, 15, 16, 46, 47, 57, *M. c.* or $vg.^{1-4}$.)

The vagus appendages rarely serve as locomotor or respiratory organs. They show a marked tendency to become unpaired; they may dwindle into insignificance, or they may be retained as highly specialized sense organs (chilaria and metastoma of merostomes; genital papillæ and pectens of scorpions).

The vagus neuromeres, on the other hand, are well-developed, but they fuse with one another so quickly that it is very difficult to distinguish their boundaries after the early embryonic stages. Their motor elements are greatly reduced and the sensory ones correspondingly enlarged, owing to the reduction of the corresponding trunk muscles and the absence of appendages, or their conversion into sense organs. In them is located an important decussation of the longitudinal tracts passing from the cord to the brain, and *vice versa*; and the vagus neuromeres are the most anterior ones in which such a crossing takes place. (Figs. 65, 66, 114, *v.dec.*)

The vagus nerves have special relations with the heart, intestine, and integument. They are the only segmental nerves that are persistently directed backward into foreign territory, a result that is due in part to the forward concentration of the vagus neuromeres, and in part to the backward growth of the nerves and the atrophy of their native metameres. (Figs. 38, 42, 57, 70, 71.)

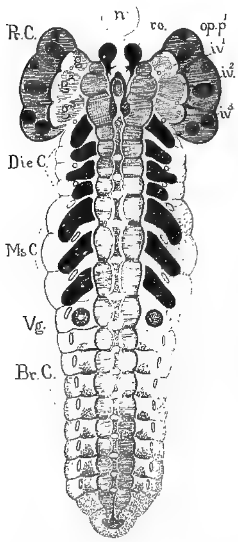


FIG. 14.—Diagram of an insect embryo (Acilius) in mercator projection.

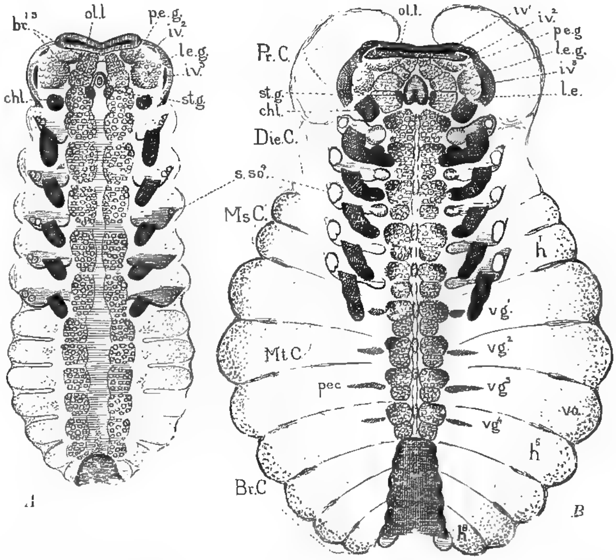


FIG. 15.—Scorpion embryos in mercator projection.

The interpolation of the vagus neuromeres between the mesencephalon and the branchiencephalon is a very important and striking feature in the morphology of the arachnids. They form a compact group, or distinct brain region, which in its anatomical and physiological characters, and in the distribution of its nerves, is very similar to the vagus region of vertebrates.

5. The Branchiocephalon.

This group of metameres, four or five in number, is the least specialized of any so far considered. The appendages may be well-developed (Limulus and many crustacea) or they may be rudimentary. In the higher forms, this region is chiefly notable as the site of the respiratory organs, *i.e.*, the tracheæ, gills, lung-books, and heart. (Fig. 3, *br.c.*)

The mesoderm is complete, each metamere containing well developed somites and lateral plates. (Figs. 16, 142.) The most characteristic organs found in these metameres, such as the cartilaginous branchial bars and the segments of the heart, arise from the mesoderm.

The neuromeres usually remain separate, but there is a tendency for the anterior ones to move forward and join the vagus group. In vertebrates, the entire group has joined the vagus neuromeres, forming the most posterior part of the medulla. (Fig. 58.)

Nerves.—In the arachnids, the great complex of vagus and branchial nerves has already made notable progress in that separation of components from the primary segmental nerves, and in their regrouping into compound nerves whose constituent parts have a common function, that is so characteristic of vertebrates.

We may recognize, for example, the beginning of the lateral line nerve in the combined sensory components of the first three vagal appendages of the scorpion. In Limulus, the primitive condition of the vertebrate cardiac nerves is seen in the eight pairs of segmental cardiac nerves that arise from the vagal and branchial neuromeres. (Figs. 59, 78, c^{7-14}.) The visceral arch nerves are represented by the branchial nerves, and the hypoglossal, by the combined group of motor components that supply the great, branchio-thoracic muscles. (Fig. 77.) The intestinal nerves are also indicated; i^{1-10}.

It is only necessary to unite the vagal and branchial neuromeres into a more compact mass, and to complete the union of the sensory, branchial, hypobranchial, cardiac, and intestinal components into compound nerves, to realize the characteristic condition so familiar in vertebrates. (Compare Figs. 57 and 58.)

It will be observed that the similarity exists, not only in the union of the originally separate components into the same physiological groups, but that the number of neuromeres and components is approximately the same; that their topographical position is the same; and that the general course and distribution of the resulting nerves is the same.

The Endocranium.

All the higher arachnids are provided with a cartilaginous endocranium that is the forerunner of the primordial cranium of vertebrates. It may be traced back to such primitive arthropods as Branchipus, Apus, and other phyllopods. In Branchipus, it is a small plate of cartilage, lying on the hæmal side of the mesencephalon, and serving for the attachment of the mandibular muscles.

In the higher arachnids, it is more voluminous, serving mainly for the attachment of the leg and jaw muscles, and for the great longitudinal muscles that move the cephalothorax on the branchial section of the body. Its structure is similar to that of the primordial cranium of vertebrates, and it has the same topographical relation to the brain and to the alimentary canal. The rudiments of the following parts may be recognized: occipital ring, trabeculæ, pituitary foramen, and palato-pterygoid arch. (Figs. 209–220.)

The Mesoderm.

Origin of the mesoderm. To understand the peculiarities of the cephalic mesoderm, we must consider its origin as a whole.

In Limulus, the mesoderm arises in part from the telopore, a shallow, terminal depression overlying a confused mass of proliferating nuclei destined to form mesoderm, yolk cells, and endoderm. (Figs. 128 and 140.)

As the embryo elongates, the depression maintains its terminal position, changing to a longitudinal groove, and finally taking the form of a typical primitive streak. (Figs. 129, 130, 140, *t.p.*). From the primitive streak, a sheet of mesoderm extends forward and laterally, finally breaking up into somites and lateral plates.

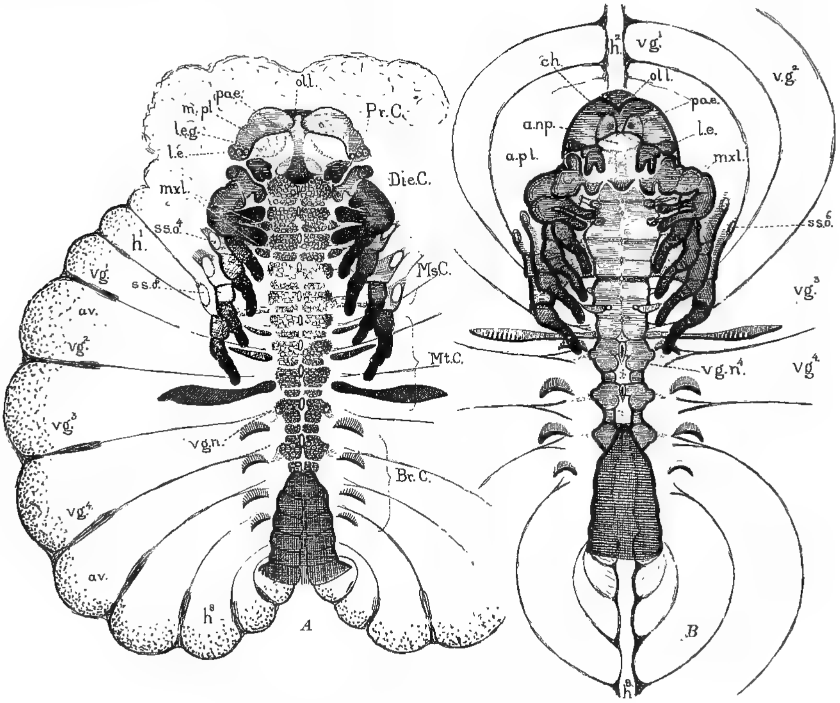


Fig. 16.—Scorpion embryos in mercator projection.

In the abdominal, or branchiocephalic and vagal regions, the somites are hollow, contain true cœlomic cavities, and are quite distinct from the overlying ectoderm. The corresponding lateral plates are sharply segmented, and they are united, for a short period, with the overlying ectoderm. They appear to be formed from the ectoderm by a local, inward proliferation, that takes place, not only in the region of the germ wall, but along the lines that mark the anterior and posterior boundaries of the lateral plates. (Fig. 128, *a.*)

On the peripheral margins of the expanding mesodermic area, no segmentation of any kind is visible. Ectoderm, mesoderm, and yolk cells form a common, thickened rim, or germ wall, similar in general appearance to the early stages of the primitive streak, and extending along the entire lateral margins of the germinal area. (Figs. 140–142.)

The post-oral mesoderm therefore arises from three distinct sources. The axial portion, consisting of the double line of mesoblastic somites, arises from the primitive streak; it represents the trail of mesoderm cells left behind as the teloblasts of the primitive streak migrate backward. The greater part of the lateral plate mesoderm is formed from the proliferating cells of the germ wall, as it spreads over the surface of the yolk in a lateral direction. But on the median side of the germ wall, the definitive ectoderm continues to proliferate inward for a considerable distance along the lines that separate the lateral plates. The cells thus produced form a part of the lateral plates, and the proliferating lines break the lateral sheet of mesoderm into distinct segments.

The dicephalic and mesocephalic (thoracic) mesoderm of arachnids presents a most important modification. It forms at first, a well defined band on either side of the nerve cord. Each band then becomes divided into distinct cœlomic chambers or somites; but segmented lateral plates are absent, the mesoderm of that region consisting of scattered cells that are not visible in surface views. (Figs. 15, 16, 19–21.) From the thoracic somites, or head cavities, arise the muscles of the appendages, the cartilaginous cranium, and the secreting cells of the coxal gland, or head kidney.

The procephalic mesoderm is scanty and unsegmented, forming a thin walled, unpaired cœlomic vesicle that breaks down into scattered cells. The procephalic mesoderm appears to arise from the primitive cumulus before apical growth begins.

Comparison.—With the progress of cephalization in the arthropods, there has been, therefore, a steady decrease in the volume of mesodermic structures. In the higher arachnids, mesoderm is almost absent in the procephalon, and the lateral plates are absent in the dicephalic and mesocephalic regions. The result, or cause, if you will, is the absence of the thoracic sections of the heart and of the longitudinal, intersegmental muscles; the shortened thoracic tergites then fuse with one another and with the procephalon to form a continuous unsegmented shield, or cephalic buckler.

In the vertebrates, the decrease in volume of the cephalic mesoderm is carried still further, affecting the anterior head regions, as well as the more posterior ones, that in the arthropods are usually well equipped with mesodermic structures. This decrease is due chiefly to the progressive atrophy, or fusion, or condensation of what were originally freely movable parts, and the consequent reduction in the number and volume of cranial muscles. For example, practically all the hæmal, longitudinal, intersegmental muscles disappear with the fusion of the branchial region with the head. The several pairs of originally separate leg-jaws fuse into unpaired oral arches, only one of which is freely movable. The mesocephalic locomotor appendages and their voluminous muscles disappear, and also numerous endocranial muscles, owing to the union of the endocranium with the dermal skeleton. Finally the branchial appendages lose a part of their muscles in their conversion into lung-book-like gill pouches.

This progressive degeneration of the cephalic mesoderm, from before backward, has been, therefore, an ever present factor, exercising a persistent and powerful influence over the form of the head and the structure of the brain thoroughout the whole arthropod-vertebrate phylum.

The Vascular Area and Concrescence.

Vascular Area.—The mode of growth of the extra embryonic area, the concrescence of the germ wall, and the character of the mesoderm in the various regions is shown in Fig. 138.

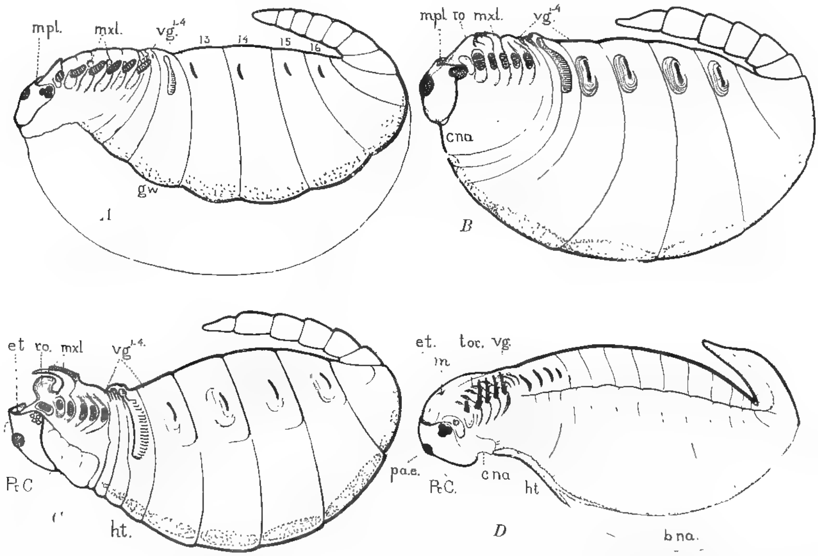


FIG. 17.—*A–C*, Scorpion embryos in side view, semi-diagrammatic. The thoracic appendages are removed in *B* and *C*. *D*, Diagram indicating relations of the cephalic organs in arachnids to those in vertebrates.

The margin of the germinal area belonging to the thoracic metameres is greatly thickened, forming large masses of spherical or oval cells containing a small excentric nucleus, and a brilliantly refractive, colorless thread, usually coiled with great regularity in the long axis of the cell. (Fig. 131.)

Some of these cells are ultimately converted into muscles, others remain as free amœboid cells, and in the adult may be found in great numbers scattered among the connective tissue lacunæ, in the anterior part of the cephalothorax.

Whether the degenerating muscle cells of the cephalothorax are to be regarded as true blood corpuscles or not is doubtful; but it is evident that owing to the increase in size of the yolk sphere, there is already established, in the higher arachnids, an extra embryonic germinal area, and that certain parts of this area may be regarded as the beginning of an extra embryonic vascular area. The peripheral ends of the vagus and abdominal lateral plates give rise to the heart, pericardium, longitudinal hæmal muscles, and to blood corpuscles.

Concrescence.—As the lateral margins of the germinal area grow faster than the median portion, concrescence of the germinal wall will ultimately occur in the precephalic and post caudal regions. In very large yolked eggs, precephalic concrescence will tend to bring the cardiomeres into conjunction, either in front of, or underneath the procephalon, that is in their characteristic position in vertebrates. (Figs. 17–23, 138, 140, 141.)

The post caudal concrescence will tend to unite the posterior margins of the germ wall behind the real apex of the body, giving rise to the various phenomena in vertebrates that have been confused with "gastrulation," "concrescence of the lips of the blastopore," and with apical growth.

The New Mouth, Cephalic Navel, or Hæmastoma.

In the arachnids, there is a special area on the anterior hæmal surface, just in front of the procephalon, that we shall call the cephalic navel. It probably occurs in all arthropods, under various modifications, as the so-called dorsal organ. It is primarily a thickening of the hæmal blastoderm, entirely outside, or beyond the germinal area. In the arachnids, the thickened blastoderm gives rise to an immense mass of proliferating cells that are ultimately invaginated into the yolk, where they degenerate and are absorbed. This infolded area of degenerating cells forms the central point toward which all the surrounding organs converge; the germ wall, with its appropriate structures advancing toward its sides and posterior margin, and the procephalon toward the anterior one. There is thus formed, either in front of, or below, the procephalon, a vortex center toward which all the surrounding organs move, and into which is infolded the remnants of the hæmal blastoderm (Figs. 23, 127, 138, 139, *c.nv.*) The opening between the enteron and the exterior, thus virtually established on the hæmal surface, finally closes in the arthropods, but in the vertebrates a permanent opening is established at this point, that becomes the new mouth, or the *hœmastoma*.

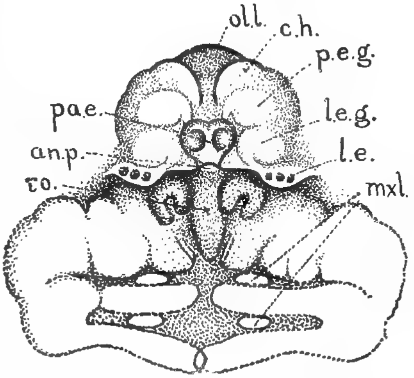


FIG. 18.—Anterior end of an embryo scorpion, showing forebrain completely covered by the palial fold.

Although the cephalic navel ultimately closes in the arthropods, prophetic signs of its future function are not lacking, for on the site where it is formed, there are frequently developed adhesive discs (phyllopods), or root-like outgrowths (cirripeds, copepods) that serve as organs of attachment, or for the absorption of nutriment.

The cephalic navel of arthropods may be regarded as one of the inevitable products of apical growth on a spherical yolk surface, just as the belly navel of vertebrates is a product of the peculiar method of closing up the hæmal surface. The center, around which the converging lips of the cephalic navel are formed, is the degenerating area of hæmal blastoderm, often called the dorsal organ.

The Closure of the Old Mouth or Neostoma.

In the arachnids, there is a progressive enlargement and fusion of the anterior cephalic neuromeres, that gradually leads toward the narrowing of the passageway for the stomodæum, and ultimately to the closing of the mouth. The backward growth of the rostrum and the transfer of the optic ganglia to the region overlying the mouth, due apparently to remote, but persistent and cumulative causes, are contributory factors in bringing about this result.

These conditions at first lead to a profound modification of the mode of life, making a liquid, or finely divided diet a necessity, and ultimately to the utilization of the cephalic navel as a new entrance to the alimentary canal.

Conclusion.

In the arachnids, the body is built up by successive generations of new groups of metameres, or tagmata, at definite historic periods in the evolution of the phylum.

The process of cephalizing the anterior regions of the body consists in the gradual and extensive elimination of motor elements and the establishment of a definite sequence of functions and organs, according to an inherently necessary order.

The first five tagmata embrace the first sixteen metameres and lay the foundations for the head in vertebrates. Each tagma is characterized by a special number of metameres, by peculiarities in the number and structure of its neuromeres, sense organs, ganglia, nerves, mesoderm and endo-skeleton, and by their sequence and mode of growth, that are in essential agreement with those in the corresponding divisions of the vertebrate head.

The arachnid body consists of metameres added to the primitive head, which represents the remnants of the cœlenterate body. The greater part of the arachnid body and its primitive head forms the vertebrate head. Nearly all the vertebrate body consists of a new generation of metameres, not represented in arachnids.

The conditions created by apical growth, by cephalization, and by the increase in the volume of the yolk sphere, lead to the closure of the old mouth, and to the formation of a new one on the hæmal surface, the primitive dorsal organ forming the starting point for the cephalic navel, that ultimately becomes the new mouth.

CHAPTER II.

OUTLINE OF ARACHNID THEORY; CONTINUED.

I. Comparison of Adult Arthropods With Adult Vertebrates.

The preceding analyses have shown, that beneath a heavy disguise of contour and surface detail, the structural plan of an arachnid and of a primitive vertebrate is after all the same. Let us now consider several types of adult arthropods and see how they compare with vertebrates.

I. Orientation of Neural and Hæmal Surfaces.

It will be seen that although the location of the eyes and the shape of the body indicate the usual position of the animal during locomotion, they afford no certain evidence as to which is the neural and which the hæmal surface, for the pattern formed by the sense organs on the neural surface of the cephalothorax of some arthropods may be very similar to that on the hæmal surface in others, and this fact must be borne in mind when comparing them either with ostracoderms or with true vertebrates.

In the phyllopods, and in many other crustacea that swim neural side up by means of oar-like cephalic appendages, the center of gravity usually lies below the attachments of the swimming appendages. In such cases the parietal ocelli and lateral eyes lie near their original embryonic position, on the upper, or neural surface, as they do in vertebrates. (Figs. 7, 9, 244, 247 and 260.)

Where locomotion is effected either side up, as in Limulus, the prevalent mode of life may be indicated by the position of the eyes and legs, and by the shape of the body. Limulus, for example, uses its sixth pair of legs as pushing poles, as it moves over soft bottoms, or crawls along partly buried in sand, with little more than the median and lateral eyes exposed. During the adult stage, however, it frequently swims, neural side up, for considerable periods, and persistently does so in the larval or trilobite stages, the sloping, anterior margin of the shield, like a well turned bow of a boat, holding the head up and the body properly balanced. The same modes of life and dual methods of locomotion undoubtedly occurred in many trilobites and merostomes, and when the free swimming life predominates, one or more pairs of appendages are enormously enlarged to form heavy, oar-like swimming appendages. The lateral eyes may then lie well forward on the head, between the neural and the hæmal surfaces (Fig. 5).

In Bothriolepis (Figs. 247 and 248), we have a similarly shaped body, with similar oar-like cephalic appendages, and from the various positions in which they are found in the deposits, there can be no doubt that they crawled, partly buried in soft mud, with the ocular, or neural side up, but swam with the neural side down, the center of gravity lying below the attachment of the arms toward the bottom of the boat-shaped head. The same was probably true of Cyathaspis (Fig. 244), Tremataspis (Fig. 236), Pteraspis, and probably to a less extent of Cephalaspis (Fig. 232).

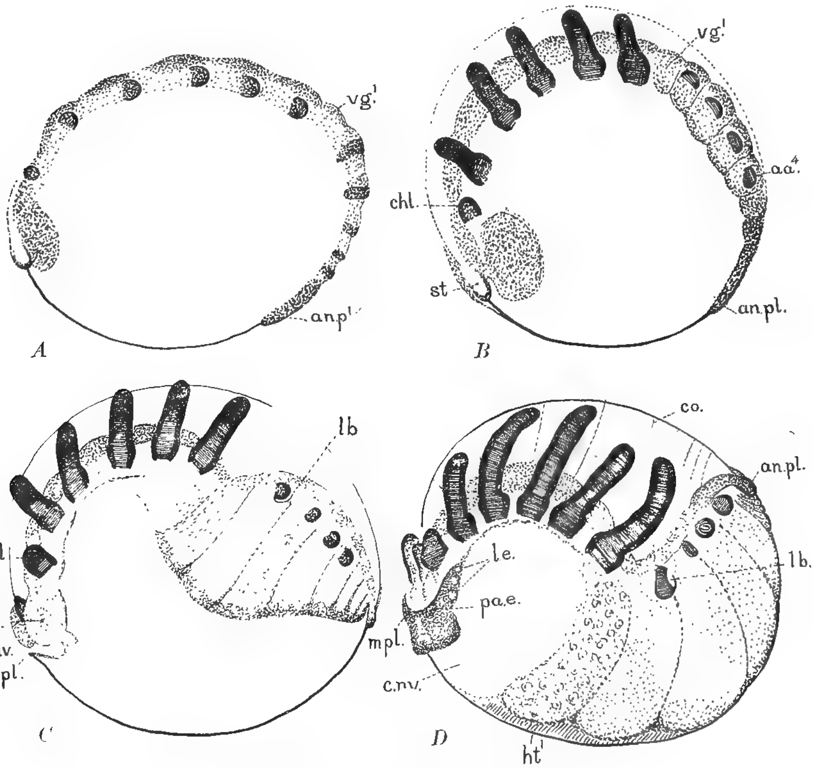


FIG. 19.—Embryos of a spider in side view.

The prevailing position among vertebrates is unquestionably with the neural side uppermost, although, as we have just seen, the most primitive vertebrates may move about with either side up. It is by no means true that the prevailing position of the invertebrates is with the neural side down. In many annelids, there appears to be no fixed position for the neural and hæmal surfaces. In most crawling arthropods (insects and spiders), the neural side is directed downward, but probably in the vast majority of phyllopods, cladocera, copepods, merostomes, and trilobites, and in the larvæ of decapods and cirripeds, the prevailing position, when swimming freely, is with the neural side uppermost, and that is the approximate position in practically all the adult cirripeds.

It is thus clear that the position of the animal during locomotion has no morphological value whatever. It is necessary to emphasize this point, because the ancient superstition, to the effect that it is always the same surface of a vertebrate or of an invertebrate that points heavenward, or that it is the baptismal name of a surface that determines its identity, is still deeply rooted in the minds of an incredible number of zoologists.

II. COMPARISON OF ADULT ARTHROPODS AND VERTEBRATES.

Bunodes.—The form that perhaps most nearly realizes the generalized arachnid type we have tried to portray is Bunodes, a small, silurian merostome from the island of Oesel, Russia. (Fig. 13.) In my visit to this island in 1901, a large collection of these forms was obtained from which I have made a large scale model, showing in detail the essential features of the hæmal surface. This animal is remarkable for the fact that it has no recognizable exoskeleton. The fossils consist of well defined, but very thin, carbonaceous films, in a fine chalky matrix. They are found side by side with small eurypterids that are covered with a delicate chitenous membrane, still retaining apparently its original, chemical structure, and close to fragments of Tremataspis, consisting of perfectly preserved, calcareous, dermal plates. It is therefore probable that Bunodes had neither a chitenous nor a calcareous exoskeleton.

The general form of the body is intermediate between that of Limulus and that of a trilobite, or of a typical merostome. All the five head divisions, except the diacephalon, are clearly indicated, and they are surprisingly like those in larval Limuli (Fig. 152). There is a distinct procephalon, six thoracic, two vagal (chelarial and opercular?), and five branchial metameres. The most remarkable feature is a pair of short, slender antennæ clearly seen in one specimen.

For the sake of exposition we may picture to ourselves the manner in which an adult arachnid, or other arthropod, might be moulded into a vertebrate, although it is manifestly impossible for any adult animal to be converted into another. We may start with a form like Limulus, or Bunodes, or an eurypterid, or with an adult phyllopod, like Branchipus, or a cladoceran, or cirriped.

In practically all these animals, extensive lateral, or pleural folds develop on the sides of the cephalothorax, that either extend in a nearly horizontal plane, to form a broad, shield-shaped cephalothorax, with backwardly directed cornua, as in the marine arachnids (Fig. 155), or the folds may be directed toward the neural surface, forming, in extreme cases, the bivalve shield, or mantle, of phyllopods (Fig. 273), ostracoda (Fig. 307), cladocera (Figs. 8 and 9), and cirripeds (Fig. 275). It may enclose the head, or the entire body, in a large peribranchial, or atrial chamber, which contains, or into which opens, the nutrient, excretory, respiratory, and genital organs. Another characteristic feature is the often enormous labrum, or rostrum, that shows a persistent tendency to migrate backward, forming an overhanging lid to the mouth (Fig. 7). The rostrum and the

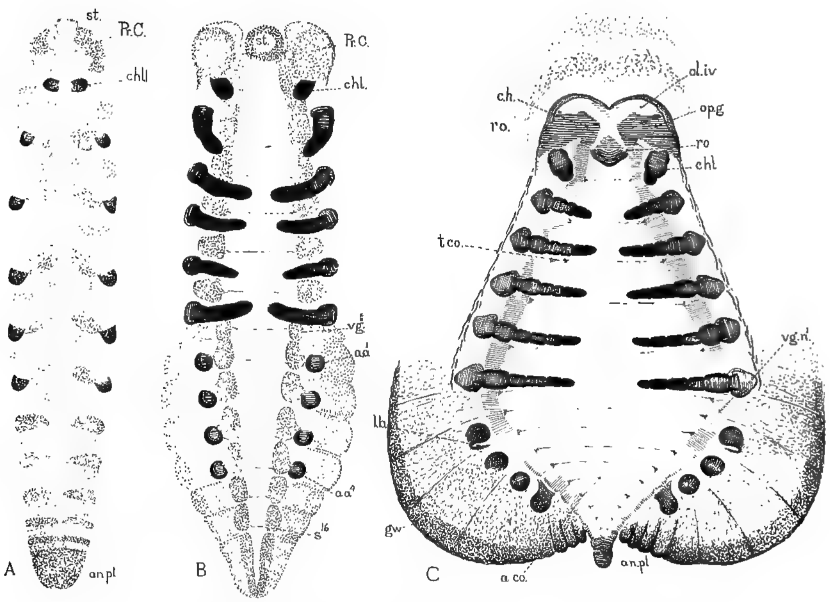


FIG. 20.—Spider embryos in mercator projection. Camera-outlines

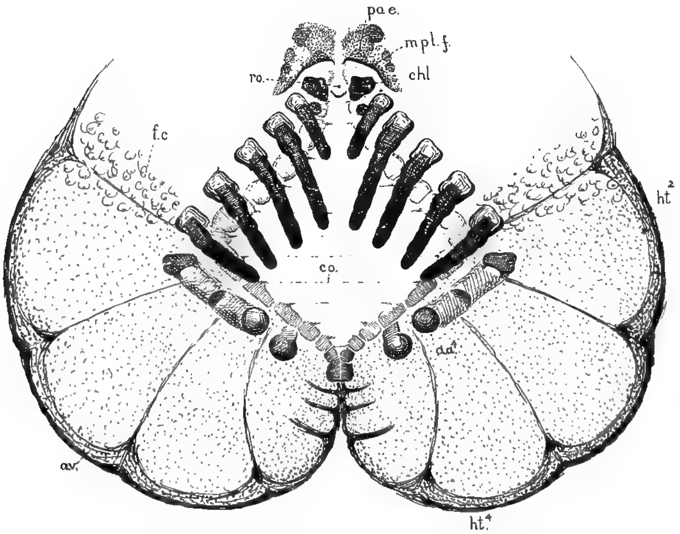


FIG. 21.—Spider embryo in mercator projection. Camera-outlines.

atrial folds, together with the branchial and oral appendages, thus tend to enclose the mouth in an ever deepening chamber. When this condition approaches its extreme development—cirripeds, cladocera, etc. (Figs. 273–275)—the mouth becomes very inaccessible, and food can only reach it in a finely divided condition, carried there by roundabout ways, in the currents of water produced by the swimming, the oral, or the branchial appendages. Or the mouth may become completely closed, as in many dwarf, or parasitic cirripeds. (Figs. 280 and 281.) Under these conditions the form and general appearance of a phyllopod-like arthropod, with its large branchial, or atrial, chamber, and its oar-like cephalic appendages, approaches that of some simple ostracoderms, like Cyathaspis, or Pteraspis. (Comp. Figs. 176 and 244.)

If we compare an adult Limulus viewed from the neural surface, with Cephalaspis seen from the same surface (Figs. 11 and 12), it will be seen that such an arachnid could be made into an ostracoderm by the union and backward growth of the anterior margins of the cephalothorax, thus enclosing the mouth and appendages in a large branchial chamber, like that in some phyllopods (Figs. 9–10). The eyes and olfactory organs could remain in their original embryonic position near the center of the head; the olfactory organs in front, the three parietal ocelli in the center, and the lateral eyes on either side. (Fig. 12.) The enlarged coxal joints of the anterior thoracic appendages, extending on to the hæmal surface, would form the visceral arches about the mouth, the free appendages forming the external gills and the jointed, oar-like arms. A varying number of infolded branchial appendages, similar to the lung books of arachnids, would initiate the true gill pouches, and finally the elongated post-abdomen would form the beginning of the flexible trunk, with its pleural or lateral folds, from which the post-cephalic appendages later arise.

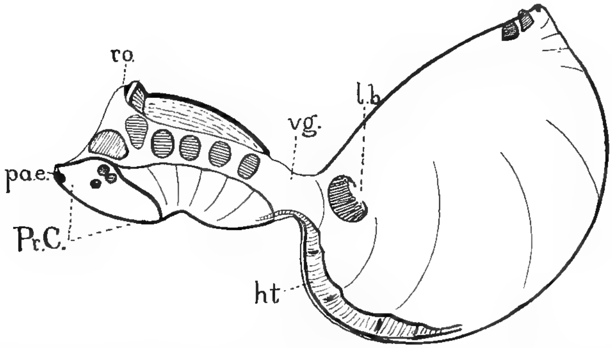


FIG. 22.—Young spider, showing the procephalon, transferred from the neural to the hæmal surface, and the location of the thoracic appendages, mouth, heart, and respiratory organs. Thoracic appendages removed.

From the cephalaspids we may easily derive the remaining ostracoderms. In Bothriolepis, the old cephalo-thoracic portion remains comparatively small, while the abdominal buckler has become greatly enlarged and closed on its neural surface to form a true atrial chamber that encloses the gills and cloaca. (Fig. 5.) The jointed, oar-like appendages, which belong to one of the posterior mesocephalic segments, are attached to the angle of the cornua, that are here very small compared with those of Cephalaspis.

Bothriolepis retains the hinge-like joint in the vagus region, which is such a prominent feature in trilobites, merostomes, and other arachnids. The same joint is a conspicuous feature in Dinichthyes, Coccosteus, etc., a group of primitive, fish-like animals that probably unite the typical ostracoderms with the true vertebrates. (Fig. 250.)

In Tremataspis (Figs. 236 and 237), there are probably several pairs of small cephalic appendages, comparable with external gills, that protruded from the openings on the oral surface; the larger, oar-like pair, at the beginning of the series, being especially noteworthy. The exhalent branchial currents and the excretory products, no doubt pass out of the posterior end of the atrial chamber, as in Bothriolepis.

The assumed changes above described affect, in the main, the external form of the animal. The internal structure might remain essentially as it now is in arachnids, and, except for certain organs, it would harmonize with the structural plan in vertebrates. For example, it would be necessary, in order to complete the transformation of an arachnid into a vertebrate, to close the old mouth and to connect the new one and the gill pouches with the enteron. The factors involved in these changes are described elsewhere. For the present, it is enough to recognize the fact that these events have taken place, in some way and at some time, whatever the method or cause may have been.

On the other hand it will be observed that many internal organs, that we are accustomed to consider as characteristic of vertebrates, are already present in the arachnids, in their proper position and relations, and merely have to be enlarged or improved, or even left as they are, to agree with those in vertebrates or ostracoderms.

For example, there is already present in Limulus, in addition to the brain, sense organs, and other structures that have been considered, a head kidney, *cox. o.*, heart, *h*, aortic arches, *a. o.*, and cardinal sinuses, *card. s.* foreshadowing those in vertebrates. (Fig. 2.) There are infolded gill sacs and gut pouches in arachnids, that are precursors of the gill clefts, thyroids, and other enteric diverticula in vertebrates. (Figs. 179–182.) There is in Limulus and other arachnids a large cartilagenous endocranium and gill bars, so similar in form, location, and histological structure to those of vertebrates, that they might readily pass for those of some primitive, unknown member of that class. (Figs. 210–220.) There is, in Limulus, an internal, dermal skeleton, made of chiten, it is true, but nevertheless consisting of a network of trabeculæ, cancellæ, Haversian canals, lacunæ, and canaliculæ, so much like those of certain ostracoderms (Pteraspis) that it is doubtful whether fossilized fragments of one skeleton could be distinguished from those of the other, if their real origin was unknown. (Figs. 196–207.) And finally, there is present in all arthropods that have been carefully studied in regard to this organ, a median, subneural cord agreeing in position, development, and in some cases in function, with the notochord of vertebrates. (Figs. 221–231.)

It is evident, therefore, that the resemblance in form and general appearance between the ostracoderms and the marine arachnids is not a fanciful one, to be classed as a meaningless coincidence, or as due to mimicry, to parallelism, or to a particular mode of life. The resemblance is real, and pervades the whole organism, and can be satisfactorily explained only on the assumption that there is a close genetic relationship between the two classes.

III. Comparison of Arthropod and of Vertebrate Embryos.

A comparison of adult arachnids with adult vertebrates helps us to see the morphological relations that exist between the two types, but it cannot tell us how one arose from the other. That is the function of comparative embryology, for the rise of one great class from another takes place during the malleable embryonic periods, when transitional stages are created by a slow yielding to the impact of successive readjustments between organs developing under unequal and unstable conditions.

Hence the supreme test of any broad theory of phylogeny is its ability to present an unbroken series of embryonic stages, naturally or inevitably leading from one type to the other, and to point out the efficient causes for them. This embryonic series should include, at the proper period, the characteristic anatomical structures of both types. The established direction of growth shown by various systems of organs, and the general conditions that control growth in the lower type, should persist in the higher, supplying a past cause for the creation of the fundamental features of the new type, and a present one for those now appearing in it. There should be no changes demanded that necessitate the sudden destruction of old organs, or the abrupt creation of new ones; that interrupt the continuity of individual life, or that break, or entangle, the necessary morphological relations of one organ to another. This dual embryonic series should run parallel with, and should supplement and elucidate the series of adult forms left along the trail made by the two types in their slow process of evolution.

I have made a series of models that show how the embryos of vertebrates and arachnids conform to these requirements. (Figs. 24–34.) They are intended to illustrate the principal stages in the development of a primitive vertebrate supposed to be descended from arachnids. The series begins as an arachnid embryo and leads, without any greater changes than are found in the development of the higher animals, through the typical embryonic stages of forms like Limulus and scorpion, into a vertebrate embryo of the fish-like or amphibian type.

The series shows us that the early stages of vertebrate embryos, in all essential respects, run parallel to, or are identical with, those of arachnids; and that the same morphogenic forces which created the cephalothorax of arachnids find their full expression in the head of vertebrates. It shows that both embryos begin their growth from the same surface of the egg and spread over the yolk in the same directions, enclosing the opposite side in the same manner; that there has been no transfer of the nerve cord from one surface to the other, as claimed by Gaskell, and that the medullary plates in both types are homologous, and not, as claimed by C. L. Herrick, one dorsal, the other ventral.

Form Controlling Factors in the Early Stages.—Apical growth and the volume and composition of the yolk sphere are important factors in the development of the embryo, because the physical and chemical composition of the yolk sphere controls the rate of radial growth, while the circumference of the yolk sphere, and the ratio between the rate of apical and bilateral growth, determines the relative time and place at which certain organs arise, and the physical conditions under which they develop. Owing to the relatively large volume of the yolk sphere in the arachnids, neither the cœlenterate nor trochosphere stages can assume the form of the ancestral, free swimming animal, *i.e.*, a nearly spherical body growing in each of three dimensions at about an equal rate, for they are reproduced in the arachnid egg under totally different conditions. They appear at a time when cell growth is beginning on the outer surface of a relatively large sphere of inert material, and the various organs must be mapped out in one plane, like a Mercator projection of the earth's surface. Moreover at these early stages, the development of the deeper lying organs is delayed, owing to the impenetrability of the yolk and the lack of respiratory facilities.

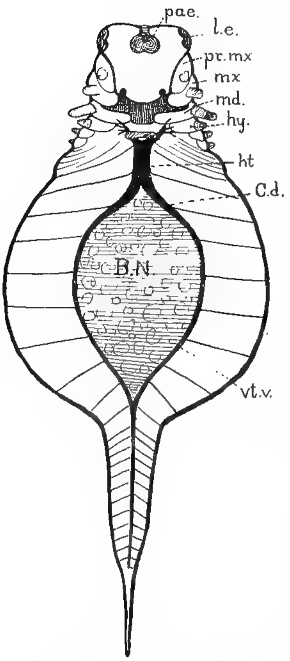


FIG. 23.—Diagram illustrating a hypothetical, transitional condition, between the embryo of a marine arachnid and that of a primitive vertebrate. It shows the convergence of procephalon, appendicular arches, and mesodermic lateral plates around the dorsal organ to form the cephalic navel, or the anlage of the hæmostoma. The uncovered yolk, that is surrounded by the concrescing germ walls and cardiomeres, constitutes the belly navel, *B. N.*

Thus all the early stages must be expressed in the form of a film in which the rate of growth, in the three dimensions, is very unequal. This film increases in length by a process of apical growth, which takes place at one end only; in breadth by bilateral growth, and in thickness by radial growth. These early conditions are identical for all segmented animals, and it is only necessary to fix the location of the growing apex, and the direction of bilateral growth, in order to fix, beyond question, the identity of the head and tail ends and the neural and hæmal surfaces.

The Gastrula, Cœlenterate, or Trochosphere Stage.—The first stage after cleavage (Fig. 24, *A*), shows the primitive cumulus, the primary center for the origin of the germ layers. The central depression, *gst*, marks an area of inward proliferation which gives rise to the endoderm, yolk cells, and procephalic mesoderm. This stage represents the radiate or cœlenterate phase, and is to be regarded as the true gastrula of the arthropod-vertebrate stock. The central depression deepens and later forms the stomodæum, the outer opening being the neurostoma. The stomodæum, at a very early period, is enclosed, or surrounded by a nerve ring consisting of the stomodæal ganglia and their commissures, which probably represents the remnants of the circumoral nerve ring of the cœlenterates. The stomodæum is, therefore, caught in a trap, the bars of which are continually growing stronger, and from which it never escapes.

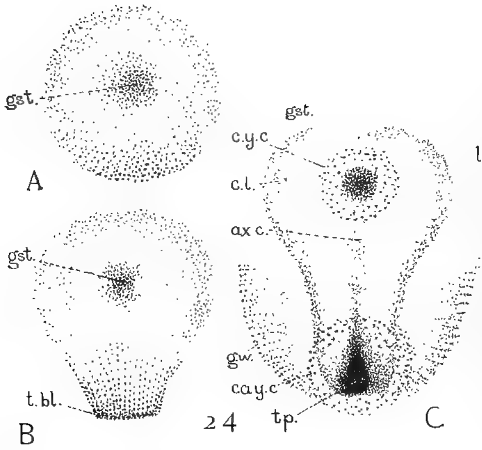
Transition from Radiate to Bilateral Symmetry.—The blastodisc, or cell layers covering the primitive cumulus, gradually spreads out over the surface of the yolk in all directions. Then, on the posterior side of the disc and independently of the central depression, a second thickening appears, in which cell growth and proliferation is especially active. It marks the beginning of apical growth and of bilateral symmetry, and lays the foundations for the first metameres. The anterior portion of the primitive cumulus gives rise to the procephalic lobes. (Figs. 24, 25.)

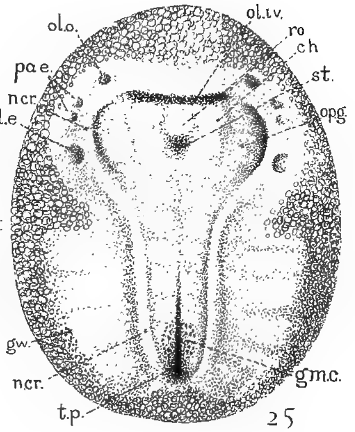
The Telopore.—The rapid cell division at the apex of the developing trunk may give rise either to an elongated axial groove (insects), or to a terminal infolding, or telopore (arachnids), the so-called "blastopore" of authors. Later it may be changed to a typical primitive streak (Limulus and scorpion), or there may be no infolding whatever (Cymothoa). This axial or terminal ingrowth (Fig. 25), is not to be regarded as a modification, or as an extension of the process of gastrulation in the procephalic lobes. It is merely a local exaggeration of the marginal growth of the blastodisc. The infolding is a secondary result of the rapid tangential proliferation that takes place at the head of the comet-like outgrowth. It may or may not be present.

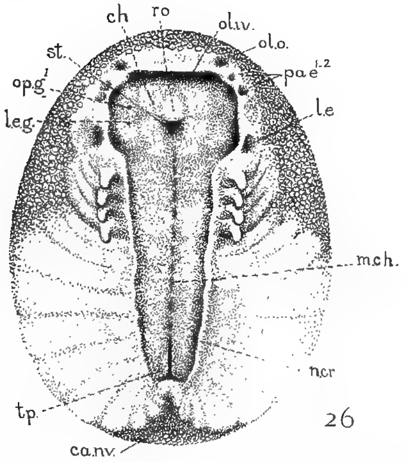
The Germ Wall.—At the close of the primitive cumulus stage, a germ wall, *g. w.*, is formed on the lateral and posterior margins of the blastodisc. With the formation of the trunk, it forms the lateral boundaries of the developing metameres. (Figs. 25, 26). The germ wall, which is merely a thick band of proliferating cells, similar to the teloblasts at the caudal end, spreads laterally over the yolk surface (Figs. 31, 32), leaving behind, in addition to the ectoderm and yolk cells, a sheet of underlying mesoderm that gradually breaks up into somites and lateral plates.

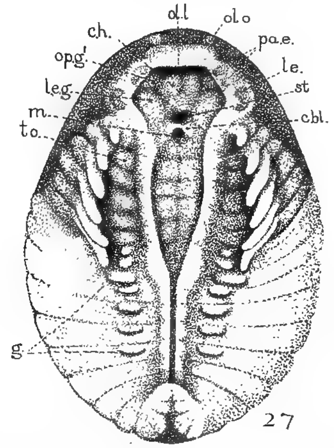
Differentiation, therefore, takes place along two main axes; from the median line laterally, and from the head end backward; hence the anterior median part of the germinal area, which now includes the primitive head and the new body, is always the oldest and shows the greatest histological differentiation; the marginal and caudal part is the youngest and is the least differentiated.

Concrescence of the Germ Wall.—As the gradually widening germinal area advances over the yolk, the germ walls of the more posterior segments form a ∧, the arms of which gradually unite, forming a double, primitive streak-like band of nuclei behind the telopore. (Figs. 16, 21, 25, 26, 27, 138.)









FIGS. 24 to 34.—A hypothetical series of arachnid and vertebrate embryos. The purpose of the series is to show the continuity in the methods of growth and organic differentiation in vertebrates and arachnids. It begins with the typical arachnid stages and leads up to those characteristic of primitive vertebrates, where without interruption they are carried on to completion.

FIG. 24.—*A* shows the radially symmetrical germ disc, or primitive cumulus, with its centrally located gastrula ingrowth; *B*, beginning of apical, or teloblastic, growth, and the appearance of bilateral symmetry; *C*, the formation of the medullary plate; the unequal expansion of the thickened margin of the germ disc, or germ wall, *g. w.*, and the infolding of the teloblast to form the telopore, *t. p.*

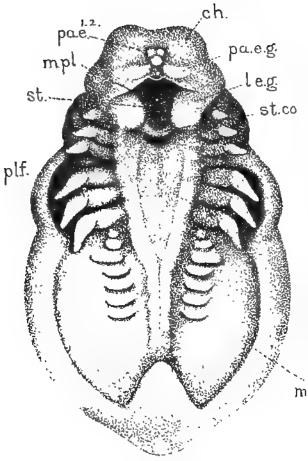
FIG. 25.—The open medullary plate stage, with its neural crests, the marginal infoldings that mark the beginning of the forebrain vesicle, and the forebrain sense organs on the outer slope of the neural crest.

FIG. 26.—Shows the appearance of the thoracic appendages; the segmentation of the lateral plate mesoderm in the abdomial region; the beginning of the postanal concrescence of the germ wall; and the infoldings for the middle cord, or notochord. The telepore is replaced by a primitive streak.

FIG. 27.—Shows the appearance of the gustatory lobes, the vagus and abdominal appendages, and the elevation of the caudal lobe. The olfactory organs have moved forward, in front of the head, and the median eyes have been transferred to the inner limb of the neural crest. The cerebellum appears as the suprastomodæal commissure.

FIG. 28.—The palial fold has covered nearly the whole of the forebrain, and the optic ganglia are crowded backward and upward toward the oral region. The pleural folds appear, and the thoracic folds, or the thoracic shield, extend over the posterior thoracic appendages, forming the beginning of the opercular or branchial fold.

FIG. 29.—The optic ganglia have united over the stomodæum to form the tectum opticum. The neural crests of the branchial region have closed, except over the mouth which lies just behind the stomodæal commissure, or cerebellum. The uncovered space marks the location of the choroid plexus of the fourth ventricle.



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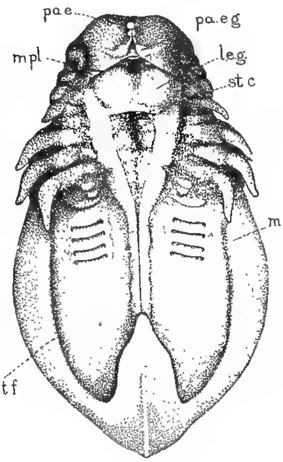

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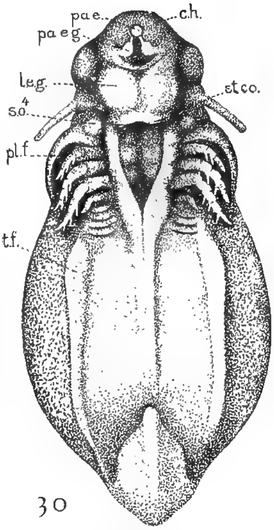

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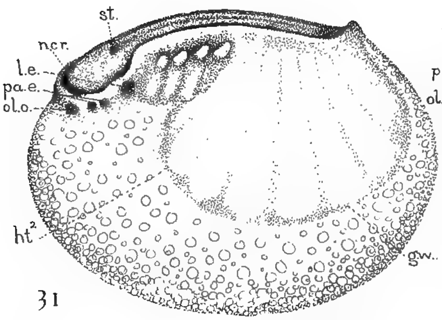

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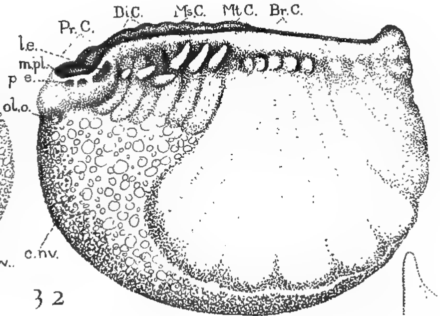

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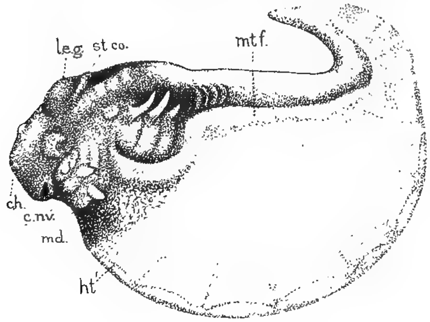

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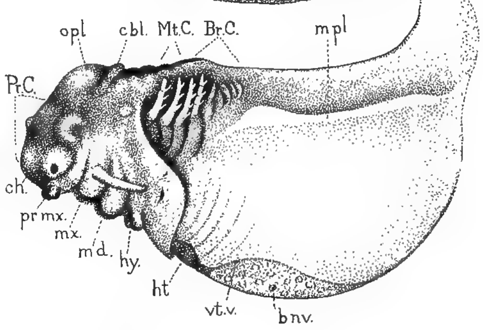

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FIG. 30.—The embryo now presents typical vertebrate conditions. The old mouth is practically closed. The posterior thoracic and vagus appendages appear as the external gills, and the pleural fold as the postcephalic lateral fold that gives rise to the pectoral and pelvic appendages.

FIGS. 31 and 32.—Side views of Figs. 26 and 27, showing the extension of the germ wall over the yolk, and the elevation of the procephalic lobes above the general level of the yolk.

FIG. 33.—Side view of Fig. 29. It shows the projection of the procephalic lobes beyond the anterior surface of the yolk, thus allowing the oral arches, or the basal arches of the anterior thoracic appendages, to approach the hæmal surface of the forehead. The lateral eye has been carried into the brain vesicles, appearing through the skin as the kidney-shaped retina.

FIG. 34.—Side view of Fig. 30. At least four pairs of oral arches have united on the hæmal suface, giving rise to the premaxillary, maxillary, mandibular, and hyoid arches. Vestiges of the free appendages persist as the oral arch papillæ, tentacles, or balancers. The large thoracic segmental sense organ opposite the fourth thoracic appendage and behind the hyoid arch has now become the auditory placode.

Thus the embryo elongates, apparently, in two different ways; by true apical growth at the original apex of the embryo, and by the concrescence of the adjacent parts of the germ wall, behind the apex. Failure to recognize the meaning of these two processes in vertebrates has led to much confusion.

As the telopore is merely a locally exaggerated marginal growth, its products are not primarily different from those of the germ walls that concresce behind it. But it will be observed that in their derivation and in their serial arrangement, the two sets of products stand in totally different relations to one another, and to their surroundings. (Figs. 138, 157.)

In vertebrates, as well as in arachnids, neither the telopore, nor the concrescing margins of the germ wall have anything to do with a true gastrula, nor is their mode of growth comparable with the cœlenterate method of gut formation. As indicated elsewhere, post-anal concrescence is the inevitable result when a living film, extending by apical and marginal growth, spreads over a spherical surface.

The Nervous System follows in the paths first laid down by the expanding germ layers. The procephalic lobes, developing from the territory of the primitive cumulus, and the lateral nerve cords on either side of the line of apical growth. A slipper-shaped medullary plate is thus formed that in both arthropod and vertebrate embryos has essentially the same structure, location, and mode of growth. In both types we may recognize the marginal sense organs of the procephalic lobes and the central, stomodæal infolding. This infolding, with a rostrum-like elevation on its anterior margin, is frequently a conspicuous marking in the middle of the cephalic lobes of amphibia (Rana, and Necturus) (Fig. 25.)

In this stage, the olfactory lobes make their appearance as a deep fold across the anterior border, and the edges of the neural crest begin to grow over the lateral margins of the medullary plate. A little later, the thoracic appendages appear as gill arches and external gills. (Figs. 26–28.)

The Primary Sense Organs.—In the following stages (Figs. 27–34), the primary sense organs on the margins of the cephalic lobes move into, or toward, their final position, and the gustatory organs make their appearance on the inner margins of the basal lobes of the thoracic appendages. The olfactory organs, *ol*, *o*, move toward the anterior median line but remain in the surface ectoderm, outside the brain chamber; the two pairs of ocelli are caught in the palial fold and carried onto the membranous roof of the brain vesicle to form the parietal eye; the kidney-shaped lateral eyes lie on the outer edge of the fold, not quite inside of the brain chamber. (Fig. 27.)

Meantime the **cornua,** *c*, of the thoracic shield and the edges of the abdominal pleurites appear. (Figs. 28, 33.)

The hæmal side of the cephalothorax is unsegmented. The greatly thickened germ wall in this region concentrates around a point between the anterior end of the heart and the forebrain, where a great mass of cells, the remnants of the hæmal blastoderm, are engulfed in the yolk and absorbed. (Fig. 33, *c.nav.*)

Vertebrate Stages.—Up to this point, our vertebrate-arachnid embryo has been passing through the cœlenterate and arthropod stages of its development, the later ones, as we have represented them, being essentially like those of Limulus and the scorpion, although not presenting any characters foreign to a vertebrate. In the following stages, the vertebrate characters appear.

The changes that most affect the general shape and appearance of the brain are the transfer of the lateral eye placodes to the inside of the cerebral vesicle, and the union of the optic ganglia over the neural surface of the brain to form the ganglion habenulæ and the tectum opticum, or optic lobes. (Fig. 28.) As the latter increase in size, they crowd the stomodæal commissure and its ganglion backward, over the posterior part of the midbrain region, where they form the rudiment of the cerebellum. (Figs. 29, 30, 107 and 108.)

When the convex, kidney-shaped lateral eye placode is transferred to the brain wall, it becomes a concave, horseshoe-shaped retina. Still later, it becomes a circular one, with a median fissure and centrally located nerve, both conditions being the direct result of its ancestral shape and mode of growth. (Fig. 106.)

The Auditory Pit develops from a prominent, disc-like placode, or segmental sense organ, which in Limulus lies on the cephalothoracic shield, opposite the third or fourth thoracic segment. (Figs. 29–30.) With the concrescence of the anterior oral arches on the hæmal side of the head, the disc shifts its position to that part of the head where it makes its first appearance in vertebrate embryos. (Figs. 33–34.)

The Heart has been formed in typical arthropod fashion, by the concrescence of the lateral plates of the vagus, and the anterior abdominal metameres, which accounts for the fact that, in both arthropods and vertebrates, the anterior heart nerves arise from the corresponding vagus and branchial neuromeres. (Figs. 32 and 33.)

In the formation of the vertebrate heart, new factors may arise in the greatly increased volume of the yolk sphere. In this case the branchial metameres, lying near the equator of the egg, must extend their lateral plates completely round the yolk before a heart segment can be formed. Hence, in the larger yolked eggs, it is only the vagal and anterior branchial metameres that are in a position to form heart segments in time to nourish the growing head structures. If the younger and shorter caudal metameres produced heart segments, they would necessarily arise later and would be separated from the head by the barrier of the abdominal yolk navel. (Fig. 34.) The heart would then be a single tube at either end and a paired tube in the middle. (Figs. 23, 139, *C.*)

The thoracic, and the post branchial cardiomeres have been eliminated in vertebrates, as they have been in arachnids, and the heart develops, as nearly as one may determine, from about the same group of vagus and branchial metameres in both cases. But the posterior end of the vertebrate heart still extends partly round the yolk navel; hence the divided posterior end and divergent vitelline veins; and it is crowded into an area on the hæmal surface that is growing shorter while the heart is growing larger, hence the auriculo-ventricular curvature.

The Cornua of the cephalothoracic shield are retained as the **opercular fold,** which extends over the posterior appendages, as suggested for Cephalaspis, to form a respiratory, or atrial chamber. The projecting margins of the abdominal segments or pleurites are retained as the lateral fold, from which the paired, post-branchial appendages arise. (Figs. 29–34.)

The Oral Arches and the Hæmostoma.—Both the formation of the hæmostoma, or new mouth, and the transfer of the basal joints of the anterior thoracic appendages to the hæmal side of the head to form the oral arches, are the inevitable results of the processes that have been steadily going on during the phylogeny of the arachnid cephalothorax. These processes are: the increased size of the yolk sphere; the increased size of the forebrain neuromeres; and the progressive degeneration of the cephalic mesoderm. The way in which these changes affect the location of the jaws and the shape of the head, during the early stages of development, is shown in Figs. 31–34. It will be seen that as the forebrain increases in volume and in precocity, the apex of the head is elevated and thrust forward off the surface of the egg. As the hæmal ends of these anterior metameres are greatly reduced in volume, or absent, the other head structures, which were originally neural or lateral in position, such as the anterior mesoblastic somites and the appendages, are drawn toward the hæmal side of the head. Here they converge around the ingrowing, hæmal surface, or cephalic navel (dorsal organ) that represents the beginning of the buccal infolding, the basal joints of the appendages forming the beginning of several pairs of oral arches, *i.e.*, premaxillæ, maxillæ, mandibles, and hyoids.

The more posterior arches are not subject to these conditions; hence they tend to remain in their original position on the neural or lateral surface. But in the later stages of the higher vertebrates, even they may be transferred to the hæmal surface. (Figs. 307, 308.)

The mouth parts of our embryo are now in the ostracoderm and cyclostome stage, one that is seen temporarily in all higher vertebrate embryos (see development of the jaws in the frog) (p. 257), and permanently in the adult cyclostomes and ostracoderms. (Figs. 159–174.) The true vertebrate condition is attained by the union of two pairs of arches to form a single, fixed, upper jaw, and the union of a third pair to form a movable, unpaired, under jaw, or mandible.

* * * * * * * * *

The older stages of our arachnid-vertebrate embryo, Fig. 34, are characterized by an increase of the **cranial flexure,** bringing the heart close under the anterior end of the brain, and producing that forward dislocation of the hypobranchial muscles, so characteristic of vertebrates; by the opening of the gut pouches into the lung-books; by the appearance of true vertebrate appendages as post-cephalic outgrowths of the marginal fold; by the increasing size of the cartilage cranium and gill bars; by the substitution of a subdermal skeleton for an epidermal one, and by the conversion of the arthropod lematochord into the notochord.

CHAPTER III.

EVOLUTION OF THE NERVOUS SYSTEM IN SEGMENTED ANIMALS.

I. Meaning of the Term Brain.

In the vertebrates, the term "brain" vaguely signifies the specialized anterior end of the neuron. In the invertebrates, the term may be even more vague, in that it is often used to signify only that part assumed to lie originally in front of the œsophagus, that is, the supra-œsophageal ganglion. Or the term may signify that ganglion, plus a varying number of post-oral neuromeres.

The lack of precise definition in both cases is significant, and justifies the use of the term, as we shall use it here, namely, to signify a varying number of neuromeres consolidated in the region of the primitive mouth.

The number of neuromeres thus set apart, their specialization, and the intimacy of their union, gradually increases throughout the arthropod-vertebrate series, and furnishes an impressive picture of persistent, progressive specialization.

In the arthropods, there are many oscillations in the total number, and in the grouping, of the brain neuromeres. The primary causes of their union are too complex to be analyzed, except in the broadest way; but we may readily recognize a steady progression toward a definitely organized collection of neuromeres that it is entirely proper to call a brain in the vertebrate sense, for it contains approximately the same total number of neuromeres as the vertebrate brain; and it is divided into similar groups of neuromeres, each of which is associated with nerves, sense organs, and other structures similar to those in vertebrates.

The evolution of the brain cannot be effectively studied apart from the body regions to which it belongs, for each moulds the other and reflects the other's changes. The events that created the vertebrate brain, and whose influence is still effective in moulding its form and function, are to be found in the arthropods. There, all the initial phases in the successive incorporation of one region of the trunk after another into a more complex "head," and of one part of the cord after another into a more and more complex "brain," have taken place, and probably nearly all the more important steps in the process are there crystallized into recognizable form.

The five groups of neuromeres included in the first fifteen or twenty that make up the vertebrate brain may be definitely identified with the corresponding divisions of the arthropod brain. We cannot hope to identify more than that since those that follow and which make up the greater part of the spinal cord were acquired after the evolution of vertebrates from arachnids had taken place.

In other words, the ancestors of vertebrates were animals provided with a comparatively small number of neuromeres, 21 ±, most of which had already been consolidated into a complex brain of the vertebrate type. One of the important events in the early evolution of the new or vertebrate type was the rapid increase in the number of metameres by the regular process of apical growth. The new metameres formed a new trunk or body, while nearly the whole of the old arachnid trunk (head, thorax, and abdomen, 14–16 metameres) was still further consolidated to form the head of the new type. The whole process thus presents a striking analogy to the way in which the primitive body of segmented animals was formed as a new outgrowth from the body of its cœlenterate ancestor, which then became the head of its descendant. (Fig. 35.)

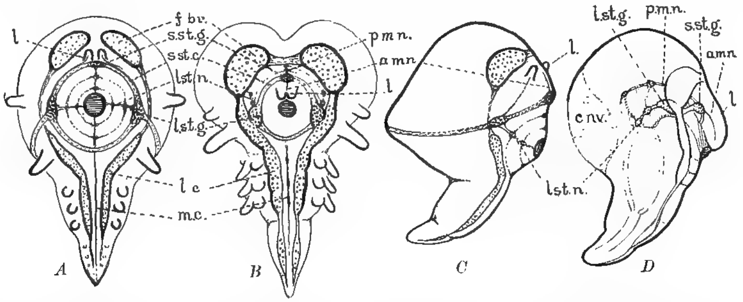

FIG. 35.—Diagrams to explain the probable relations between the structure of a trochosphere and the early embryonic stages of a primitive arthropod; *A*, Trochosphere in mercator projection, seen from the neural, or sub-umbrella surface; *C*, same from the side seen as a solid object; *B*, early stage of an arthropod embryo, seen in mercator projection; *D*, same seen as a solid object, from the side. In *A* and *C*, the circumoral area, with its system of radial and circular nerves, forms a part of the sub-umbrella of the trochosphere. In *B* and *D* this area is supposed to be infolded, giving rise to the proximal portion of the stomodæum, from which the system of stomodæal nerves and ganglia arise. The ancestral coelenterate body, according to this interpretation, is represented in the arthropod embryo by the procephalic lobes and stomodæum; the arthropod trunk, with its lateral and median nerve cords, is a new formation, arising as a local outgrowth from the ancestral cœlenterate body, or from the procephalic lobes of the arthropod embryo. On the aboral surface of the trochosphere is the area of yolk deposit and the "closing in" point, a pauperitic, degenerative region that is called the cephalic navel.

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II. THE STOMODÆAL NERVES.

We recognize two distinct systems of nerves in segmented animals. One belongs to the stomodæum, and probably represents the remnants of the circular and radial sub-umbrellar nerves of a cœlenterate-like ancestor; the other consists of longitudinal and transverse nerves that developed in the tentacle-like out-growth that gave rise to the body of the new animal. (Fig. 35.)

The stomodæum is looked upon as representing, in part, the infolded sub-umbrella. When invaginated, it carried with it the primitive system of circum-oral nerves, which then arise as circular and longitudinal nerves from the walls of the stomodæum. The outermost circular nerve (prototroch nerve(?)), is represented by the supra-stomodæal commissure with its anterior median, and two lateral, ganglia. These nerves and ganglia are without doubt very ancient structures, and their position and mode of development clearly indicate that they belong to a different system of nerves from those in the remaining part of the head or trunk.

There is probably a distinct post-œsophageal ganglion and commissure belonging to this system, although I have not succeeded in locating it, or in distinguishing it from the more anterior post-oral commissures. The supra-stomodæal commissure always sends nerves to the labrum, or rostrum, which receives nerves from this source only. The innervation of this pair of appendages, their median position in front of the mouth, and between the right and left halves of the forebrain, distinguish them from all others, and indicate their probable origin from tentacle-like organs of some very remote ancestor.

Originally the stomodæal nerves appear to have been intimately connected with the two median longitudinal nerves of the trunk, *i.e.*, with the median cardiac, on the hæmal side, and the median sympathetic on the neural. Both these connections are lost in the adults of the higher arachnids, *i.e.*, in Limulus, although in the scorpion the connection with the cardiacs seems to be retained.

The dividing line between the cœlenterate nervous system of the primitive head and that belonging to the bilateral outgrowth from it, cannot be accurately determined, and indeed there is no reason to suppose the two were ever distinct systems, the post-oral nerves being merely extensions of the older ones in the head.

III. THE FRAME-WORK OF THE NERVOUS SYSTEM.

The nervous system of segmented animals may be reduced to a system of longitudinal and transverse strands or cords.

Longitudinal Cords.—In the arachnids, eight longitudinal nerve cords may be recognized: a median hæmal one, from which arises the cardiac ganglion; a median neural one, or middle-cord (Mittelstrang of Hatschek), from which arises the so-called median sympathetic nerve; a pair of ventral cords, which give rise to the main axial nervous system, or neuron (brain and spinal cord); the paired pericardials; and the lateral sympathetics.

The Median Nerve, "*Median Sympathetic*," or "*Middle-Cord*," of arthropods appears to have extended backward, from the posterior part of the œsophageal region, or of the circumoral nerve ring, the whole length of the body. I have not been able to determine the peripheral distribution of its fibers. The main nerve and its sheath undergo many modifications. In the higher arthropods and vertebrates, the nerve itself atrophies and ceases to form a functional part of the nervous system. It serves, however, as a center for the development of voluminous, resistent envelopes from which is evolved the notochord. The history of the middle chord will therefore be described in the chapter on the evolution of the notochord

Transverse Cords.—Numerous transverse, or circular bands intersect the longitudinal ones, and lay the foundations for the transverse commissures, and for the segmental peripheral nerves. The latter usually lead by smaller branches into a subdermal plexus, from which the nerve ends are distributed to their respective terminals.

The ventral cords and the middle cord are confined to that surface of the embryo that is the first to develop. Their position during the early stages is the same in all segmented animals, and their presence definitely locates the primitive oral, or neural surface of the body.

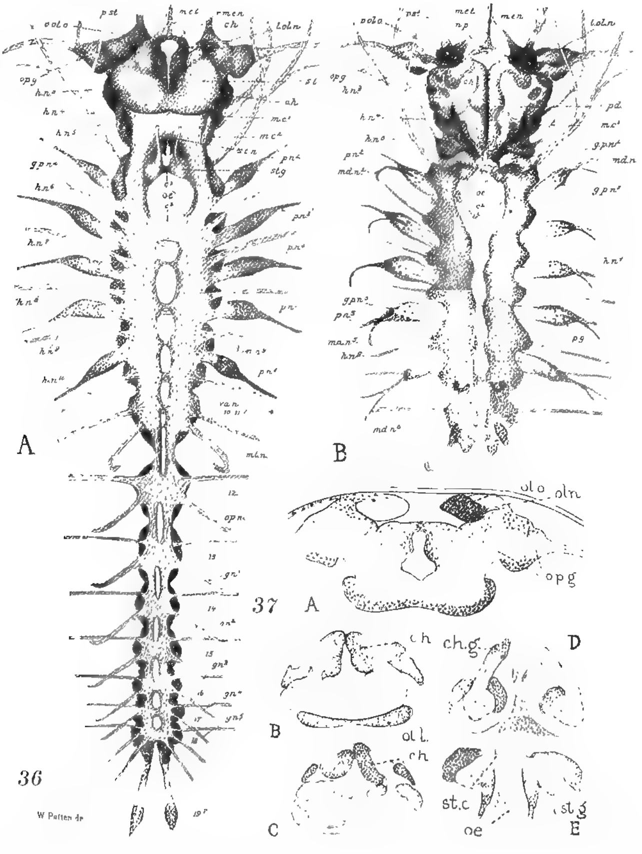

FIG. 36.—Brain and nerve cord of a young Limulus in the second larval stage. A, Hæmal surface; *B*, neural surface.

FIG. 37.—Sections of same. A, Through the optic ganglia and olfactory organs; *B*, through the middle of the hemispheres and the posterior part of the forebrain; *D*, through the cheliceral ganglia; *E*, through the suprastomodeal commissure and the lateral stomodæal ganglia.

The longitudinal cords serve to conduct nervous impulses in a longitudinal direction; in them are located the great majority of the nerve cells. The transverse bands serve to conduct nervous impulses in a centripetal or centrifugal direction. The comparatively few nerve cells that belong in them, as a rule, lie near their central or peripheral terminals.

The Process of Specialization. –The axial or central nervous system undergoes progressive evolution, or specialization, in a transverse and in a longitudinal direction.

The first process consists in the segregation of similar nerve fibers and cells into concentric, overlying longitudinal zones or tracts, the most notable example of this being the assembling of motor elements toward the hæmal surface, and of sensory ones toward the neural surface of the cords.

The second is the transverse division of the cords into blocks, or neuromeres, which then, singly or in groups, become the centers of some particular function. The linear specialization of the neuron is due to the gradual elimination of the heart, digestive and locomotor organs, from the anterior body metameres, and to the increased size of the sensory and ingestive organs. These changes lead to a great reduction in the number and volume of the motor nerve elements in the anterior metameres, and to the location of functional centers in the neuromeres according to a definite order, which follows that established in the corresponding groups of metameres. See page 209. This order, which is initiated at a very early period in the history of segmented animals, is as follows: olfactory; coordinating; visual; ingestive (*i.e.*, masticatory, swallowing, and gustatory); auditory; locomotory; respiratory (cardiac and branchial); digestive, and urogenital. This process of cephalization progresses in a cephalo-caudal direction, the functional centers becoming more and more sharply localized in the direction and order named above.

IV. The Differentiation of Peripheral Nerves.

The primary system of transverse nerves forms the foundation of the peripheral nervous system. The evolution of these nerves consists mainly in the resolution of the primary network into special nerve bundles composed of fibers having similar central and peripheral terminals.

The principal stages of the process appear to be as follows: 1. Each neuromere is at first connected with several pairs (four?) of transverse nerves, all of which may contain both motor and sensory elements. 2. The number of nerves for each neuromere is ultimately reduced to two main pairs, an anterior and a posterior. 3. The roots of the anterior nerves gradually shift toward the neural surface of the cord; the posterior ones retain a more hæmal position. The two series of nerves thus formed, are called the neural and the hæmal nerves. 4. The neural nerves develop ganglia on their proximal ends, and in those regions of the body where appendages are developed, supply only the appendages. The hæmal nerves are without ganglia and supply the remaining parts of the metamere. 5. In the cephalothoracic, or head region, the neural and hæmal nerves remain separate (vertebrates and arthropods), while in the more posterior regions they may unite, for a longer or shorter distance, forming single nerves with two sets of roots, ganglionated neural roots, and non-ganglionated hæmal roots. 6. Both neural and hæmal nerve roots contain motor and sensory elements, but at an early period in the evolution of arthropods the sensory elements become more and more predominant in the neural nerves, and the motor elements in the hæmal ones, this condition being most strongly marked at the anterior end, and diminishing gradually in a caudal direction.

Factors that Modify the Arrangement of Peripheral Nerves.—The more important factors that modify the primitive segmental arrangement of peripheral nerves are as follows: *a.* the location, isolation, and size of the peripheral terminals; *b.* the elimination of other terminals; *c.* the organic union of similar terminals belonging to different metameres; *d.* the relative age of the metamere in which they belong.

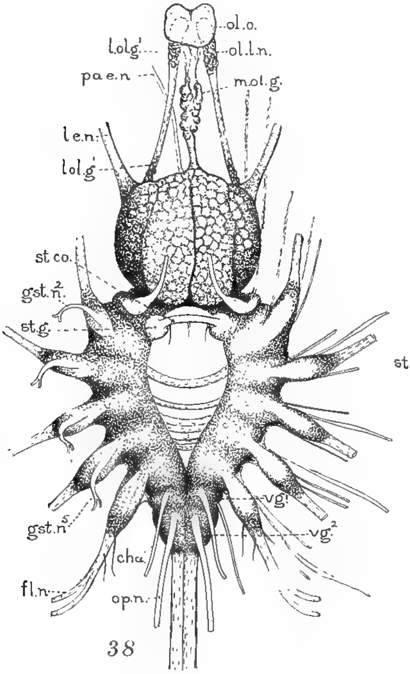

FIG. 38.—Brain of a young Limulus about three inches long; neural surface.

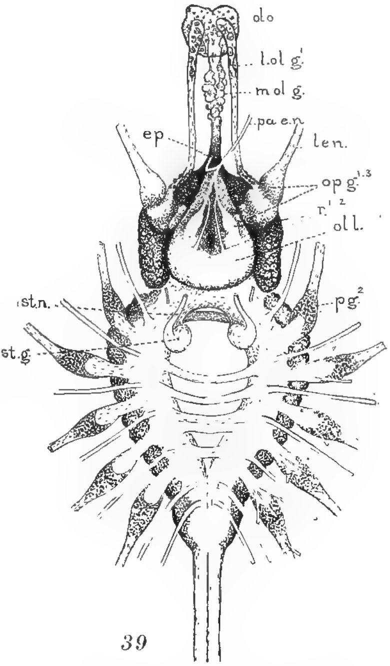

FIG. 39.—Same; hæmal surface.

a. The segregation of like nerve fibers into peripheral nerves, or into nerve tracts in the central nervous system, is determined by the time and place of origin of the peripheral terminals.

Wherever there are highly specialized organs, morphologically isolated, the associated nerve fibers and nerve cells show a similar isolation or segregation, the growth of each correlated part keeping pace, in the main, with the growth of the other. The primary sensory organs are superficial in position and lie in the ectoderm, close to the lateral margins of the neuron. The motor ones are deeper, more lateral or hæmal in position. The corresponding nerves have, in the main, similar relative positions, and these factors have controlled from the outset the segregation of motor components in a hæmal direction, and the sensory ones in a neural direction, both as regards their location in the peripheral nerves and in the central nervous system. With the invagination of the nerve cords, these conditions were still further exaggerated by the union of the neural crests in the median dorsal line, and by the position of the mesoblastic somites. (Fig. 137.)

The wide separation of the neural and hæmal nerves, as for example in the thorax of Limulus and the scorpion, is due on the one hand to the location and specialization of the appendages, coxal sense organs and ganglia, and on the other to the location of the more peripheral trunk muscles and sense organs. It no doubt had its origin at a very early period in the evolution of metameres.

b. *Elimination.*—In the arthropods there is a progressive elimination from the anterior metameres of the motor, nutritive, cardiac, and respiratory organs, leaving little but the leg and jaw muscles, and the primary sense organs, such as the eyes, olfactory, gustatory, auditory, and tactile organs. The nerve elements associated with those organs disappear with them. Those that remain increase in volume and independence with their corresponding peripheral terminals, while their central terminals tend to completely monopolize their appropriate neuromeres. In this way the primitive character of the segmental nerves may be lost or greatly modified. This is the case in the procephalon, where the only peripheral nerves that remain belong to the eyes and olfactory organs, all other peripheral elements having been eliminated, if they ever existed there.

c. *Union.*—Where organs belonging to different metameres perform the same function their nerves tend to unite, forming a common bundle, or nerve, or tract. Such compound nerves, consisting of the united branches of separate segmental nerves, may themselves simulate independent segmental nerves, and greatly disguise the original segmental arrangement. Examples of this mode of segregation are seen in the segmental cardiacs, the hypobranchial, the intestinal (Figs. 57, 58), and to a lesser degree, the gustatory nerves of Limulus.

c. *Historic Factor.*—If we attempt to homologize the nerves in one part of the head with those in another, or with those in the trunk, we meet with insuperable difficulties because, as we have seen, each group of metameres has a history of its own that is different from that of all the others, and this history is reflected in the structure of its nerves and neuromeres. The attempt to homologize the structures in the head with those in the trunk or tail, except in the most general way, is an illogical and hopeless undertaking, for the caudal metameres belong to later generations that came into existence under new conditions and were provided with different organs from those in the old. Except for a small number of the most anterior ones, the trunk and caudal metameres of vertebrates did not exist in the arthropods. They arose with the vertebrate stock and never developed any organs comparable with the cephalic appendages, jaws, gill arches, or visual organs. Hence it is clear that there can be no exact homology between the head metameres of an arachnid or a vertebrate and a trunk metamere of the same animal. For that reason, therefore, we may not consider the cranial nerves, or cranial neuromeres, or cephalic sense organs, as modifications of those in the trunk, or *vice versa*, without conveying an entirely false impression of their real history and meaning.

* * * * * * * * *

In the lower arthropods, the peripheral nerves are generally arranged throughout the whole body, in typical segmental fashion. In the higher arachnids, due to the operation of the above described factors, this clear cut metamerism declines, or is greatly obscured. The broad distinction between cranial and spinal nerves becomes clearly established, and the extensive elimination of motor elements, as well as the local segregation of sensory and motor components of different nerves into compound nerves having a similar function and distribution, has given to the entire system the same structure and general arrangement of parts seen in the vertebrates.

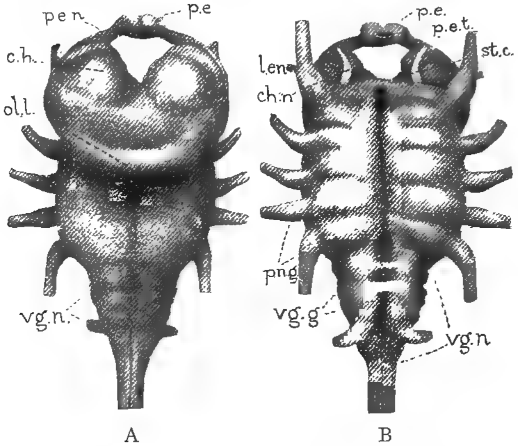

FIG. 40.—Models of the brain of a young scorpion, just hatched. *A*, Hæmal surface; *B*, neural surface.

In Limulus, for example, this process of specialization has produced the highly characteristic olfactory, pineal eye, and lateral eye nerves, as well as the compound system of gustatory, branchio-thoracic (hypoglossal), cardiac, and intestinal nerves. These nerves are already so complex and highly modified that the original segmental arrangement is now exceedingly difficult or impossible accurately to determine.

The same conditions, but in a still more exaggerated form, are seen in vertebrates, and in part justifies the revolt of certain American neurologists against the apparently hopeless task of determining the segmental value of vertebrate cranial nerves and their relation to the dorsal or ventral roots of spinal nerves. They have laid great stress on the analysis of nerves into their functional components; but in perfecting a highly artificial system, they have neglected the deeper morphological problems involved in their more primitive segmental arrangement. It is clear that both the old and the new method must be retained. But neither method alone applied to the vertebrates can ever give us a true picture of their ancestral condition. That can only be obtained from the arthropods where the highly specialized condition seen in the vertebrates has its origin.

V. Neuromeres and Metamerism.

Metamerism of the body and the subdivision of nerve cords into blocks or neuromeres are characters that were probably slowly evolved in bilateral animals; not inherited, even in a rudimentary form, from cœlenterate ancestors.

The evolution of neuromeres probably began in the trochozoa. They are well developed in the annelids and in the arthropods, especially in the abdominal regions. In the higher arthropods, the clear-cut distinction between adjacent neuromeres of the head is greatly obscured by their fusion into larger groups, and by the segregation of their constituents into new groups, according to their function. In vertebrates, the post-cephalic part of the neuron, which has been more recently acquired, and which is not represented in arthropods, is never divided into distinct neuromeres, and probably never was so divided.

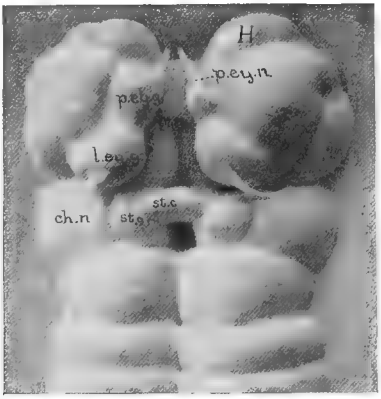

Fig. 41 —Model of the forebrain region of an embryo scorpion, stage *G*, Fig. 18.

Even in the arthropods and annelids, it is doubtful whether there is any such thing as a neuromere, complete in itself and devoted to a single body joint or metamere. There are certainly none in Limulus, or in the scorpion, and the lower down we go, as for example into the phyllopods, the less sharply defined the neuromeres become; that is, the ganglionic masses are more diffuse, and the peripheral nerves more numerous, and not so strictly segmental in their origin or distribution (Branchipus).

In Limulus and scorpion, where there appears to be such an exact and exclusive association of the body segment with its neuromere and nerves, there is no such exclusive association in fact, because many motor neuromeres and the central ends of many sensory fibers are located in some neuromere anterior to the one where the nerve fibers leave the cord to reach their peripheral terminals. That is, the central nerve terminals and the centrally located nerve cells, in many cases lie in different metameres from the peripheral organs with which they are associated. (Figs. 59, 60.)

This condition appears to prevail in the most primitive arthropod neuromeres, hence that complete functional and morphological correspondence, supposed to occur between a body joint and a nerve cord joint, does not exist. Metamerism has developed to a different degree in the two systems and affects them in quite a different manner. The morphological segmentation of the nerve axis does not coincide with that of the body, and the functional segmentation of the nerve cord does not coincide with its morphological segmentation, for both motor nerve cells and sensory dendrites are frequently located in a neuromere in front of the metamere in which the corresponding nerve fibers leave the cord, and in which they have their peripheral terminals.

A partial explanation of the lack of correspondence between functional and morphological metamerism of the nerve cord is afforded by what takes place in embryo scorpions. Here each neuromere is composed of two distinct segments, and as the space between the abdominal ones increases, the anterior segment of one neuromere unites with the posterior segment of the one in front of it, thus completely changing the original grouping of the half neuromeres. It is not clear whether this takes place in Limulus or in the other arthropods I have studied, but it probably does, otherwise it is hard to understand how the cell bodies of the motor neurones are located in the neuromeres in front of the one from which the corresponding motor nerves leave the cord.

It is therefore clear that Loeb's attempt to prove that each abdominal neuromere in Limulus is a complete reflex center for its corresponding gill, is based on a misconception of the structure of the nerve cord. His interpretations of his experiments are incorrect because, as we shall show later, they are based on a misunderstanding of the structure of a neuromere and the distribution of its nerves.

VI. The Primitive Sense Buds.

The main nerve trunks in the arthropods represent bands of metamorphosed sense organs, and they coincide with the lines along which such sense organs were distributed in the remote ancestral forms. The transformation of these primitive sense organs into nerve cells constitutes an important step in the evolution of the central nervous system. Many details in this process are still retained in the embryos of arachnids.

In the scorpion, the entire brain and cord is an aggregate of innumerable, closely packed sense buds which, under a low power, produce a mottled, or pitted appearance that is very characteristic. (Figs. 15 and 16.) Under a higher power, and in sections, each bud appears pear-shaped, with a goblet-shaped cavity opening to the exterior at one end, and leading into a narrow vertical canal at the other. They consist of typical sensory cells, having the same shape, arrangement, and rod-like ends as those in the segmental sense organs on the outer margins of the coxæ. (Fig. 74, *E*.)

The primitive sense buds appear as soon as the six thoracic appendages are outlined (stage *B*), and are at first uniformly distributed over the entire cord and cephalic lobes, with the sole exception of the olfactory lobes. (Fig. 15.) At a later stage, *E*, those on the lateral margin of the cord are distinctly larger than the rest, forming two dark bands. From the buds on the posterior lateral margin of each neuromere, arise the ganglion cells at the roots of the post-thoracic nerves (spinal ganglia). The buds on the smaller, or originally posterior segment of the neuromere give rise to the cluster of motor nerve cells which are found near the anterior nerve roots.

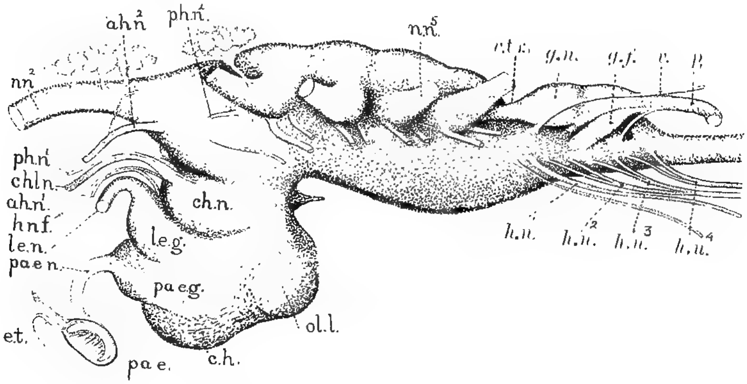

FIG. 42.—Brain of adult scorpion, from the side.

As development proceeds, the central cavity of the bud closes, the sensory cells lose their cylindrical form, and their hair-like, or rod-like outer ends disappear; finally each bud forms a small cluster of ganglion cells.

In the late embryonic stages of the scorpion, the metamorphosed sense buds form long conical masses of cells with the proliferating apices directed inward. Their appearance is then much like the cell clusters formed by neuroblasts. (Figs. 227–228.)

Cell division in the sense buds diminishes after their metamorphosis, the ganglion cells reaching an approximately fixed number at an early embryonic period. This, however, does not apply to the minute cells in the hemispheres, in the olfactory lobes, or in the pedal ganglia of Limulus, for these cells appear to increase in number steadily, at least as long as the animal continues to grow in size.

In Limulus the cells descended from a given sense bud, during the late larval periods, form well defined clusters of pear-shaped ganglion cells, with a special neuroglia investment. Each cell of the same cluster appears to project its fibers along the same path, to the same terminals. (Figs. 61–64.)

In Limulus it has not been possible to identify each nerve-cell cluster with the antecedent sense buds, for the latter are best seen in the embryos of scorpions, while my most detailed work on the cord has been done on Limulus. But the conditions in the two animals are so similar that there can be no reasonable doubt that an arthropod neuromere consists of distinct clusters of nerve cells, each surrounded by a special sheath of neuroglia, each projecting its fibers along the same paths to the same terminals, and each directly descended from one or more embryonic sense buds.

In the early stages of the neuron in vertebrates, as in the late stages in the scorpion, the nerve cells are often arranged in parallel vertical rows, which may be interpreted in the same manner as in arthropods, that is, as the ontogenetic remnants of ancestral sense buds.

There are many familiar instances where nerve cells arise from the same points in the ectoderm as the sensory ones. It is highly probable, in such cases, that the nerve cells are ultimate phases in the specialization of sense cells. For example, in Acilius, a few cells of large size leave the embryonic retina at a comparatively late stage; they finally join the optic ganglion and become giant nerve cells, having such a peculiar form and location that they may be readily recognized through life (Patten). Ganglion cells may also arise from the gustatory epithelium in Limulus, or from the epithelium of lateral line organs in vertebrates. But in none of these cases has it been clearly shown, to my knowledge, that a functional and structurally complete sensory cell is bodily metamorphosed into a ganglion cell. However, just such a metamorphosis as this does take place in Limulus and Branchipus, where the large rod-bearing visual cells are converted into true ganglion cells, which still retain indications of their primitive grouping into ommatidia and remnants of the visual rods. (p. 162 and Fig. 109, *A*.)

The transformation of well developed sense buds into ganglion cells, as just described for the neuron of arachnids, is not, therefore, without precedent.

In most arthropods, the primitive sense buds, while undoubtedly present in some form, are not as well developed as they are in scorpions. Hence certain authors have failed to recognize their real character, and have interpreted them as neuroblasts, or even as nutritive folds, or as folds produced by growth pressure. Such interpretations are untenable. It is true that the sense buds may be represented by small conical groups of cells, or nuclei, arising from the proliferation of a single deep-lying cell, or nucleus, or "neuroblast." But the formation of these neuroblasts is to be regarded as an abbreviated method of repeating the sense bud stage so clearly seen in the scorpion.

Even these neuroblasts may be omitted, or their appearance postponed to a relatively late embryonic period; the entire cord then has its origin in a few terminal neuroblasts (or telo-neuroblasts), as in Cymothoa.

CHAPTER IV.

THE SUBDIVISIONS OF THE BRAIN.

I. THE PROSENCEPHALON, OR FOREBRAIN.

The fore brain of arthropods is that part of the neuron that usually lies in front of the stomodæum. In the embryos it is the anterior expansion of the medullary plate called the procephalic lobes. As nearly all traces of mesoderm and appendages have disappeared from this region, there is but little evidence accessible to indicate the presence there of metameres. In many arthropods the lobes are divided into three main divisions, with no recognizable separation, at any time, between them and the postoral sections of the nerve cords; hence we may, for the present, regard the main divisions as greatly reduced metameres, and the central portions as neuromeres.

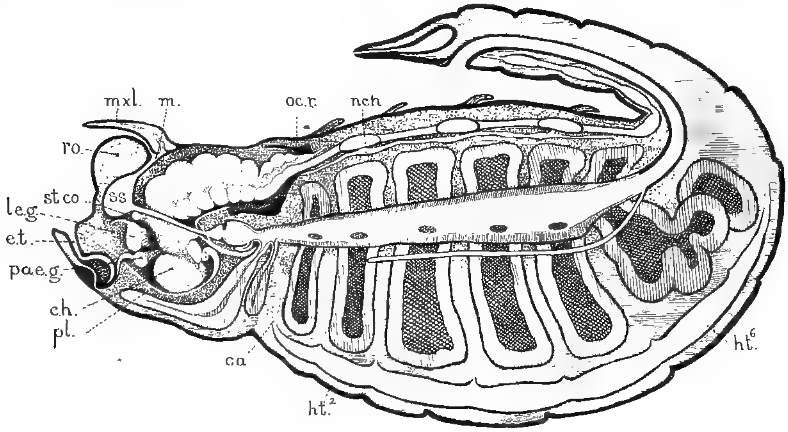

FIG. 43.—Sagittal section of a young scorpion.

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Acilius.—The structure of the procephalic lobes is best seen in the embryos of those insects which lead an active larval existence, as for example in Acilius. (Fig. 14.) Here they are divided transversely into three similar parts, which probably represent all there is left of three procephalic metameres. Each metamere is also divided into three parts: *a.* a median one, representing a forebrain neuromere, corresponding to the postoral neuromeres; *b.* a middle part, representing a segment of the optic ganglion; and *c.* a lateral one, forming a segment of the optic plate, each plate containing two ocelli. Between each segment of the optic ganglion and the optic plate is a deep infolding, *iv.*$^{1-3}$, which later closes, covering up the optic ganglia, but leaving the ocelli and neuromeres in their original position.

A pair of small appendages, *ro*, lie near the first metamere. Later, they fuse to form the labrum. The second metamere has no appendages. The third one is closely associated with the antennæ.

From the upper or neural surface of the first (?) and second forebrain neuromeres, are developed dense masses of small cells, with deeply stained nuclei, that give rise to the characteristic mushroom bodies of insects. They may be recognized in apparently all classes of arthropods, attaining enormous size in the ants, bees, wasps and spiders, and reaching extraordinary dimensions in Limulus. In structure and function (Limulus), they are true coordinating centers, and are to be regarded as the earliest stages in the phyllogenetic development of the cerebral hemispheres of vertebrates.

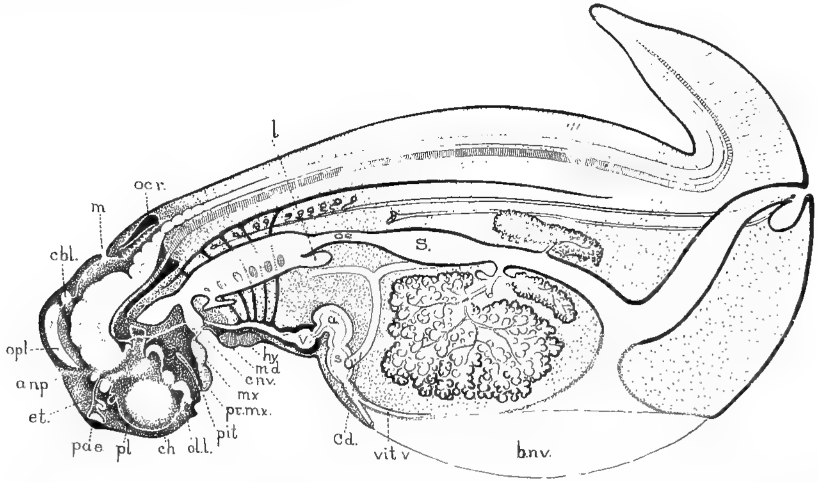

FIG. 44.—Sagittal section of a primitive vertebrate embryo, showing the relation of its principal organs to those in the arachnids; schematic.

In the **arachnids,** the cephalic lobes differ from those of Acilius: *a*. in the indistinct segmentation of the optic plate, *b*. in the relatively late appearance of the segmental sense organs (median, and lateral, eyes, and olfactory organs), and *c*. in the peculiar character of the first metamere. Other differences appear later, as we shall presently indicate.

In the scorpion (Fig. 15), which may be taken as the type, the first metamere is never divided into neuromere, optic ganglion, and optic plate, but forms at the outset a deeply grooved transverse band, *ol.o.* The walls of the infolding contain minute, deeply stained nuclei, that make it very conspicuous, both in sections and surface views. The band marks the primitive anterior end of the brain and is the anlage of the **olfactory lobes.** The infolding deepens, at first more rapidly at either end, and ultimately carries the whole lobe below the surface, and backward, underneath the brain. Here it forms a hollow, bilobed transverse band, conspicuous in all subsequent stages, when the brain is viewed from the hæmal side, but almost entirely concealed below the hemispheres when seen from the neural side. (Figs. 40–42, 43, 46, 47.)

The **cerebral hemispheres** arise as mushroom-like expansions of the second neuromere. In Limulus, they are very conspicuous in the early stages, and ultimately grow to an enormous size. They consist of dense masses of minute cells, with deeply stained nuclei, unlike any others in the nervous system. (Figs. 37 and 38.)

As these cells multiply, the hemispheres project above the surface of the brain and then mushroom, forming large, overhanging lobes. We may distinguish anterior, lateral, and posterior lobes, the latter being much the largest. In addition, there is a large lobe on the median face of each hemisphere. (Figs. 47, *B*, 48 and 49, *g.c.*) The hemispheres, throughout life, are connected with the neural surface of the second neuromere by a thick, vertical stalk, or peduncle, composed of nerve fibers.

As the hemispheres increase in volume, the posterior lobe completely overlaps the third neuromere, and the lateral and anterior lobes partly envelop the hæmal surface. In the adult, the hemispheres are irregularly convoluted, and their median faces are flattened against each other so that they form a large spherical mass that has a striking resemblance, in external form, to the hemispheres of vertebrates. (Figs. 38–48.)

In the scorpion, the hemispheres are much smaller than in Limulus and are crowded farther forward by the optic ganglia, which have almost united in the median line behind them. Later the whole prosencephalon is bent toward the hæmal surface, through an angle of something more than 90°. (Fig. 47, *A*.) When the **fore-brain flexure** is completed, about the time of hatching, the hemispheres lie on the anterior hæmal surface of the procephalon. (Figs. 42 and 43, *c.h.* or *h.*) This flexure is very marked in all arachnids, so far as known, except in Limulus.

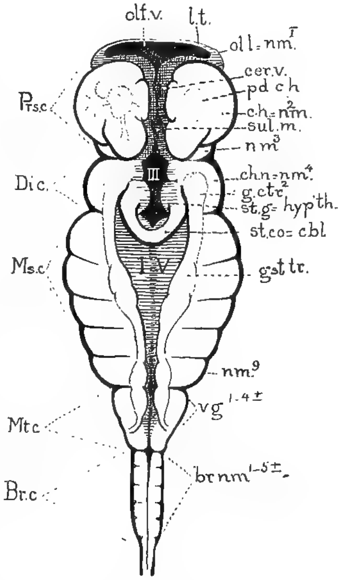

FIG. 45.—Diagram of the arachnid brain, showing the number and grouping of the neuromeres, the ventricles, the vagus lobes, and the longitudinal gustatory tracts and their relation to the stomodæal ganglia.

The third neuromere undergoes very little change. It may be recognized for a considerable period as a separate neuromere whose neural surface is covered with tufts of large ganglion cells. It is gradually incorporated into the thick mass of tissue that constitutes the body of the forebrain commissures, and upon which the hemispheres rest (basal ganglia). (Fig. 46.)

The history of the procephalic sense organs and their nerves and ganglia will be considered under their appropriate heads.

II. THE DIENCEPHALON.

The diencephalon in arthropods consists of a variable number of neuromeres surrounding the mouth. The first neuromere following the procephalic lobes (antennal neuromere of insects, cheliceral neuromere of arachnids) may be regarded as the initial neuromere of this subdivision of the brain. Its large size and its special relations, on one side with the hemispheres, and on the other with the stomodæum and the gustatory organs, lend to this neuromere and those im-

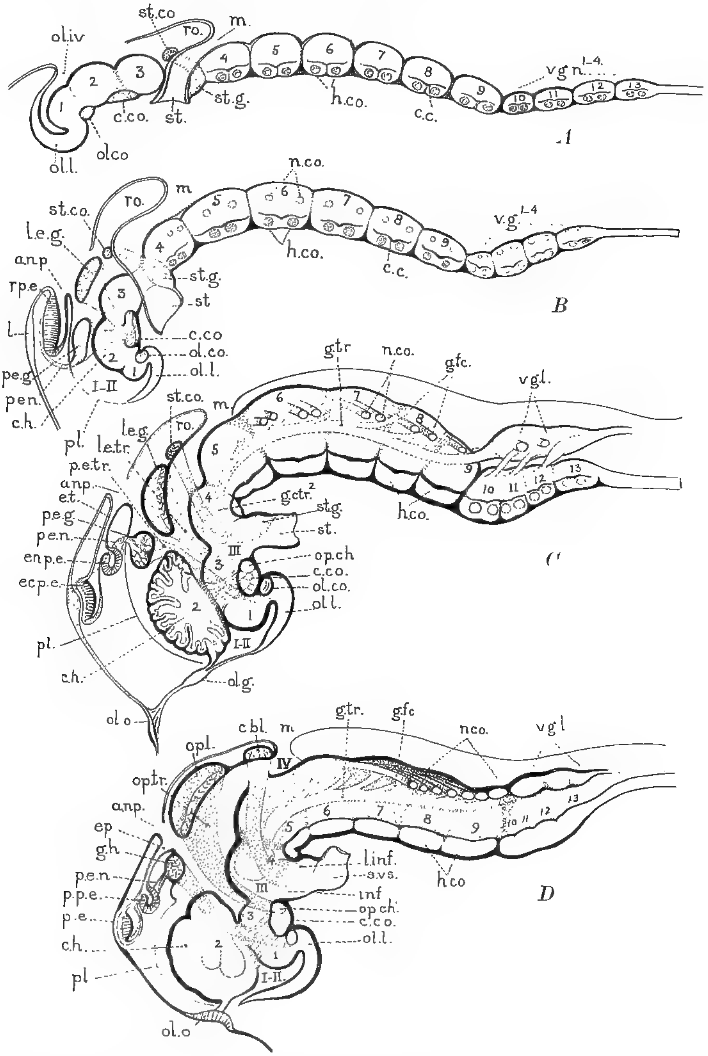

FIG. 46.—Semi-diagrammatic sagittal sections, showing the relations of the principal nerve centers in the brains of arachnids and vertebrates. *A*, Embryo scorpion (stage *B*, Fig. 15); *B*, embryo scorpion (stage *G*, Fig. 18); *C*, hypothetical intermediate condition, based on the conditions in both scorpion and Limulus. The embryonic palium and the anterior neuropore have been carried over into the adult, and the lateral eye ganglia have been projected onto the neural surface, otherwise the typical arachnid conditions remain essentially unmodified. *D* shows the probable position and relation of these parts in a vertebrate. The ventricles are indicated in Roman numerals, the neuromeres in Arabic numerals.

mediately associated with it in the circumoral region, a special distinction that justifies their elevation to the rank of a distinct brain region.

* * * * * * * * *

In the scorpion (Figs. 15, 16, 43), by the time the embryo hatches, the forebrain is bent through something more than 90°, onto the anterior hæmal surface of the egg. The angle of this bend lies behind the cheliceral neuromere, which, therefore, faces forward, connecting the forebrain, now on the hæmal surface of the egg, with the thoracic neuromeres on the neural surface. (Figs. 43–46.)

In practically all adult arachnids, the cheliceræ move forward to the very anterior end of the head and lie close together in front of the rostrum and stomodæum, instead of behind them, as in the earlier stages. The result is that the cheliceral nerves, instead of arising from the sides of the brain, like all the other nerves to the appendages, arise from the median, neural surface, and point cephalad and neurad. (Fig. 40.)

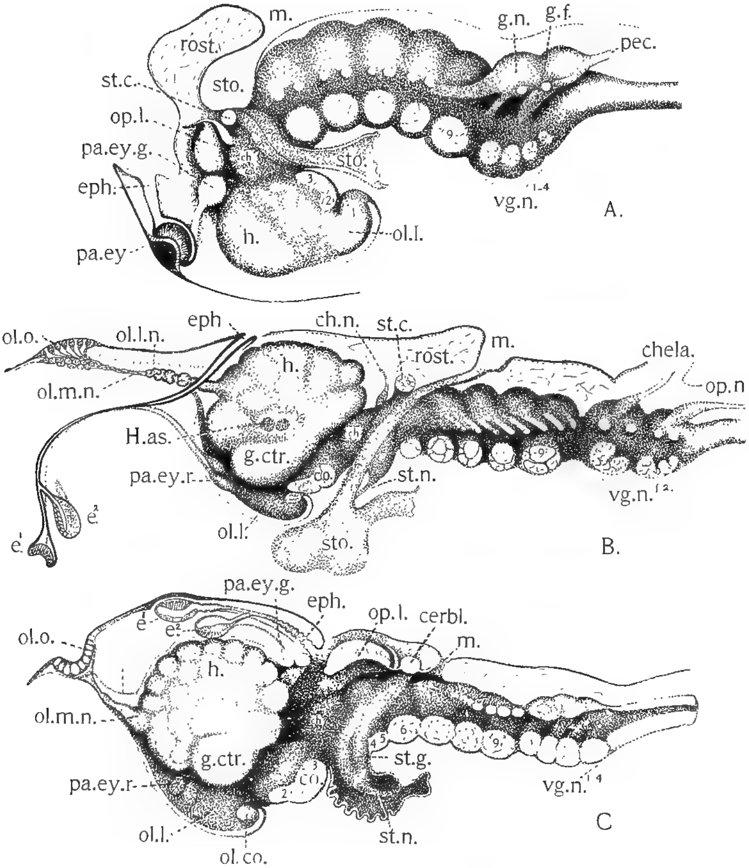

FIG. 47.—Sagittal sections of brain models. *A*, young scorpion; *B*, Limulus; *C*, a hypothetical brain, combining the principal characters of the brain of Limulus and scorpion, and with the parts in the position they are supposed to occupy in a primitive vertebrate.

In Limulus, the cheliceral neuromere is less conspicuous in the older stages because it is partly covered by the posterior, lobes of the hemispheres, which grow back over it. (Figs. 37, 38, 47 and 48.) As the cheliceral neuromere moves forward, it unites so intimately with the third neuromere of the forebrain that it is difficult to distinguish the boundaries between them. Both neuromeres help form the basal ganglia that lie underneath the lobes of the hemispheres, and which may be said to form the floor of the prosencœl. (Figs. 57, 58.)

* * * * * * * * *

Minute Structure.—The minute structure of this region has been worked out in some detail in Limulus. Two great masses of neurones that probably belong to the third procephalic neuromere are found on the median, neural surface of the brain, underneath the posterior lobes of the cerebral hemispheres (Fig. 49, *ch., H.c.*) Their neurites extend caudad and outward, and then cephalad, forming a large part of the posterior cerebral peduncle. On reaching the base of the hemispheres, they spread out into great fan-shaped masses that penetrate into the cortex of every lobe and convolution, except the median or gustatory one. (Fig. 48 and 49, *G.c.*) They run parallel with similar fibers arising from the two clusters of association cells, *H.a.s.* lying above the gustatory lobes. They terminate in minute, spherical masses of neuropile that form an indistinct, sub-cortical layer in each lobe, and near which the neurites of the cortical, granule cells terminate. Some of the fibers appear to terminate between the cortical cells. (Fig. 50.) Numerous branches from these neurites ramify in the forebrain commissure, *c.o.*, and in the cheliceral lobes, *ch.l.*

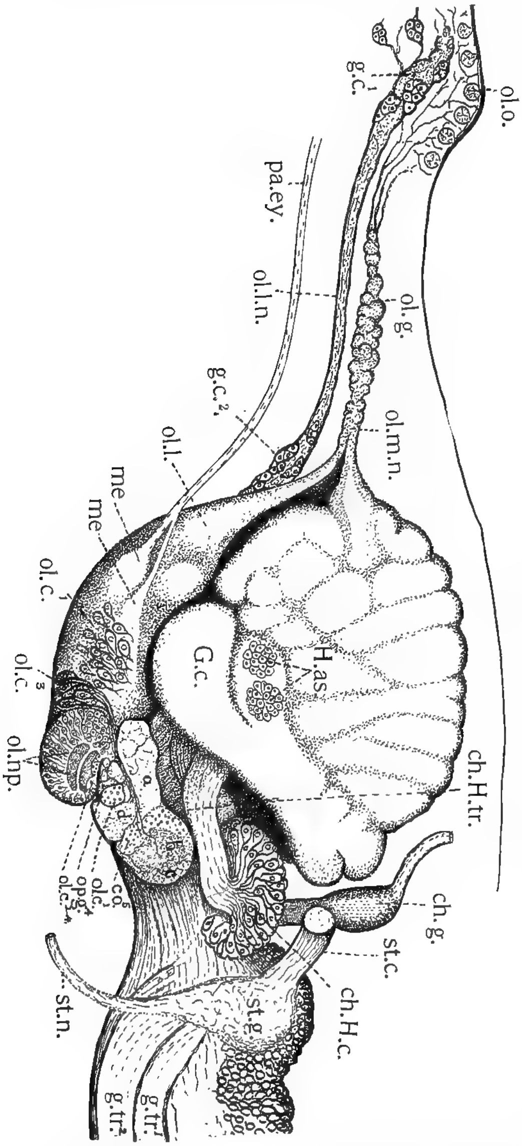

FIG. 48.—Median surface of a model of the forebrain of a young Limulus about four inches long.

The cheliceral lobes (Fig. 49, *ch.l.*) are large spherical masses of neuropile lying on the anterior lateral margin of the cheliceral neuromeres. Their lateral surface is covered with small cells, whose neurites together with many others, ramify in their interior. The most conspicuous ones are those belonging to the two sets of cerebral association cells, *ch, H.c.* and *H.as*, and the terminal dendrites of the main gustatory tract, *G.tr*^{4}.

The middle portion of the cheliceral neuromere forms the posterior portion of the great mass of commissural fibers and neuropile upon which the hemispheres rest. (Fig. 48, *b* and *c*.) One may recognize in it: coarse fibers of the lateral cell clusters, Co^5; fibers from the large, central cells of the olfactory lobes (Figs. 48 and 51, $ol.c^1$.); a dark, central mass of neuropile, *b*. in which innumerable neurites, apparently from all parts of the brain, terminate; and a thin layer of commissural fibers extending from one crus to the other, *c*.

The more anterior portion of the commissural mass (Fig. 48); represents the commissural bundles of the second and third forebrain neuromeres, *a* and *d*; and the several olfactory, $ol.c^{1-4}$, and optic commissures, $op.g.^4$.

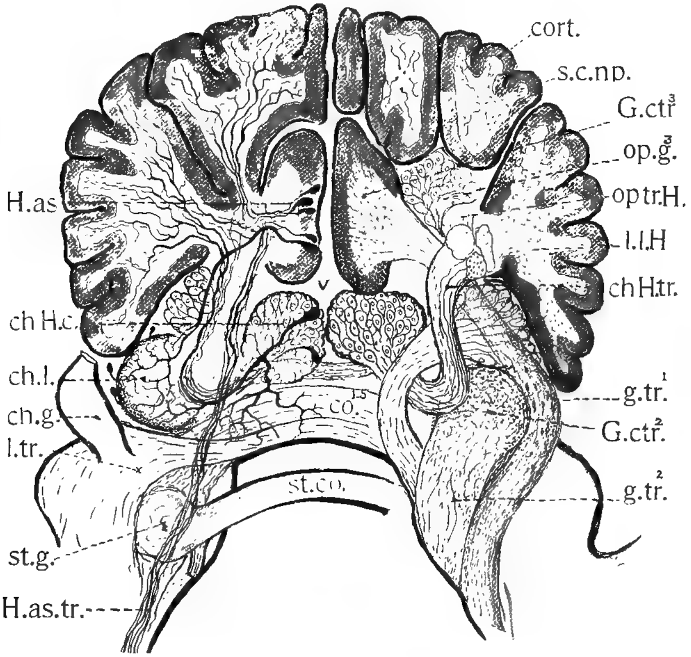

FIG. 49.—Diagonal section of the forebrain of a young Limulus (about four inches long), methylene-blue preparation stained with carmine. Camera outlines.

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The Stomodæal Ganglia and The Suprastomodæal Commissure.—The cheliceral neuromere is always intimately associated with the system of stomodæal nerves and ganglia. The lateral stomodæal ganglia lie on the median side of the nerve cords, *st. g.* The stomodæal commissure, *st.c.*, which always crosses in front of, or over, the stomodæum, forms one of the most conspicuous and constant landmarks of the arthropod brain.

In the scorpion, the anlage to the lateral stomodæal ganglion may be faintly seen from the surface, on the anterior median face of each half of the cheliceral neuromere. (Figs. 14 and 15, *st.g.*) The same anlage may be seen in sections, in Blatta, Acilius, Buthus and Limulus, as a thickening or evagination of the side walls of the stomodæum. (Fig. 53, *c.*) The evaginated part separates from the stomodæum and, uniting with the adjacent neuromere (cheliceral or antennal), forms the lateral stomodæal ganglion. In insects, a frontal, or median stomodæal ganglion arises in a similar manner from the anterior median wall of the stomodæum. (Fig. 14.)

Nerves extend backward from the stomodæal commissure into the labrum, which never receives nerves from any other source. From the deep, or hæmal, end of each lateral ganglion, a nerve extends along the side walls of the œsophagus, connected by several transverse bands with a median nerve arising from the frontal ganglion. (Fig. 35.)

In arachnids, the median stomodæal nerve seen in the insects is absent, and there are no traces of ganglion cells in the commissure.

The stomodæal nerves and ganglia represent a distinct system of nerves that cannot be compared with any others. That it is a very ancient system is shown by its vigorous growth at an early ontogenetic period. The ganglia, nerves, and commissure, form a special system controlling the peristaltic actions of the stomodæum in swallowing, grinding, or sucking food. These reflexes may possibly be directly stimulated through the sensory cells in the inner lining of the stomodæum or in the lips; but, in Limulus at least, an essential condition appears to be an initial stimulation of the gustatory organs in the jaws, or of the olfactory organ. From the gustatory organs, important nerve tracts converge toward a common center in the cheliceral neuromere, and toward the lateral stomodeal ganglion. (Fig. 114.)

Comparison of the Diencephalon of Arachnids and Vertebrates.—When the mouth of the arachnids was shut off from the exterior by the backward overgrowth of the rostrum and of the optic lobes, and by the closing up of the cerebral vesicle, the stomodæum and the adjacent ectoderm remained in the vertebrates as the epithelial lining of the third ventricle and adjoining chambers; and the opening through the floor of the brain, which served as the passageway for the old œsophagus, remained as the infundibulum. The inner end of the stomodæum, that protrudes through the infundibulum, became the sacci vasculosi; the lateral stomodæal ganglia, the lobi inferiori; and the stomodæal commissure, the anlage of the cerebellum. (Figs. 3, 46.)

The median haemal portion of the cheliceral neuromere, which is the principal center for the olfactory, gustatory, and stomodæal impulses, corresponds with the hypothalmic region, while the cheliceral lobes and the cerebral association cells, *ch.H.c*, mark the beginning of the thalamus. On the roof of the ventricle, the median ocellus persists as the parietal eye. (Fig. 47, *c.*) Let us examine these comparisons more carefully.

* * * * * * * * *

The Stomodæum.—In existing arachnids, the roof of the diencephalic region consists of the epithelium that was produced by the backward migration of the rostrum and the mouth. (Figs. 3, 46, and 47.) Owing partly to the manner in which the entire brain has slipped forward, underneath the skin, and in part to this backward growth of the rostrum, the stomodæum becomes divided into two sections, an inner one passing through a narrow opening between the crura to the enteron; the other extending backward, over its outer surface, to the mouth. The outer section is dilated in most arachnids to form a large chamber or sucking stomach. It is merely a matter of terminology whether we call the mouth the opening of the original infolding, leading directly through the brain, or the opening which lies much farther back beneath the overhanging rostrum. In the vertebrates, both the original infolding and its secondary extension may be recognized.

As we have shown elsewhere, the closing of the primitive œsophagus was due to several factors, among which were: the crowding together of the cranial neuromeres; the increasing size of the palial fold; the backward growth of the rostrum and optic ganglia along the anterior median line; and the deepening of the median, neural groove by the precocious thickening of the lateral cords. These conditions lead to the infolding of the entire neuron at an early embryonic period, and to its complete separation from the overlying ectoderm. Thus, not only were the eyes enclosed within the brain chamber, but the passage way for the stomodæum first became greatly constricted, and then the opening into it was covered over by the neural crests and optic ganglia, thus forever closing the entrance to the enteron from that direction.

The several processes seen in the arachnids, in vertebrate embryos, are blended and abbreviated into a simple marginal overgrowth and an axial depression of the medullary plate. The chamber thus formed over the cheliceral neuromere then becomes the third ventricle; the epithelium of the extra-neural part of the stomodæum merging with, and forming a part of, the epithelial lining of the adjacent cavities. The primitive stomodæal infolding may still be seen in the amphibia, as a minute pit in the middle of the procephalic lobes, near their anterior margin. (Fig. 46.) This pit lies in the position of the future infundibulum and appears to deepen, giving rise to it. The epithelium forming the floor of the depression is continuous with the epithelial layer that covers the inner surface of the adjacent brain cavities, and represents the deeper end of the stomodæum, now converted into the membranous saccus vasculosus.

From the posterior lateral walls of the infundibulum, two rounded ganglionic lobes are evaginated, the lobi inferiori. They correspond with the lateral stomodæal ganglia of the arachnids. Like them, they have direct nervous connections only with the adjacent epithelial sac (stomodæum), although the nerve centers themselves are of considerable size.

According to Johnston, the epithelial wall of the saccus contains large spindle-shaped, sensory cells, bearing a tuft of cilia which projects into the cavity of the tube (ventricle). From them arise nerve fibers that help form a nerve plexus over the outer surface of the sac. The afferent and efferent fibers form two lateral symmetrical tracts which run through the corpus mammalare to the ventral part of the thalamus.

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The Optic Ganglia.—The palial overgrowth carried the united parietal eyes over the region of the old stomodæum, thus helping to form the roof of the third ventricle, and giving rise to the ganglion habenulæ and its commissural strands.

The lateral eye ganglia also united to form a part of the brain roof, but were crowded still farther backward, beyond the tween-brain neuromeres, carrying with them the stomodæal commissure. The latter then became the anlage of the cerebellum, and the optic ganglion became the tectum opticum. (Figs. 3 and 46.)

The optic tracts extend diagonally backward and upward from the optic chiasma to the optic ganglia, and help to form the external lateral walls of the diencephalon; the primitive cerebellar tracts extend diagonally downward and forward, over the inner or ventricular surface of the diencephalon to the lobi inferiores. Thus the location and direction of these important fiber tracts still tell the history of the parts in which they terminate. (Fig. 46, *D.*)

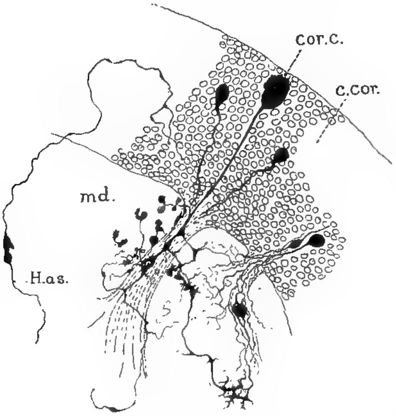

Fig. 50.—Portion of the cerebral cortex of a young Limulus. Camera, Zeiss obj. 16 mm., oc. 18. Golgi preparation.

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The Cheliceral Neuromere.—The anterior neural portion of the cheliceral neuromere is probably in part comparable with the thalamus division of the diencephalon. It contains the great masses of association cells going to the hemispheres and cheliceral lobes (Fig. 49, *ch.l.*) and also the cheliceral nerves and ganglia. (Fig. 49, *ch.g.*) The cheliceral nerves unlike all the other cranial nerves, arise from the median neural surface of the neuromere. They are probably crowded against the cerebellar commissure by the enlargement and backward migration of the optic lobes. (Figs. 47, 57 and 58.) They are represented in vertebrates apparently by the fourth nerves, which seem to arise from the roof of the brain, between the optic lobes and the cerebellum, although their roots have their origin far forward, on the floor of the midbrain region. The exceptional location and direction of these nerves in vertebrates, therefore, is in harmony with their exceptional location and direction in arachnids; and the extraordinary resemblance between them affords collateral evidence in confirmation of the explanation just given for the origin of the tectum opticum and the cerebellum. Otherwise these peculiarities of the fourth nerve are inexplicable.

* * * * * * * * *

It will be observed that the whole floor of the vertebrate brain consists of more or less modified neuromeres. Those structures which now form the roof of the brain, such as the palium, ganglion habenulæ, optic lobes, and cerebellum, are not in any way comparable with neuromeres; they have no segmental value, and they now have no genetic relations with the neuromeres over which they happen to lie. The tectum opticum, for example, really belongs to the third forebrain neuromere, in front of the diencephalon, and except as a matter of convenience, cannot be classified as part of the mesencephalic neuromeres. (See p. 157.)

* * * * * * * * *

Summary.—Thus we have in the diencephalon of vertebrates a remarkable combination of special characters; viz. a sharp cranial flexure; a funnel-like depression in the floor, with voluminous nerve centers (lobi inferiori) on its side wall; the presence of important nerve tracts arising from the cerebellum, the olfactory and gustatory organs, and that converge toward a common center in the infundibular region; the presence of a membranous sac that contains the remnants of sensory cells, and a special set of neuro-muscular reflexes. Each of these characters is without parallel elsewhere in the brain of vertebrates. They indicate that this particular region either has some very unusual part to play in cere-

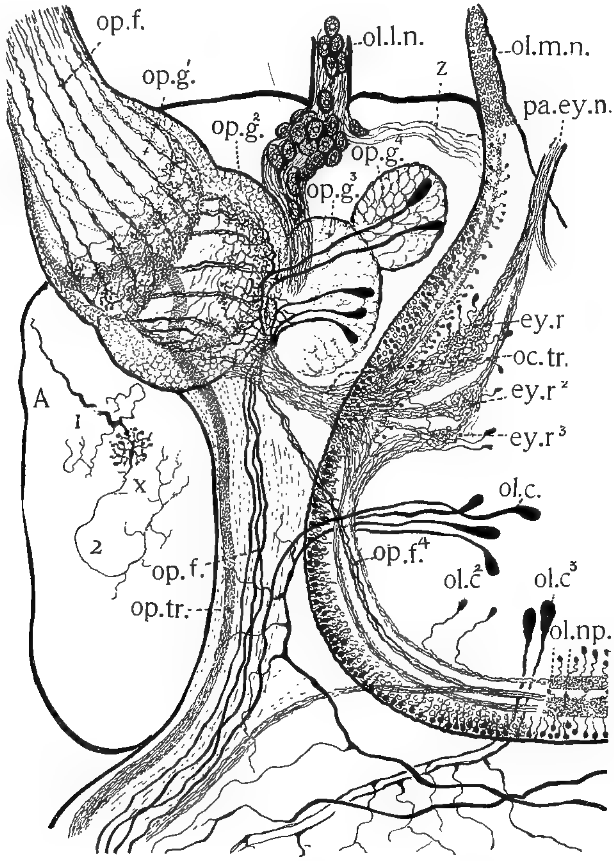

FIG. 51.—Forebrain of a young Limulus, hæmal surface. *A*. A single optic fibre, showing the arrangement of its principal branches. Methylene-blue preparation. Camera outlines.

bral activities now, or did have some such function in the past; but what that function was, or is, or what is the history and the meaning of these parts, neither vertebrate anatomy or physiology gives us the slightest clue.

But when we compare these conditions with those in the arachnids, their meaning is sufficiently clear. The infundibulum is the passageway for the old stomodæum, and the latter is the saccus vasculosus. The lobi inferiori are the lateral stomodæal ganglia; the nerve plexus of the saccus, the stomodæal nerves; the tween-brain flexure is the one which occurs in arachnids between the supra- and infra-stomodæal ganglia; the remarkable centralization of fiber tracts in the infundibular region is the retention of the ancestral condition seen in arachnids, where fiber tracts from the olfactory and gustatory organs, and from the stomodæal commissure, converge toward the swallowing centers, or the ganglia that control the neuro-muscular apparatus of the stomodæum.

In both vertebrates and arachnids, there is: *a.* but one passage, or opening, in the floor of the brain, and in both cases that passage is of similar relative dimensions; *b.* it lies just behind the hemispheres and the lateral eye nerve roots; and *c.* just in front of the anterior end of the notochord; and *d.* in front of the first pair of somatic motor nerves; *e.* in both cases, the opening lies approximately between the right and left halves of the fourth and fifth neuromeres; *f.* in both cases evaginations from the median face of the half neuromeres form special ganglia (stomodæal ganglia, lobi inferiores), quite unlike any other cranial ganglia; *g.* in both cases, these ganglia have similar associations with the stomodæal commissure (cerebellum), with the epithelial tube lying in the opening through the brain floor, and with the olfactory and gustatory organs; *h.* and although of considerable size, the ganglia have no direct nerve connections with any organs external to the brain.

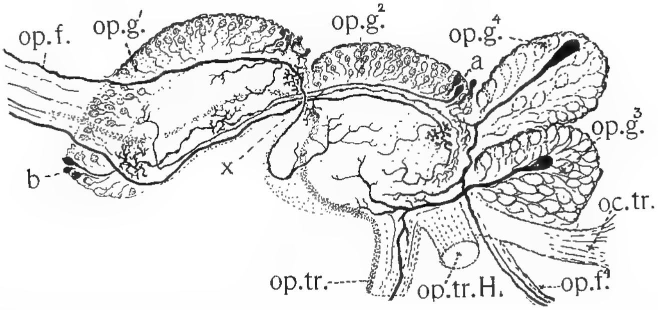

FIG. 52.—Semi-diagrammatic, longitudinal section of the lateral eye ganglion of a young Limulus.

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The diencephalon, therefore, of arachnids and vertebrates, may be defined as one, two, or more, neuromeres surrounding the primitive stomodæum, and uniting the primitive forebrain (supra-œsphageal ganglion) with the midbrain, or thoracic neuromeres. It lies in the angle of the oldest, and most striking cranial flexure, and marks the anterior termination of the notochord. The chamber lying between and above these neuromeres (the third ventricle) was for a certain period an extension of the stomodæum, or an antechamber to that portion that actually perforates the brain floor. The final closing of the entrance of this antechamber took place probably at a point just back of the cerebellum (rhomboidal fissure). (Figs. 3, 46, 58.)

III. The Mesencephalon.

In typical arachnids there are six thoracic neuromeres. The first one (two or three) (cheliceral neuromere) has already been described as the tween-brain, the remaining ones constitute the midbrain. They differ from all other neuromeres in their great breadth, and in the enormous size of their ganglia and gustatory nerves.

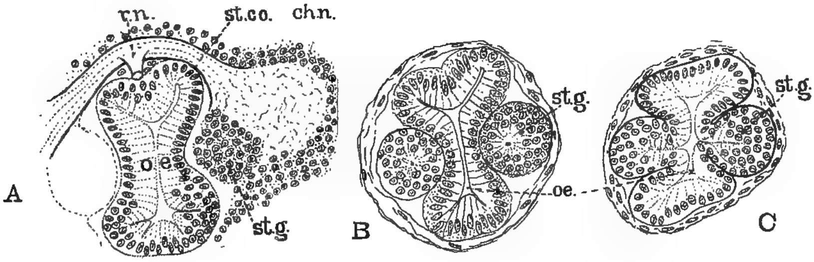


Fig. 53.—Longitudinal, horizontal sections of the head of an embryo scorpion, showing origin of the lateral stomodæal ganglion. *A*, At the level of the suprastomodæal commissure; *B*, at a lower level, showing the inner end of the lateral stomodæal ganglion; *C*, still deeper level, showing its origin from the sides of the stomodæum. Camera outlines.

In the scorpion, they rapidly increase in size with the growth of the appendages, forming a compact group in which the original segmentation is clearly indicated by the arrangement of the nerves and cross commissures. They are never so completely fused in the adult as to lose their identity, differing in this respect from those in the forebrain in front of them, and in the vagus region behind.

In the adult scorpion, the cross commissures are very short, and the thick cords, or crura, are but slightly separated, leaving a very small opening for the passage of the œsophagus. (Figs. 40–43.)

In Limulus, this opening is larger, the anterior ends of the crura are widely separated, and the elongated anterior commissures are bent into wide loops by the backward movements of the œsophagus. (Figs. 38–39.) These conditions, and the absence of a tween-brain flexure, give the brain of Limulus a different outward appearance from that of the scorpion, although structurally they are very much alike.

The great size of the neuromeres and the divergence of the crura make this the broadest and most voluminous part of the brain, giving it a rhomboidal outline, when seen from above.

Mesencoele.—The mesencoele is formed in part by a marginal, epithelial overgrowth, and in part by a deep median depression or infolding, between the two cords. The epithelial overgrowth is formed along the whole margin, as a thin overarching shelf that projects about a third way over each cord. (Figs. 136, 227 and 231.) Later, the cords settle bodily below the surface, and as there is no delamination of a superficial epithelium, a wide opening is left that is gradually closed in by the union of the thin edges of the two overgrowths.

As the two cords in this brain region remain horizontal, the potential mesencœle is broad and shallow, except in the middle line where it extends to the bottom of the deep median fissure.

In the more posterior parts of the brain, in the vagus and branchial regions, similar overgrowths occur. But the cords are much narrower here and their margins are brought together, like the closed covers of a book, by the deep median infolding, so that the chamber is converted into a deep, narrow fissure. The bottom of this fissure is converted into a "canalis centralis," when the neural commissures grow across the fissure, just above the floor. (Figs. 55, 69.)

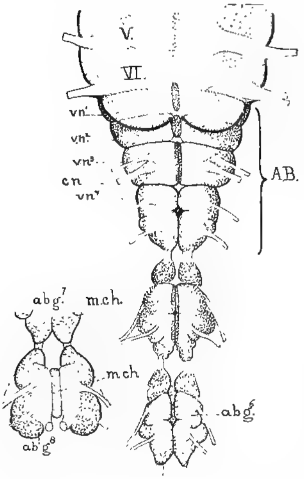


FIG. 54.—Vagus and branchial neuromeres of an embryo scorpion about ready to hatch. Camera outline.

* * * * * *

Comparison with Vertebrates.—The midbrain neuromeres of arachnids are represented in vertebrates by the group of conspicuous neuromeres forming the floor of the brain, from the infundibulum to the vagus region. The region is characterized by: *a*. its great width; *b*. its enormous cranial ganglia, widely separated from the crura and associated with the oral and hyoid arches; *c*. by the segmentally arranged gustatory organs; and *d*. by the unusual distinctness of the neuromeres in the early embryonic stages, in marked contrast with the regions just in front and behind.

In vertebrates confusion has arisen from the failure to distinguish between the true neuromeres on the floor of the brain and the various structures that have been forced out of their original positions onto the roof of the brain. The cerebellum and the optic lobes, as we have indicated above, are of very unequal value, and in no wise comparable with neuromeres. Their position in vertebrates is a purely secondary one, a long way caudad to their original position and connections. The optic lobes, that in vertebrates form the roof to the midbrain, clearly belong to the procephalic neuromeres, while the primitive cerebellar "neuromere" is a special commissure primarily associated solely with the diencephalon. The area covered by these structures therefore, varies greatly, and has no constant relation to the underlying neuromeres.

If we remove the cerebellum and optic lobes from the brain of a vertebrate embryo (frog), it will be seen that the underlying neuromeres form a natural group, that corresponds approximately with the posterior four or five thoracic neuromeres of arachnids. It is impossible, at present, to accurately fix either the anterior or the posterior boundaries of this group, for we do not know how many, if any, have been added to the cheliceral neuromere to form the diencephalon, or whether or no the last, or sixth, thoracic neuromere has fused with the first vagus. There should be, according to our provisional interpretation, five neuromeres, from the fifth to the ninth inclusive, in this region; and that number corresponds pretty nearly with the estimated number of neuromeres, and with the number of head cavities, segmental nerves, and visceral arches that are known to occur there. (Fig. 58.)

IV. The Metencephalon, or Vagus Neuromeres, and V, The Branchiencephalon, or Branchial Neuromeres.

The Metencephalon.—In many arthropods, the transitional region between one group of metameres and the next is often marked by an abrupt change in the size of the pertinent organs, and by their union in the middle line and ultimate disappearance; at the same time, in the next following segments, the same kind of organs may be greatly enlarged. These conditions are similar to those seen at the point of incomplete fissure in annelids.

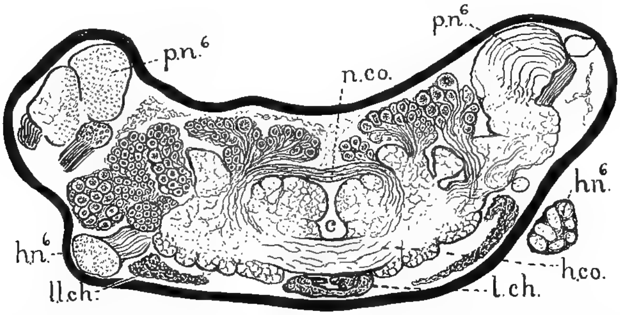


Fig. 55.—Section through the first vagus neuromere of Limulus, showing the neural and hæmal commissures, central canal, and lemmatochord.

The most striking cleavage zone of this character in the arthropods is the vagus region. It lies between the thorax and abdomen, and is one of the most conspicuous transitional zones in the whole body. It is present in many insects, crustacea, trilobites, etc., but its character is best known in the arachnids.

In Limulus, there are two vagus metameres, the chilarial and opercular, whose neuromeres form an important part of the brain. The external boundaries of the two metameres are at first similar to those of the other abdominal segments. (Figs. 141, 142.) But ultimately, the only remaining external traces of the chilarial segment are the chilarial appendages and the narrow ridge on the posterior margin of the thoracic shield. (Fig. 152, *ch.pl.*) The tergite of the opercular metamere is a narrow wing plate, still clearly outlined on the lateral margins, but in the middle it is completely fused with the abdominal shield *op.pl.* The hinge of the cranial buckler comes between the tergites of the chilarial and the opercular metameres. (Fig. 155.)

The chilarial and opercular neuromeres are completely fused with each other and with the posterior end of the midbrain; and in the adult only the commissures and the distribution of the corresponding nerves afford a clue to their identity. (Figs. 65, 66, and 70.)

In the scorpion the first four abdominal metameres belong to the vagus group. At an early period, there is a pair of rudimentary appendages on each of these four metameres. (Figs. 15 and 16.) In young scorpions, the first two pairs form minute papillæ near the unpaired genital opening. The third pair form the pectines, and the fourth, in part, the first pair of lung books.

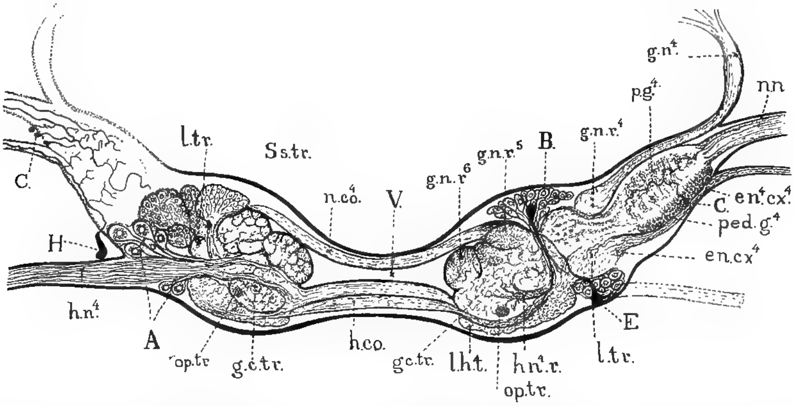


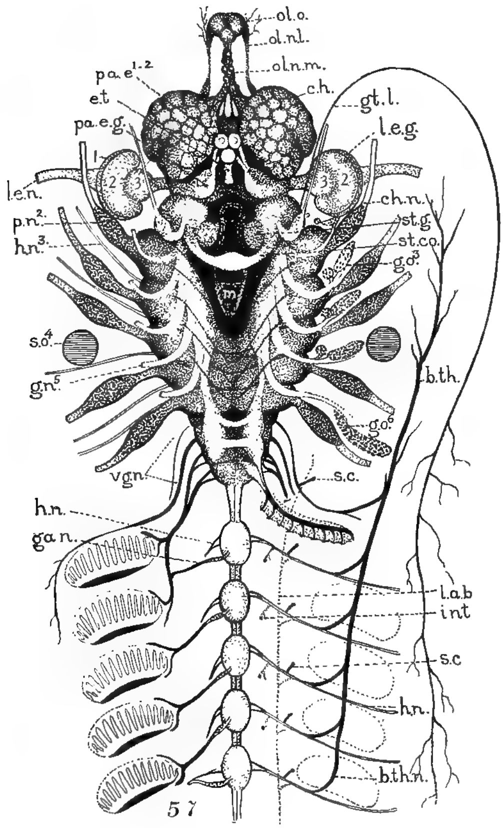
FIG. 56.—Cross-section of the mesencephalon of a young Limulus brain. On the right, the section passes through the fourth pedal ganglion, with its gustatory, entocoxal, and pedal nerves, and the ascending roots of the fifth and sixth gustatory nerve roots. On the left, the section passes through the root of the fourth hæmal nerves, showing its relation to the commissures and to the great longitudinal tracts. The figure is constructed from methylene blue and von Rath's preparations. The capital letters indicate the same neurones as in Figs. 65 and 66.

The four neuromeres become fused into a dense triangular mass, crowded forward beneath the midbrain. Its posterior end is elevated, producing a pronounced hind-brain flexure. (Figs. 40, 43, 54.) The vagus neuromeres are relatively narrow, and as the corresponding appendages are crowded toward the middle line, their pedal nerves arise in a characteristic manner from the neural surface, not from the sides.

* * * * * * * * *

The Branchiencephalon.—In the arachnids, the anterior vagus metameres are characterized by their highly modified tactile or sensory appendages, the posterior ones only being respiratory. In the transitional forms between vertebrates and arachnids, respiratory segments were doubtless added to the head, from time to time, thus leading to the union of the entire group of branchial neuromeres with the posterior portion of the brain.

We therefore look on the hindbrain of vertebrates as composed of two main parts successively added to the midbrain, namely: *a.* the vagus section, consisting of from two to four fused neuromeres, associated with appendages that have undergone extensive reduction and modification, the most important remnants forming organs of a tactile or gustatory nature; this characteristic group of neuromeres is largely sensory, and now forms the hindbrain, or metencephalon of arachnids; and *b.* a second group of neuromeres belonging to the branchial segments, and



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Olfactory
olfactory organ
Coordination
hemispheres
Visual
parietal eye
lateral eye
Swallowing
stomodaeum
infundibulum
Chewing
and
Gustatory
leg-jaws
oral-arches
Locomotor
Auditory
Equilibrium
Vagus
tactile
lateral line
Respiratory
cardiac
branchial
hypobranchial
sympathetic
Digestive
excretory
genital

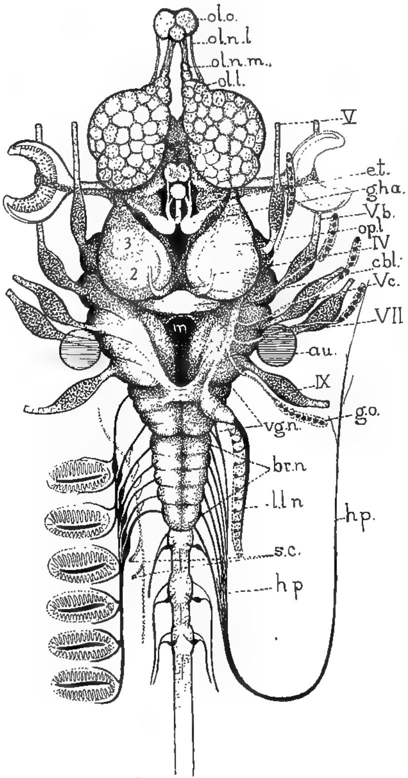

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FIG. 57.—Semi-diagrammatic figure of an arachnid brain and nerve cord. It represents, in the main, the conditions in Limulus. The parietal eye and the vagus lobes and nerves, however, have the location and arrangement characteristic of the scorpions.

FIG. 58.—Here the same parts are shown in the position they are supposed to have in vertebrates. The principal changes are in the position of the optic ganglia, which have moved backward and upward to form the optic lobes; the pedal ganglia have become the cranial ganglia of the fifth, seventh, eighth, ninth, and tenth nerves; the coxal gustatory organs lay the foundations for the principal lines of canal organs. The branchial neuromeres have fused with the brain, and the components of the several branchial and vagus nerves going to the same kind of organ have united, forming compound nerves distributed respectively to the respiratory organs, sense organs, heart, intestine, and the great branchio-thoracic, or hypo-branchial muscles. The similiarity in the linear distribution of the principal functions, or the nerve centers controlling them, is shown by the inscriptions between the figures.

which were mainly associated with the gills, heart, and viscera; they united with the brain at a later period.

The combined vagal and branchial neuromeres of arachnids form the hindbrain, or medulla, of vertebrates. (Figs. 57–58.)

In arachnids, all the branchial neuromeres do not form a part of the brain, except possibly in certain specialized land forms; but they already show the beginning of that functional segregation of sensory, branchial, cardiac, and motor nerve fibers that is so characteristic of the hindbrain neuromeres of vertebrates. (See cardiac and hypobranchial nerves).

In arachnids (scorpion and Limulus) there are in all seven vagus and branchial neuromeres, which is close to the estimated number in this region in vertebrates. However, this number probably varies in vertebrates, as it does in arachnids, and only an approximate numerical agreement and serial location is offered as having significance. The segregation of the vagal and branchial nerves (in both vertebrates and arachnids) into the groups mentioned above, is of much greater significance than the agreement in the number of neuromeres.

CHAPTER V.

MINUTE STRUCTURE OF THE BRAIN AND CORD OF ARACHNIDS.

METHODS.

In order to better understand the minute structure of the brain, it is essential to first determine the structure of one of the isolated neuromeres of the spinal cord. I have used for this purpose one of the branchial neuromeres of Limulus. But even here the structure is so exceedingly complex that it is possible to work out or to represent but a very small part of it in detail. Our observations on the structure of an invertebrate neuromere will be of special interest, because they are based on the gross anatomy and embryology, upon the minute structure as obtained by several methods of analysis, and upon the physiology.

For the development of the primitive sense buds and the early embryonic stages of the cord, I have used the scorpion. For the distribution of the fibers and cells, I have used the methylene blue "intra vitam" method on Limuli from 2 to 6 inches long; the brain and cord being mounted whole, or sectioned. The adult nervous system has been tested for its physiological reactions, and the distribution of the peripheral nerves has been followed with care. Its minute structure was worked out from sections prepared by several methods, the most satisfactory ones being the usual Golgi method, and von Rath's picro-osmic-platinum chloride mixture, followed by methyl alcohol.

I. THE BRANCHIAL NEUROMERES IN LIMULUS.

Development.—In Limulus and in the scorpion, during the late embryonic stages, a thin epithelial overgrowth forms on the lateral margins of the cords, and a deep infolding appears in the median line between them. The lining to the median infolding is in part converted into the epithelium of the canalis centralis, in part into the inner neurilemma, or neuroglia, and into the lemmatochord.

The lateral cords themselves sink bodily below the surface, without separating off a surface epithelium, and are covered by an ectodermic layer formed from the marginal overgrowth united to the local (interganglionic) remnants of the middle cord. (Figs. 227, 231.) As in the arthropods generally, they lie in a horizontal plane, separated by the median infolding that forms the middle cord. In the vertebrates, similar conditions prevail, except that the median margins of the lateral cords are more deeply infolded than the lateral ones, thus bringing the neurogenic surfaces of the cords face to face. Thus the two lateral cords of the arachnids form the lateral walls of the neural tube of vertebrates, the middle cord canal (canalis centralis) being at the inner surface, the neural crests on the outer one, and the nerve fiber layers on the lateral wall of the tube. (Figs. 134–137.)

* * * * * * * * *

Commissures.—In arachnids, two main sets of transverse commissural fibers are formed in each neuromere, the neural and the hæmal commissures. The hæmal commissures are the first to arise. They make their appearance on the hæmal side of the epithelium of the median groove as two separate bundles, an anterior and a posterior one. (Fig. 64, *a.h.co.* and *p.h.co.*) The hæmal commissures are important features in all arthropod neuromeres, and represent in part the remnants of the transverse fiber tracts that extend round the body and unite the longitudinal cords. Seen in sagittal sections of the adult cord, they appear as two large irregular bundles, separated by a narrow space through which the neuroglia of the median canal and median fissure is continuous with that of the lemmatochord.

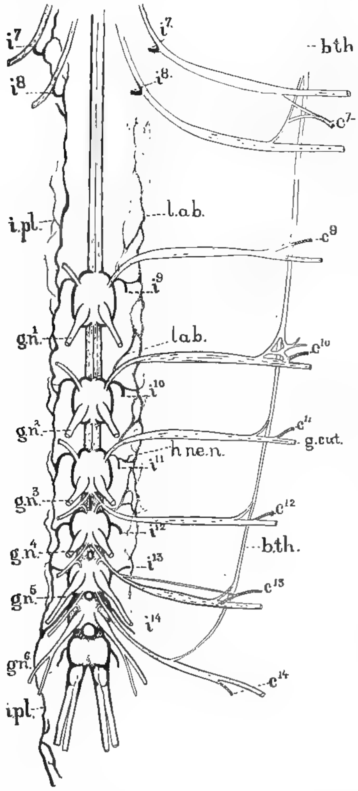

FIG. 59.—The branchial and abdominal neuromeres of a young Limulus three inches long. The intestinal plexus, *i. pl*, longitudinal abdominal, *l. ab*, general cutaneous, *g. cut*, segmental cardiacs, *c*, and the great branchio-thoracic nerves, *b. th*, are shown.

At a much later period a new set of commissures appears above the floor of the median groove, thus converting that part of the groove into a canal; a large anterior one, *an.n.co.*, a small middle one *m.n.co.*, and a small but sharply defined posterior one, *p.n.co.*

As the longitudinal commissures approach the neuromere, they divide into distinct neural and hæmal tracts *h.tr.* and *n.tr.* In the main, the fibers in each tract either terminate in neuropile masses situated on the corresponding side of the neuromere, or run straight through it, the neural tracts passing above the neural commissures, and the hæmal tracts below the hæmal commissures.

The peripheral nerves consist of two main pairs. (Figs. 59, 60.) The anterior pair is the more complex. Owing to the central relation of its fibers, its position on leaving the cord, and its relation to the great muscle masses, it may be spoken of as a hæmal nerve. It is comparable with the motor or ventral root of a vertebrate spinal nerve. It is a mixed, non-ganglionated nerve, and contains general cutaneous, somatic motor, cardiac, and visceral, or intestinal elements.

The posterior nerve is more voluminous, but less complex than the anterior one. It arises from a large conical "ganglion," consisting of neuropile and ganglion cells, situated on the posterior neural surface of the cord. (Fig. 63, *C.*) It supplies the gill muscles and the sense organs of the corresponding branchial appendage. The majority of the elements are sensory, and are confined in the main to the neural side of the nerve. It is therefore a neural ganglionated nerve, comparable with the posterior, or ganglionated root of a vertebrate cranial, or spinal nerve.

Cell Clusters. —The nerve cells in the neuromere are arranged in clusters that are remarkably constant in their size, location, and relation to fiber tracts. Each cluster probably represents the remnants of one or more primitive sense buds.

In exceptional cases, the methylene blue fails to affect the cells and fibers, but stains rather sharply the neuroglia, thus giving excellent pictures of the nerve cell clusters and their sheaths. (Fig. 61.) The clusters are mainly confined to the neural surface and lateral margins of the neuromere. The more important ones are as follows:

a. A cluster of large cells in two or more groups, on both neural and hæmal sides of the anterior lateral margin. (Fig. 61, *A.*) Their axones cross to the opposite side, forming part of the anterior hæmal commissure, entering the hæmal nerve as its third root. (Figs. 61 *h.r.*[3] and 62, *a.*) Before crossing, each axone gives off a large collateral, a′, that extends backward into the longitudinal hæmal tracts.

b. A very large cluster of medium size cells (Fig. 61, B.), whose axones, *b.* converge into a large bundle, directed vertically. On reaching the hæmal surface of the cord, each fiber divides, one branch entering the main longitudinal hæmal tracts and extending backward, as a coarse unbranching fiber, to the more posterior neuromeres. (Fig. 62, *b.*); the other branch, b′, crosses to the opposite side, in the posterior part of the anterior hæmal commissure, behind the fibers forming the third root of the hæmal nerve. They are probably association elements. (Figs. 61, 62 and 64.)

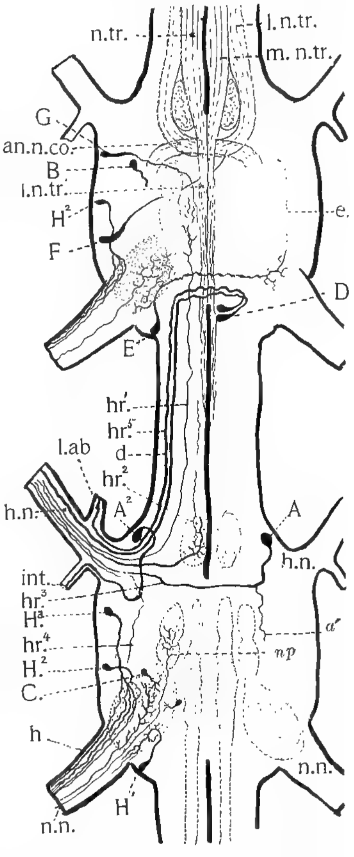

FIG. 60.—Two branchial neuromeres, seen from the neural surfaces, showing the location of the principal masses of neuropile, fiber bundles, and neurones.

c. Numerous clusters of minute cells, on the neural surface of the pedal ganglion. Their axones terminate in the large mass of interwoven fiber bundles that constitute the exceedingly complex core of the ganglion. Probably sensory. (Figs. 62, *C.* and 63 *C.*)

d. A cluster of about thirty very large motor cells on the posterior median part of the neural surface. Their axones form a compact bundle which extends vertically and then crosses to the opposite side, the two crossing bundles constituting a large part of the posterior hæmal commissure. (Figs. 60, 61, 62 and 64, *D* and *d.*)

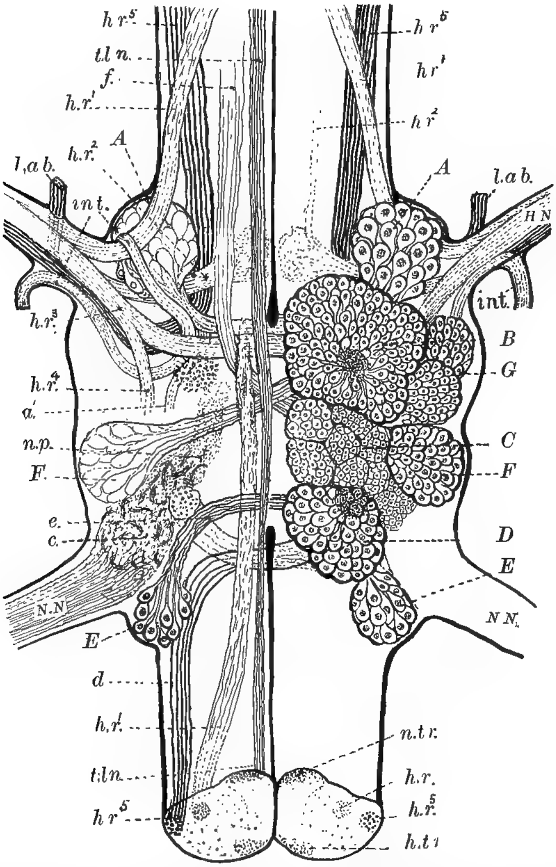

FIG. 61.—One of the anterior branchial neuromeres of a young Limulus. On the right, the principal cell clusters of the neural surface are shown; on the left, the principal nerve roots, fiber tracts, and neuropile centers. The capital letters indicate the cell clusters, and the small letters, the corresponding fibers; $Hr.^{1-5}$, the five roots of the hæmal nerves. Composite figure, based on methylene blue and von Rath's preparations.

The crossed fibers extend backward along the hæmo-lateral side of the cord to the next posterior neuromere, forming the fifth root to the hæmal nerve, $h.\ r^5$. They are very conspicuous in sections on account of the large size and pronounced coloring of the axis cylinders and their sheaths. On approaching the next following neuromere, the bundle becomes more compact and gradually moves toward the outer margin of the cord, where it turns sharply forward and outward into the hæmal nerve. It there divides into two bundles; one *l.ab*, constitutes the nerve supplying the hæmo-neural and longitudinal abdominal muscles; the other, extending onward into the main trunk, forms the branch that supplies the branchio-thoracic muscles (hypoglossal elements).

e. A group of large cells, lying on the posterior hæmal side of the pedal ganglion. (Figs. 60, 61, 63, and 64, *E* and *e.*) Their axones are directed diagonally forward, inward and upward; they then cross over to the opposite side, and return again to the hæmal surface where they extend forward as fine unbranched fibers on the lateral margins of the longitudinal, hæmal tracts.

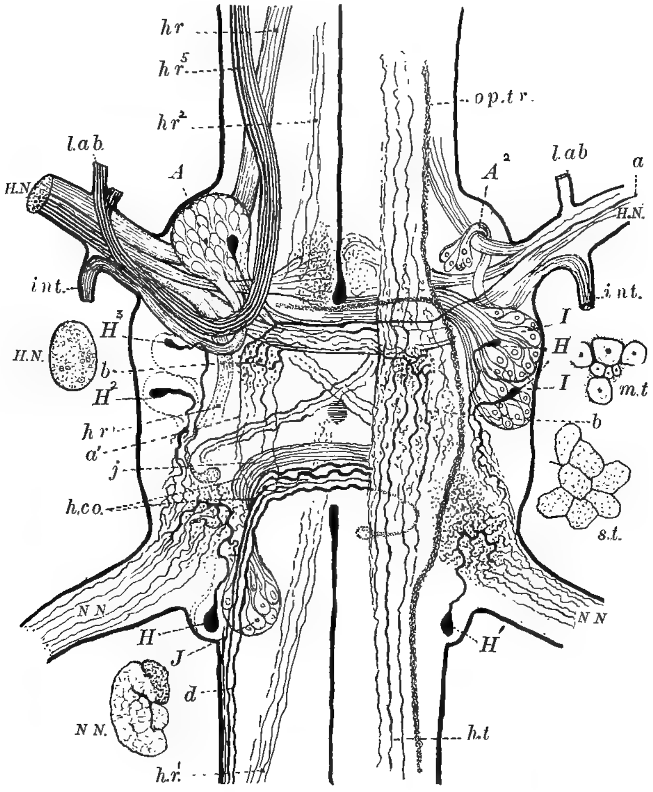

FIG. 62.—Anterior branchial neuromere of a young Limulus seen from the hæmal surface. On the right, the superficial, longitudinal, hæmal tracts are shown; on the left, the underlying hæmal cross commissures, and their relation to the principal groups of neurones. Outside the main figure, on the left, is a cross-section of a neural nerve, *N. N'*, and a hæmal nerve, *H. N*, On the right, the minute structure of some of the nerve tubes in the hæmal nerve, *m. t*, and in the neural nerve, *s. t*, is shown.

The crossing bundles constitute apparently the whole of the posterior neural commissure. (Fig. 64, *p.n.co.*). Before and after crossing, the axones give off numerous dentrites which ramify in the neuropile core of the pedal ganglia (Fig. 63, *E.*) Probably association fibers.

f. A medium sized cluster on the anterior lateral margin of the pedal ganglion.

(Figs. 60, 61, 63, 64, *F*.) Their axones form a rather loose bundle (ill defined in sections) extending downward, inward, and forward along the neural portion of the cord, to the next anterior neuromeres. Before and after crossing, the large irregular fibers give off numerous collaterals which ramify diffusely in the central fibrous portions of the neuromere. (Fig. 63, *F*.) Termination unknown; probably association fibers.

g. On the anterior lateral part of the neural surface, small clusters not clearly defined, that send axones diagonally inward and forward. (Figs. 61 and 63, *G*.) The scattering axones appear to cross in both the anterior neural and the anterior hæmal commissures. Some appear to send collaterals backward to the next posterior neuromere. Termination unknown.

h. Along the lateral hæmal margin, on either side of the pedal ganglion, are several groups of cells that are usually very conspicuous. (Fig. 62, H^{1-2-3}.) They differ from the other neurones in that each cell gives rise to a large number of dendrites and axones. The dendrites are minute and their innumerable branches fill the core of the pedal ganglion, often giving it a dark blue, finely granular appearance. The axones are large, irregularly branching fibers extending outward, as bundles of parallel fibers, onto the hæmal surface of the pedal nerve. These neurones are the only ones of their kind and are characteristic of the pedal nerves, both in the thorax and in the abdomen.

The axone bundles from the several clusters, H^{1-3}, converge toward the hæmal side of the pedal nerve where they form a distinct bundle, readily recognizable in sections. (Fig. 68, *h*.) They are the motor nerves that supply the gill muscles.

i. Two large groups of neurites on the anterior hæmo-lateral margin, sending great bundles of fibers forward and inward into the anterior portion of the anterior hæmal commissure. (Fig. 62, *I* and 64, *i*.)

j. A large group of cells on the posterior hæmal margin, projecting their fibers forward and then across to the opposite side, in the anterior portion of the posterior hæmal commissure. (Figs. 62, and 68, J, von Rath's preparations.) The cells and fibers of this group have not been identified by the methylene blue process.

NERVE-ROOTS.

The Neural Roots.—The neural or branchial nerve arises from a large ganglion on the posterior neuro-lateral surface of the neuromere, and extends upward (neurally) and outward to the gill. In cross sections (von Rath's preparations) near the neuromere, it consists of two portions, the larger one formed of a coarse polygonal meshwork of neuroglia, each mesh crowded with black dots, representing the cut ends of innumerable nerve fibers. (Fig. 62, *s.t.*) These sensory fibers constitute about three-quarters of the entire nerve. Most of them terminate in very fine dendrites, in the large oval mass of neuropile that constitutes the posterior lateral portion of the core of the pedal ganglion. (Fig. 63). A small group of fibers extends beyond the main core into the median neural region of the neuromere. (Figs. 60 and 61, *n.p.*) This neuropile center is very dense and stains with great intensity in von Rath's preparations.

The hæmal fascicle consists of small nerve tubes with sharply defined axis cylinders, separated by a wide, clear space from the outer sheath. They are motor fibers arising from the peculiar hæmal neuromeres, H^{1-3}. (Fig. 62, *m.t.*) They supply the branchial muscles.

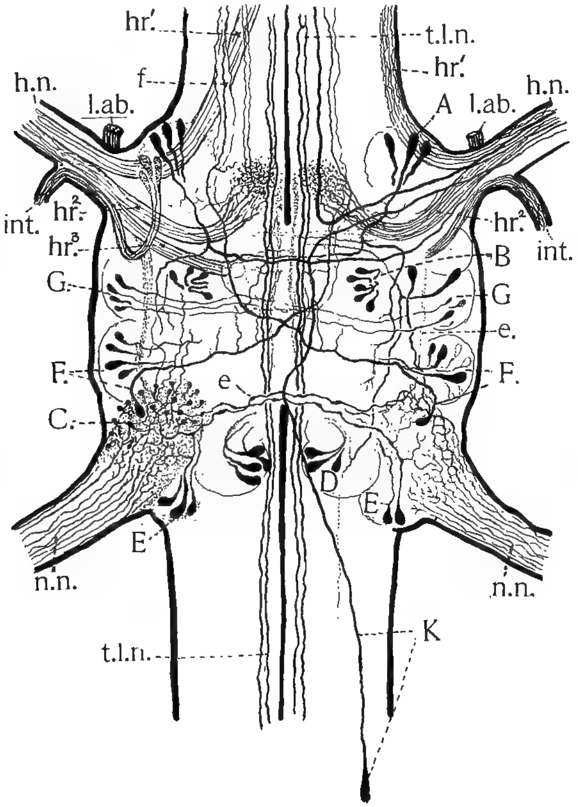

FIG. 63.—Anterior branchial neuromere of a young Limulus, showing the course of the principal neurones. Neural surface; methylene-blue preparation.

The oval mass of neuropile in the ganglion of the branchial nerve consists of an extraordinarily complex system of interwoven bundles of very fine fibrils. In this neuropile the following fibers terminate: 1. the dendrites of about three-quarters of all the fibers of the branchial nerve: these fibers are sensory. 2. the collaterals of the motor neurones, H^{1-3}. 3. the collaterals of the *E* neurones whose axones cross in the posterior neural commissure, and 4. the dendrites of the minute *C* neurones that constitute the principal cellular covering of the ganglion.

The Hæmal Nerve Roots.—The hæmal nerves arise from the anterior hæmal margin of the neuromere and extend upward and outward. In the more posterior segments, their apparent point of attachment shifts forwards to a point midway between the two neuromeres, but without changing the root terminals. (Fig. 59.) They contain the following fascicles:

a. A bundle of large motor fibers arising from the *D* neurones on the neural surface of the opposite side, in the next anterior neuromere. (Figs. 61, 62. $h.r^5$.) It runs along the hæmo-lateral margin of the cord, becoming more and more distinct as it approaches the next following neuromere. There it bends outward onto the anterior hæmal surface of the hæmal nerve, dividing into two fascicles. One forms the small, purely motor nerve supplying the hæmo-neural and the longitudinal abdominal muscles, *l.ab.*; the other passes into the main part of the nerve, and separates farther on, as the branch that supplies the branchio-thoracic muscles. (Fig. 59, *b.th.*) (hypoglossal elements.)

b. A large fascicle of pale fibers (Figs. 61 and 62, $H.r'$), that extends along the anterior neural margin of the nerve. On entering the cord, it runs diagonally forward, inward, and upward, terminating in an elongated mass of neuropile, on the median, neural surface of the next anterior neuromere. Its peripheral termination is unknown. Probably cardiac.

c. A large central fascicle, $H.r^2$, terminates in a conspicuous, isolated mass of neuropile of the same side, near the anterior median region of the same neuromere. Some of the fibers pass through the neuropile, neurad, and cephalad, joining the median, longitudinal, neural tracts. Probably general cutaneous fibers.

d. This fascicle, $H.r^3$, is not easily followed in sections, but its fibers are frequently seen in methylene blue preparations. They spring from the large neurones *A*, on the opposite side of the neuromere. Their collaterals are shown at *a'*. (Figs. 61, 62.)

e. This fascicle extends backward toward the neuropile center of the branchial nerve, $H.r^4$. (Fig. 61.)

f. The intestinal fascicle is a small bundle of fine fibers, *int.* In the anterior segments, it leaves the cord with the hæmal nerve; in the more posterior ones, it arises separately. (Fig. 59, I^{1-14}.) In the first ganglion (Fig. 61, *int.*), it runs along the posterior side of the hæmal nerve and then turns sharply forward over the neural surface of the sensory root, $H.r^1$, to a small, ill defined group of cells lying in group *A*.

We find, therefore, in the hæmal nerves, the following roots or fascicles: two sensory roots terminating in neuropile on the neural surface of the cord, on the same side, one in the same neuromere, $H.r^2$, the other in the one next in front of it, $H.r^1$. (Fig. 60.) Two roots, ending in cell groups on the opposite side of the cord, one group, *D*, on the posterior neural side of the next anterior neuromere, the other, on the anterior neural surface of the same neuromere, *A*. A fifth root, $H.r^4$, extends caudad, disappearing in the neuropile near the base of the neural nerve. The intestinal branch should perhaps be counted as a separate nerve.

It is only in the second neuromere that it is anatomically a branch of the hæmal nerve; in the more posterior neuromeres it arises from the side of the neuromere and entirely separate from the hæmal nerve roots.

Commissures.—The transverse commissures of the cord may be divided into two sets: *a.* the primary, or hæmal commissures, passing underneath the epithelium of the embryonic median groove, and representing the primitive nerve tracts uniting the right and left cords; and *b.* the secondary, or neural commissures, crossing the neural fissure above the floor of the median groove. The neural commissures, phyllogenetically and ontogenetically form much later than the hæmal, and only after the median groove becomes deep enough to bring the superior median margin of the two cords into contact.

The anterior and posterior hæmal commissures are separated by an opening in the floor of the neural canal through which the neuroglia passes to the underlying lemmatochord (Figs. 64 and 68.)

The anterior hæmal commissure consists of several indistinct bundles. So far as could be determined, the anterior portion consists of fibers from neurones I; the middle portion from neurones A; and the posterior portion from neurones B (Fig. 64).

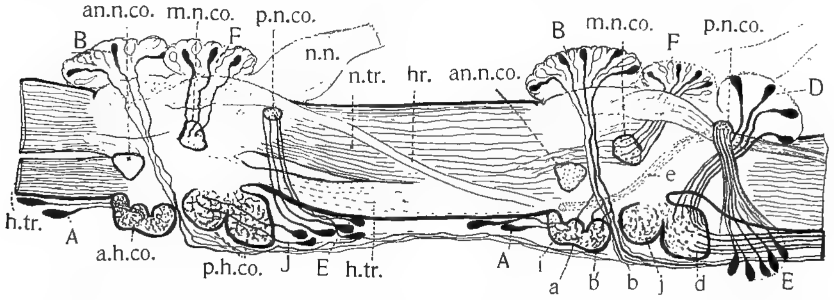

FIG. 64.—Sagittal section of two anterior branchial neuromeres, showing the relation of the principal neurones and fiber tracts to the cross commissures.

The posterior hæmal commissure contains fibers from group J (anterior bundle) and from group D (posterior bundle).

The hæmal commissures therefore contain, among fibers of undetermined character, crossed motor axones and various collaterals.

The neural commissures are three in number; an anterior, a middle and a posterior one. (Fig. 64.) The sources of the fibers in the anterior neural commissure could not be certainly determined. Those of the middle commissure *m.n.co.*, are derived from neurones, F, and those of the posterior commissure from neurones E. No other fibers could be located in these commissures. The neural commissures appear to be largely composed of association fibers.

The Neuropile Centers.—The neuropile centers are dense masses of interwoven terminal dendrites. They appear in von Rath's preparations as dense black masses of fine fibrils, and in methylene blue, as masses of fine blue dots or lines, according to the character of the stain.

The principal centers are : *a.* a large oval center at the root of the pedal nerve, forming the medullary core to the pedal ganglion. (Fig. 60.) A prolongation of it extends cephalad and mesad, forming a compact, oblong mass, near the center of the neural surface of the neuromeres; *n.p.* *b.* A center for the cephalic root of the hæmal nerve, H*r′*, extending along the median neural surface of each ganglion. *c.* A center for the middle root of the hæmal nerve, Hr^2, on the anterior median face of the neuromere. *d.* The hæmal tracts; large, spindle-shaped tracts, one on either side of the median line, on the hæmal surface. (Figs. 62, 67, 68, *l.h.tr.*) (e) Four small masses, on the hæmal surface, between the anterior and posterior hæmal commissures and the longitudinal hæmal tracts. For longitudinal tracts in sections, see Figs. 67 and 68.

II. THE CEPHALIC NEUROMERES.

We are now in a position to describe the arrangement of cells and fibers in the cephalic neuromeres.

The brain neuromeres, in the main, closely resemble those of the cord. The principal differences in form are due to their linear union and to the lateral divergence of the crura. The histological differences are due mainly to the absence of motor neurones such as the hypobranchial, intestinal, and cardiacs, to the greater size and isolation of the pedal ganglia, and to the presence of the large gustatory nerves.

Cell Clusters.—The nerve cells are arranged in clusters, of varying sizes, that have special neurilemma sheaths, as in the cord, but they are so crowded together that it is difficult to determine the exact arrangement. They cover the neural surface and lateral margin of the crura, leaving the commissures, part of the gustatory tracts, and the hæmal surface exposed. (Figs. 65 and 66.)

The Commissures.—Each neuromere has several bundles of cross commissures that have terminal relations similar to those described for the branchial neuromeres. Owing to the divergence of the crura they form long, backwardly directed loops in which the commissural fascicles are difficult to identify, except where they approach the crura.

In very young crabs, sagittal sections show that the commissures of each neuromere are surrounded by distinct membranes. There are two groups of commissures for each neuromere, corresponding to the neural and hæmal commissures of the cord, and no doubt containing similar components. In the adult, the median portion of the anterior thoracic commissures form compact bundles with a common neurilemma sheath; near the crus, the several fascicles separate to their respective terminals. (Fig. 56.) The more posterior thoracic commissures, and those in the hindbrain, are shorter, and the neural and hæmal fascicles are widely separated, leaving a space between them, which represents the beginning of the fourth ventricle. (Figs. 46, 47 and 55.)

The neural commissures.—I have not been able to work out the relation of all the commissural elements in detail, although some of them stand out very clearly. For example, in methylene blue, the posterior neural commissures are often very conspicuous. They extend diagonally forward (anterior ones) and outward on to the neural surface of the crura, over the great gustatory tracts, to the cell clusters *E*, on the posterior hæmo-lateral margin of its neuromere. (Fig. 65, *E*, *p.n.co.*)

A bundle of these fibers, on the anterior side of the second thoracic neuromere, indicates that the cheliceral neuromere, in spite of its distinctly pre-oral position, has its commissure behind the œsophagus. In most cases, one may recognize two sets of these neural fibers to each neuromere, an anterior one, arising from the neurones *E*, and a posterior fascicle, ending in a separate mass of neuropile on the lateral half of each crus.

The hæmal commissures contain several sets of fibers. The ones most clearly seen in methylene blue preparations are rather large fibers which arise from neurones A (Fig. 66) and after crossing, enter the roots of the hæmal nerves.

Between the nerve roots and the commissure, are two sets of longitudinal fibers extending outward and backward along the hæmal surface of each crus, one on the median side, one on the lateral. (Fig. 66, left.) Most of the longitudinal fibers come from the opposite side through the hæmal commissure; some of the lateral ones probably come from neurites, *B*, on the neural surface of the same side, corresponding with group B of the cord.

The Hæmal Nerve Roots.—It will be recalled that the cranial hæmal nerves supply the integument of the cephalothorax. The branches, which in the abdominal nerves run to the great longitudinal muscles, to the branchio-thoracic muscles, to the heart and to the intestines, are absent from the six pairs of thoracic, hæmal nerves. Hence they have but a single root, mainly, if not wholly sensory, and representing root two, $H.r^2$, of the branchial neuromeres.

In most preparations, the hæmal roots appear to extend only part way through the crus, terminating abruptly in the main longitudinal tracts on the median side (Fig. 66, right side). They appear to end there in a mass of neuropile, like that of the second root of the abdominal nerves, $H.r^2$. In other preparations, many fibers are seen to enter the hæmal commissure and terminate in the *A* neurones of the opposite side, which no doubt correspond to the A neurones of the abdomen.

No trace of any other roots could be found. From this observation we may infer that roots two and three, $H.r^2$, and $H.r^3$, of the abdominal hæmal nerves are sensory general cutaneous; that root one, $H.r^1$, contains the cardiac elements; and that the neurones, D, are distributed to the branchio-thoracic muscles.

The Neural Nerve Roots and the Cranial Ganglia.—Owing to the greater size and specialization of their terminal organs, the neural, or pedal nerves of the head are much larger and more complex than those of the branchial region, but in the minute structure of their ganglia and nerve roots they are much alike.

Ganglia.—In the adult Limulus (Fig. 218), each cranial ganglion forms a large oval mass of neuropile, projecting a considerable distance from the sides

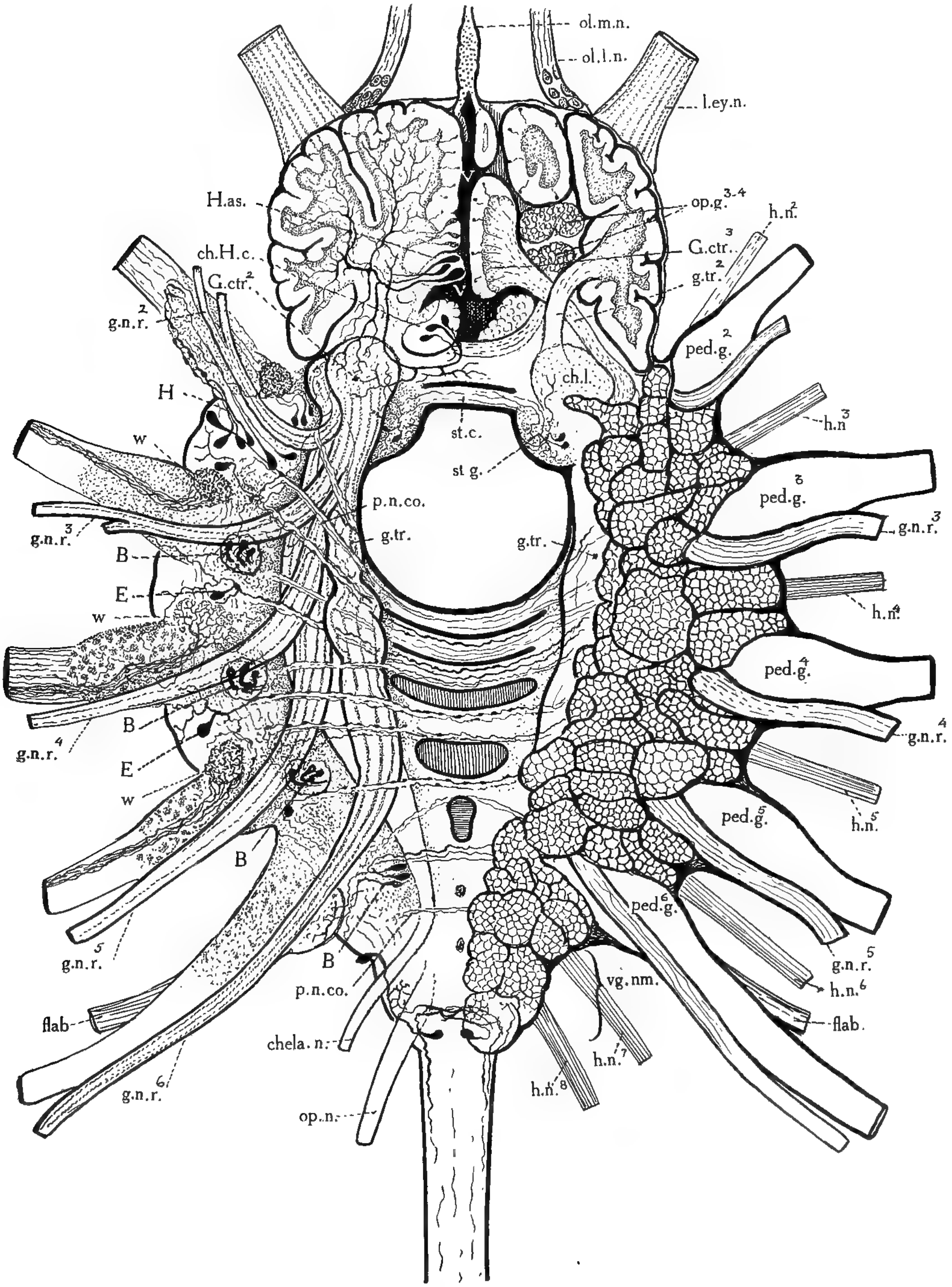

FIG. 65.—Brain of young Limulus about three inches long, seen from the neural surface. The cerebral hemisphere, on the left, is shown in optical section, at the level of the giant association neurones, *H. as*, and on the right, at a deeper level, showing the principal cerebral lobes and the gustatory tracts, *G. ctr*^{3}. and *g. tr.*^{2} Compare with Fig. 48. On the right, behind the hemispheres, the superficial arrangement of the clusters of nerve cells, and the cranial nerves are shown. On the left are seen the gustatory nerve roots, the great longitudinal gustatory tracts, the principal neurones and their relation to the neural commissures, and the principal neuropile masses in the pedal and stomodæal ganglia; methylene-blue preparation.

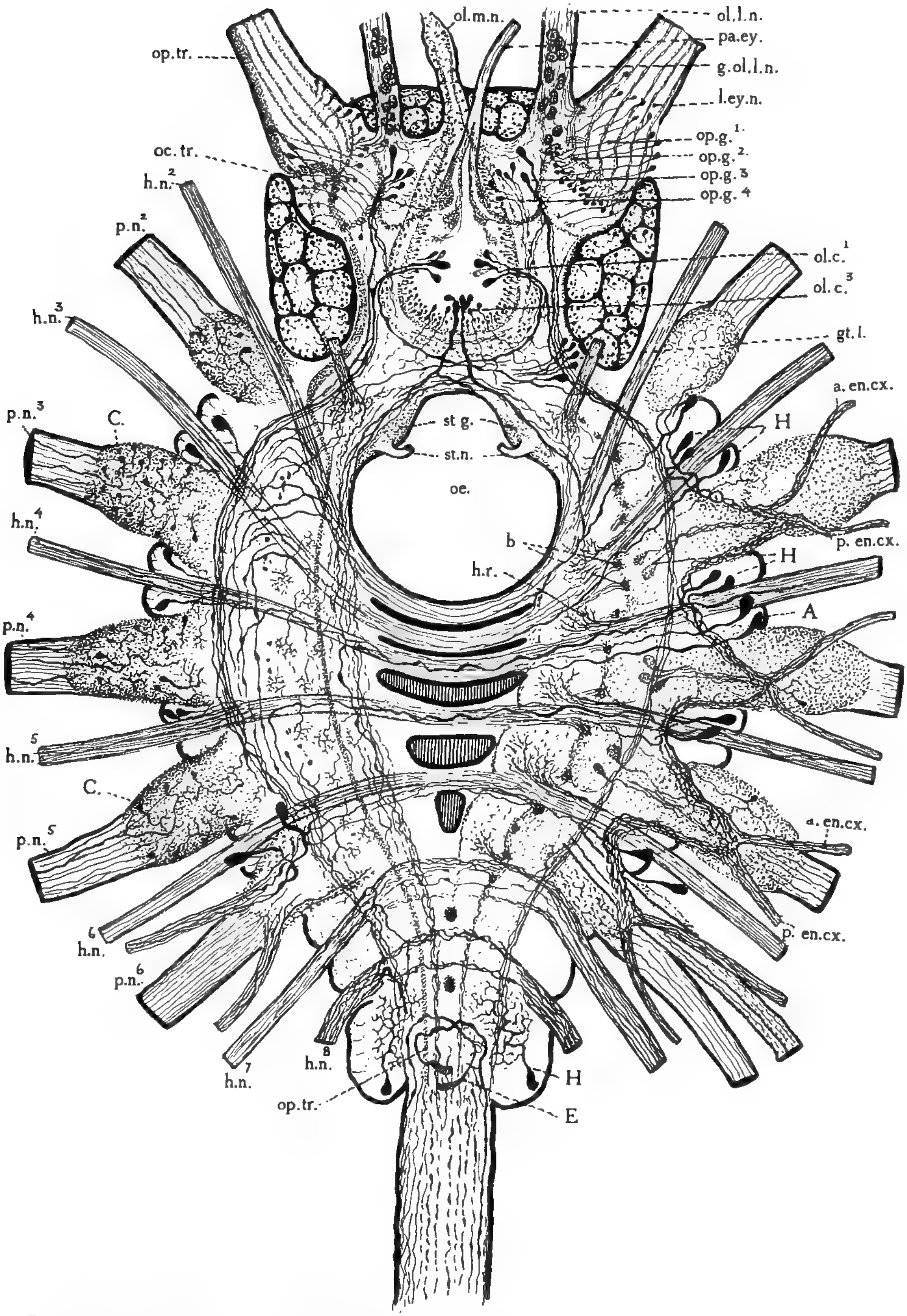

FIG. 66.—Same from the hæmal surface, showing on the left the more superficial neurones, fiber tracts, nerve roots, and commissural fibers; on the right, the deeper ones. Note the great extension backward of the fibers arising from the optic nerve, *op. tr*, and from the giant nerve cells of the optic ganglia, *op.* g^4, and olfactory lobes, *ol.* c^1 and *ol.* c^3.

of the brain. In the young (Figs. 35, 36, 38, 39), they are separated from the brain by long narrow stalks, or tracts, devoid of neurones or neuropile.

Most of the peripheral fibers terminate in the neuropile core, forming many minute irregular centers (Fig. 65). There is a special neuropile center on the anterior neuro-median side of each ganglion, formed by the terminals of a small bundle of rather distinct fibers. This center in some cases appears like a dark granular blotch, in others like a beautifully distinct, anastomosing network (Fig. 65, *w*). Their peripheral relations were not determined.

The nerve cells of the ganglia are very small and numerous. They are confined in the main to the hæmal surface, sending short, vertical axones into the neuropile, where they divide, one branch passing outward into the nerve, the other forming branches in the neuropile, which extend toward the crus. (Fig. 66, *C*).

The Motor Neurones.—On the hæmal surface of the ganglia, there are two very conspicuous bundles of coarse fibers, coming from large neurones on either side of the ganglion. A third bundle joins them, coming from cells on the neural side of the ganglion. They form the small anterior and posterior ento-coxal nerves supply that the coxal muscles. (Fig. 66, *a.en.cx* and *p.en.cx.*)

These neurones agree with the *H* neurones of the branchial ganglia, in that each one sends a considerable number of axones into the nerve trunk.

The Gustatory Nerves and Tracts.—The most striking features of the mid-brain neuromeres are the large nerve roots supplying the taste organs in the coxal spurs (Fig. 65, $g.n.r.^{2-6}$). They extend along the neural face of the pedal ganglia, sweeping diagonally inward and forward, the inner end of each root overlapping the next posterior one. The united bundles form an immense longitudinal tract along the median neural margin of each crus, between the neural and hæmal commissures.

The more posterior roots are the largest, that of the sixth appendage largest of all. The deep, inner ends of the fifth and sixth roots form large oval neuropile enlargements on the posterior median face of each crus.

Toward the anterior end, one may recognize two subdivisions to the main tract. Near the stomodæal ganglion both divisions turn outward and downward, then upward, forming a sharp semi-circular turn round the crus, giving the latter, in cross-sections, a very unusual spiral structure. The larger bundle apparently terminates in the great cheliceral lobe (Figs. 65 and 114, *ch.l*); the smaller one $g.tr^2$ forms a slight dilatation, consisting of very dense nodular neuropile, on the lateral margin of this lobe, and then passes straight forward, along the neural surface of the cheliceral neuromere to the median cerebral lobe, $G.ctr^3$.

The very large fasciculus of the sixth nerve comes, not from the coxal spurs, which here form crushing mandibles devoid of gustatory spines, but from the large spatulate organ on the outer margin of the coxa (flabellum), the function of which is to test the composition of the water passing to the gill chamber.

A small, posterior fasciculus, coming from the chilaria, joins the main gustatory tract. (Fig. 65, *chela.n.*)

In methylene blue, the gustatory tracts have a very characteristic appearance, as each fascicle contains a great many parallel bundles of extremely minute fibers that look like rows of dots.

In sections (von Rath's method), they may be recognized by their dense black masses of fine parallel fibers (except in the nodes, where they are twisted and interwoven) and by the small quantity of neuroglia contained in them. (Fig. 56, $g.n.r^{4-6}$.)

In the scorpion, a similar tract may be recognized. (Fig. 69.) But here the most conspicuous portion is the immense neuropile bodies on the roots of the first three vagus nerves. These nerves supply the genital papillæ and the pectines, and the immense size of these vagal lobes is due to the great development of sensory (tactile) organs in the pectines.

Similar lobes are seen in Limulus, but lying farther forward, and associated with the immense, flabellar nerve (gustatory) belonging to the sixth pair of legs.

III. Longitudinal Tracts.

There are several well defined longitudinal tracts in Limulus that may be traced the entire length of the brain and cord, but their relations to the various centers and to the motor and sensory terminals is exceedingly difficult to determine. In the main, the sensory elements run on the neural surface of the cords, and the motor ones on the hæmal surface.

We may distinguish the following tracts:

The Longitudinal Hæmal Tracts of the Brain and Cord.—The hæmal tracts are great sheets of longitudinal fibers covering the hæmal surface of the brain and cord. They can be seen in von Rath's preparations, along the hæmal surface of the neuromeres, hæmal to the transverse commissures (Figs. 55, 56, 67, 68, *l.h. tr*). They leave the anterior and the posterior ends of the neuromere in the nearly isolated hæmal sections of the longitudinal connectives (Fig. 64). Midway between the ganglia they cannot be distinguished from the other fibers of the cord.

In methylene blue preparations, these fibers of the cord may be followed at least from one ganglion through the next without branching, and in some cases through several ganglia. In the brain, individual fibers may be followed the whole length of the crus. (Fig. 66.)

In the brain many of these fibers terminate in small clusters of dendrites, scattered over the crura, just below the hæmal surface (Fig. 66, left side); in the branchial neuromeres they are seen on the hæmo-lateral surface just neurad of the longitudinal fibers. (Fig. 62, right side.)

The fibers of the hæmal tracts are derived from several sources. One important source is the large cluster of *B* neurones on the neural surface of each branchial neuromere. Their fibers, after reaching the hæmal surface, divide, one crossing to the opposite side in the anterior hæmal commissures, the other turning backward into the hæmal tracts. (Figs. 61 and 62.)

In the cerebral neuromeres, the hæmal tracts contain similar fibers, derived from similar cells. The latter may be seen in small clusters between the roots of the ganglia, on the neural surface of the crura. Their fibers pass vertically through the crus, joining the longitudinal tracts and the cross commissures. (Figs. 56, 65, 66, *B*, *b*, and *b.*′)

The lateral margin of the hæmal tracts of the crura receives conspicuous fibers that cross in the hæmal commissures with the roots of the hæmal nerve. Near the lateral margin of the crura they turn backward and join the lateral margin of the hæmal tracts (Fig. 66, left side). A similar, but less conspicuous, set of fibers forms on the median side of the tract.

The lateral margin of the hæmal tracts also receives a considerable number of large fibers from the third and fourth lobes of the optic ganglion, $op.g^{3,4}$, and from the crossed and uncrossed fibers of the large lateral neurones of the olfactory lobes, *ol.c′*.

The median margin receives fibers from the large central cells of the olfactory lobes, $ol.c.^3$, and from the giant association neurones in the median lobe of the hemispheres. (Fig. 49, *H.as.tr.*)

A remarkable band of fine fibers comes from the optic nerve, passing through, or over, the lateral margin of the first two optic lobes, along the lateral margin of the optic stalk, through the tween-brain, and along the median hæmal surface of the crura to the beginning of the cord. (Fig. 66, *op.tr.*) A similar band of fine fibers extends along the entire lateral margin of each hæmal tract of the cord. The two bands are united by a narrow commissure extending across the anterior margin of each neuromere. (Fig. 62, *op.tr.*?) It is not clear whether these fine fibered bands of the cord are continuations of the optic bands in the brain or not.

The great majority of the longitudinal fibers of the crura that are directed forward appear to terminate on the hæmal surface of the forebrain commissures.

The Longitudinal Neural Tracts.—These tracts lie close to the median line, on the neural surface of the cord. They receive all the fibers of the first root of the hæmal nerves, many fibers from the nucleus at the root of the pedal ganglia, and large unbranched fibers whose origin is unknown, that pass through the cord over several neuromeres.

In the crura the neural roots of the hæmal nerves appear to be absent, and the other constituents of the neural tracts could not be certainly identified. But we may recognize the following tracts which may or may not be modifications of those already described.

The lateral or pedal ganglion tracts are large and exceedingly complex, consisting of a confused mass of interlacing fiber bundles which form the lateral margins of the crura; most of their fibers come in roughly parallel bundles from the roots of the pedal ganglia (Fig. 56, *l, tr.*, right side). On reaching the tract, the fiber bundles take on a longitudinal trend. The tracts are greatly enlarged opposite the pedal ganglia, and between them they are reduced to narrow bands. (Fig. 56. *l.tr*, left side). At the anterior end of the crura, they appear to pass outside (neural) the gustatory tracts, onto the posterior neural surface of the tween-brain commissure. (Fig. 49, *l.tr.*)

The general cutaneous tracts are two large, continuous columns of neuropile on the median side of each crus. They lie between the gustatory and hæmal tracts, and extend from the tween-brain to the last vagus neuromere, (Fig. 56 *G.c.tr.*)

They usually have a slightly different color and appearance from the lateral ones, from which they are separated by numerous bundles of vertical fibers. The latter are arranged with considerable regularity, the more important sources being neurones B, sending axones hæmally, and neurones E, sending them neurally. (Figs. 56 and 65, *B* and *E.*) The principal constituents of the tracts are the crossed and uncrossed terminals of the cutaneous nerves, *h.n.* The majority of the uncrossed fibers and the optic fascicles, *op.tr*, extend lengthwise of the tracts.

Comparison of the Fiber Tracts of the Arachnid and Vertebrate Brain.—A comparison of the fiber tracts in Limulus with those in the vertebrates presents great difficulties. These difficulties are partly due to our imperfect knowledge of the brain of arachnids and of the lower vertebrates, and partly to the fact that the latter is generally studied for the purpose of explaining the structure of the higher types of brain, not for comparison with an invertebrate brain, that its own structure might be better understood. When we know more about the brain of arthropods, and less emphasis is laid on the artificial system of classifying cranial nerves, now in vogue among American neurologists, many points are likely to be cleared up which are now obscure.

Nevertheless the facts, so far as we understand them, indicate that the arachnid and vertebrate brain are in essential agreement in the distribution and relations of their main fiber tracts. The agreements to which we would call attention are:

a. In both classes, important longitudinal tracts containing the principal motor fibers extend along the hæmal surface of the brain and cord.

b. In both classes, conspicuous sensory tracts lie near the median neural surface, coming from segmentally arranged taste organs and from other sense organs, *i.e.*, tactile, temperature, or auditory, having a less precisely determined function.

c. In these sensory columns, there are local enlargements, or lobes, corresponding with special local functions; *i.e.*, in Limulus, the flabellar lobes of the eighth and ninth neuromeres; in the scorpion, the pectinal lobes of the tenth, eleventh, and twelfth vagus neuromeres; in vertebrates, the auditory and the vagal lobes of their respective neuromeres.

d. In both classes, the numerous gustatory fascicles and those from the vagus neuromeres form a very conspicuous median neural tract, extending the whole length of the brain floor. It terminates in a special center, in the dienceph-

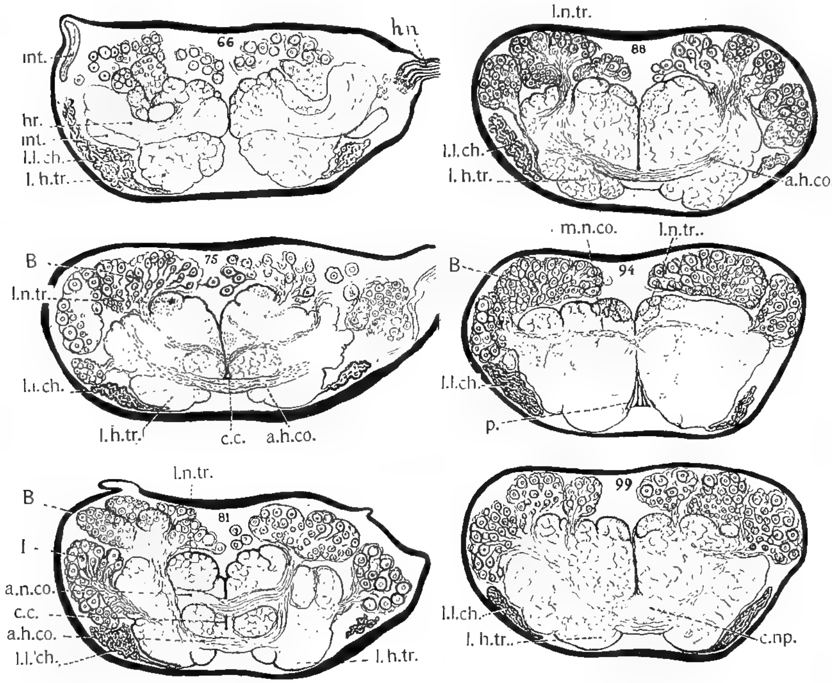

Fig. 67.

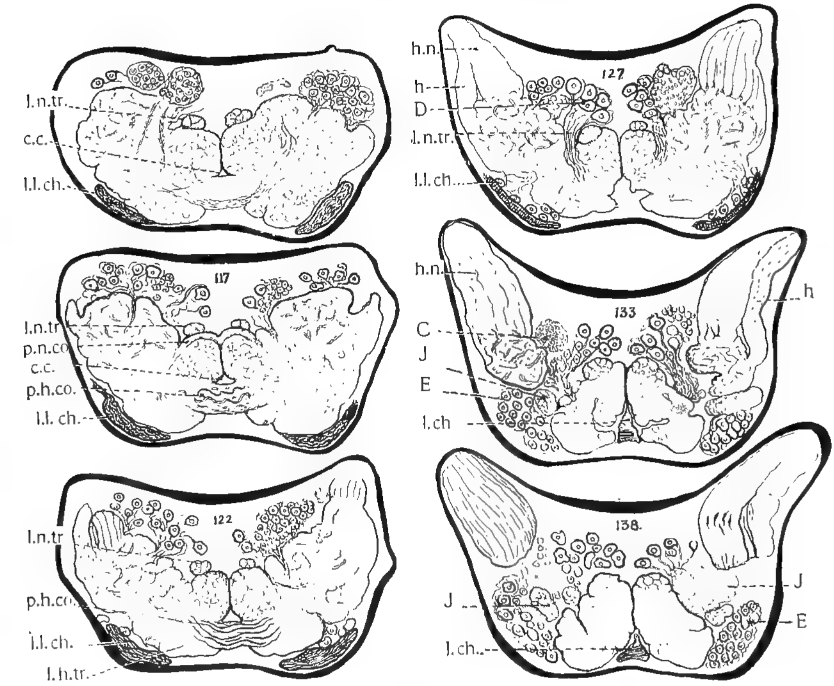

Fig. 68.

Figs. 67 and 68.—A series of sections of the first branchial neuromere of an adult Limulus, showing the location of the principal cell clusters, commissures, fiber tracts, lemmatochord, and central canal. The numbers 66 to 138 indicate the serial numbers of the sections.

alon, which is in turn connected by special tracts with the olfactory lobes, hemispheres, and cerebellum.

e. In both classes, the nerve roots are arranged in two distinct series, neural and hæmal; each series may contain both motor and sensory elements.

In Limulus, the hæmal roots enter the brain toward the hæmal surface and extend horizontally, through the crus and the hæmal commissures, to the main nucleus or cell cluster on the other side of the median line. But many fibers end in dendrites on the same side the nerve enters.

In vertebrates, a similar condition prevails in the ventral or hæmal nerves, for according to Johnston "It is a noticeable peculiarity in the origin of the nerve (*i.e.*, the third nerve of vertebrates) that a large part of the fibers arise from the nucleus of one side, and cross to enter the root of the opposite side. The same arrangement is found in the roots of other ventral nerves, but to a much less degree."

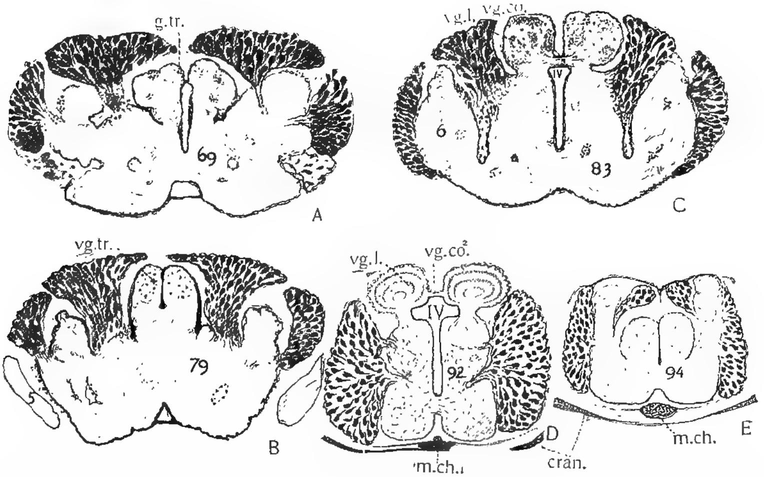

FIG. 69.—Four cross-sections of the brain in the vagus region of an adult scorpion, showing the enormous vagal lobes, the central canal, and the cephalic portion of the middle cord, or lemmatochord.

On the other hand, the neural nerves are associated with special ganglia, which arise independently of the brain, and which are attached to its neuro-lateral margin. In Limulus, these fibers end, or originate, on the same side the nerve enters the brain; very few, if any, fibers of a neural nerve arise from cells located on the opposite side of the median line.

f. In both classes, the floor of the brain is divided lengthwise into two main columns, a median and a lateral one, by an important series of vertical fibers; arcuate fibers, vertebrates, *B* and *E*, fibers, arachnids. The prolongations of these fibers run lengthwise in the hæmal (and neural ?) tracts and crosswise in the commissures.

g. In Limulus, there is in the vagus region an important decussation of impulses coming from the trunk (See section on Physiology, p. 191); and there is also there a special condensation of commissural bundles, that have been crowded together from before backward, in order to leave a large opening for the end of the oesophagus. (Figs. 57 and 58.) In the vertebrates, there is a similar backward dislocation of commissural bundles, forming a special group just back of the choroid plexus of the fourth ventricle, "commissura infirma." Johnston says (p. 287) that "Behind the choroid plexus the c. infirma contains the visceral, sensory elements proper to the segments of the VII, IX and X nerves. It is probable that the course of the root fibers of these nerves within the brain has been influenced by the crowding backward of their decussation and median nucleus by the choroid plexus." The choroid plexus could hardly have the power to dislocate the cerebral framework. The dislocation was probably brought about, as in Limulus, by the backward migration of the outer end of the old stomodæum, and when that closed, the choroid plexus grew over it, leaving the permanently distorted commissures to testify to the event.

h. In both classes, there is a remarkable ganglionated commissure extending over the neural surface of the brain, the stomodæal commissure of arthropods and the cerebellum of vertebrates. Both structures represent very primitive commissural tracts, the only ones which develop, primarily, from the roof of the brain chamber. Both commissures may be ganglionated, and they are the only ganglionated transverse commissures in the primitive brain. Both commissures develop in connection with the fourth neuromere. Both have special relations with the gustatory centers on the posterior median face of the stomodæal opening (infundibulum).

In arachnids, this commissural arch lies behind the cerebral lobes and the optic ganglia. In vertebrates, it is crowded backward by the enlarged optic lobes so that part of its fibers are directed downward and forward, toward the posterior wall of the diencephalon. (Figs. 3, 46, 57, 58.)

IV. Commissures.

Summary.—The facts, bearing on the cross commissures of arachnids, that have been brought out in the preceding pages, may be summarized as follows:

1. The right and left cords of the primitive neuron were united by a series of transverse commissures, two for each neuromere. The anterior commissure is primarily related to the anterior segment of the neuromere and to its peripheral nerve, the other to the posterior segment, and to its nerve. The commissures arise, during the early embryonic periods, as fibrous, non-cellular bands, extending across the floor of the middle groove. They are separated from one another by deeper infoldings of the groove. In the adult, they are still separate, and each contains several distinct fiber bundles, differing in origin and in histological characters.

These commissures always retain their primitive position on the floor of the neuron, hence they are called the hæmal commissures. They are the primary communicating paths between the right and left cords, and between the right and left peripheral nerves.

During the later stages, the cords increase in thickness, the median infolding forms a deep fissure, and then three new commissures appear in each neuromere, extending across the fissure above the old ones. These secondary, or neural commissures, consist largely of association fibers.

With the formation of the secondary commissures the bottom of the fissure, at certain points in each neuromere, is converted into a canal, "canalis centralis" (Figs. 55, 56, 68, 69, *c.c.*), that is lined in the earlier stages with an epithelium derived from a part of the original median infolding. (Figs. 222, 224 and 231.) The floor of the canal is formed in part by the hæmal commissures, and the roof is formed in part by the neural commissures. When the neuromeres are widely separated, there are of course wide gaps in the roof and floor of the canal between the commissures in front and those behind. In the vagus region, owing partly to the increased thickness of the crura, the canal is greatly enlarged, marking the beginning of a chamber comparable with the fourth ventricle or metencœle. (Figs. 55 and 56). Here the neuromeres are more closely united than elsewhere, and their neural commissures, together with some of those belonging to the more anterior neuromeres that have been crowded backward into this territory by the œsophagus, form a special group over the posterior part of the region of the fourth ventricle. (Fig. 47, *C*.)

In the scorpion also, the immense vagal lobes are united by two special neural commissures. (Fig. 47, *A* and 69.)

The combined neural commissures of the vagal neuromeres of the arachnids, and the more posterior thoracic ones, consist largely of somatic sensory association fibers; they probably represent the beginning of the commissura infima of vertebrates.

* * * * * * * * *

In the arachnids there is a wide gap between the forebrain and midbrain, where there are no primitive commissures. This opening, or infundibulum, is the passageway for the old œsophagus. In front of it, the character of the commissures changes greatly, in both vertebrates and arachnids. There are no neural commissures, and the hæmal ones form practically a single, but very complex mass of fibers. (Fig. 48.) In it we may recognize the olfactory commissure, representing the commissure of the first cerebral neuromere, and lying, morphologically, at the anterior end of the nervous system. Owing, however, to the inward and backward migration of the lobes, it lies, in the adult Limulus and scorpion, on the posterior hæmal surface of the forebrain. Fig. 47 *A* and *B*. The forebrain commissure also contains the commissures of the second and third neuromeres, and of the lateral eyes; but these commissures, which arise at an extremely early period, are not separated into distinct bundles. (Fig. 48.)

In Apus, the ganglia of the median ocelli unite with each other in the middle line, over the neural surface of the brain; they rest on the latter by two short stalks. In many other phyllopods and arachnids, the optic ganglia occupy a similar position, in that they lie close together, over the neural surface of the brain, behind the hemispheres. In the vertebrates, they permanently occupy this position, and have become united by secondary commissures, one in the habenulæ, the other in the optic lobes. (Fig. 308.)

The most conspicuous commissure in the arthropods and one of the first to appear, is that belonging to the system of stomodæal nerves. Its ganglia, one median and two lateral, arise from the walls of the stomodæum. It is the only commissure originally provided with ganglion cells, and the only one formed primarily across the neural surface of the brain. It has especial relations to nutrition, through its association with the olfactory, swallowing, and taste centers. It represents the primitive cerebellar commissure of vertebrates, where it appears to have had similar relations.

V. The Neurocœlia.

Summary.—The transformation of the paired nerve cords of invertebrates into the hollow nerve tube of vertebrates is affected by several independent factors. These factors make their appearance as active forces in the arachnids, and they have already established there the salient features of the vertebrate neurocœlia. These factors are as follows:

1. The infolding for the middle cord initiates the canalis centralis and the more posterior parts of the brain cavities.

2. The increasing depth of the median groove, and the increasing thickness of the two cords, brings the median edges of the cords together, and leads to the formation of the neural commissures, which form the rafters over the median groove, and aid in its conversion into a canal.

3. The formation of the palial overgrowth for the forebrain, and the marginal overgrowths in the hindbrain region, initiates the development of the broad, membrane-roofed ventricles of the whole brain.

4. The stomodæal infolding, between the forebrain and midbrain, establishes the deep and narrow third ventricle of the diencephalon.

5. The deep transverse infolding across the very anterior end of the medullary plate gives rise to the cavity of the olfactory lobes.

6. The broad chamber formed by the palial overgrowth, and into which the hemispheres project, establishes the prosencœle, or the first and second ventricles.

7. The median and the lateral eye ganglia unite above the neural surface of the brain, one forming a partial roof to the diencephalon, and the other, owing to the shape of the ganglion, forming a broad, dome-like covering for that part of the brain chamber known as the mesencœle.

8. The stomodæal commissure, forced backward by the enlarging optic ganglia, forms the first stage of the narrow arch (cerebellum) over the future metencœle.

9. In the forebrain, and in the midbrain regions, the medullary cords, in both vertebrates and arachnids, remain practically horizontal. As they are very broad (the diencephalon alone showing a marked lateral compression), and as the overgrowth is almost entirely from the sides, the resulting cavities are broad and shallow. The roof is epithelial in character, and all the nervous material, except the optic ganglia and the stomodæal commissures, forms the floor of the chamber.

10. In the region of the cord, however, the infolding combines another factor, especially prominent in the vertebrates, in that, as the median groove deepens, the two cords close like the covers of a book, bringing their outer, or neurogenic surfaces, face to face, converting the neural groove into a deep lying canalis centralis, and reducing the marginal overgrowths to the narrow strip of epithelium that roofs over the posterior fissure. (Figs. 134, 137 and 231.)

* * * * * * * * *

VI. The Neuroglia.

The neuroglia arises from the epithelial lining of the middle cord groove or canal. Referring to the early stages of Acilius (Fig. 221), it will be seen that the medulla is invaded by numerous small, dark nuclei, that spread out laterally from the middle cord, forming a uniform envelope about the medulla, the so-called inner neurilemma. Later these cells multiply and invade the medulla and surround the nerve cells, forming a coarse, nucleated reticulum or neuroglia.

In the adult, this tissue is easily recognized. In sections of the brain and cord of Limulus stained in hæmotoxylin, Lyons blue, and acid fuchsin, it is intense red, and the nerve fiber masses blue. In preparations treated by von Rath's method, it is intense black, nerve fibers gray. In sections of the adult cord (Figs. 67 and 68), the neuroglia network may be seen springing in root-like processes from the thick layer lining the central canal, as well as from the sides of the neural fissures and the surface of the medulla.

CHAPTER VI.

PERIPHERAL NERVES AND GANGLIA.

I. Components of a Neuromere.

In my first paper "On the Origin of Vertebrates," 1889, it was maintained that the primitive arthropod neuromere was a complex structure, consisting of two segments, four pairs of nerves, and a segmented middle cord.

While I have seen no reason to change my view as to the composite nature of primitive neuromeres, I do not now regard the ancestral arthropod as an elongated worm-like animal of many like metameres, but as a small-bodied one of about three imperfect segments. In the arachnid and crustacean descendants of this stock, the evolution of neuromeres, as we have explained elsewhere (Chap. XIII) was a gradual process that advanced with the successive additions of new groups of unlike metameres.

II. Nerves of the Diencephalon and Mesencephalon.[1]

A. Neural Nerves.

In Limulus, there are six pairs of thoracic neural nerves. (Figs. 36–39.) The third nerve is typical. (Fig. 79.) It divides, soon after leaving the brain, into three sets of nerves. The *gustatory nerves*, three in number, are ganglionated and terminate in the numerous sensory buds of the mandibular spines. They are absent, or very minute, in the sixth pair of legs. The anterior and posterior *entocoxal* nerves, *a.e.n.*, and *p.e.n.* are motor and supply the tergocoxal muscles; the median entocoxal nerve, *m.e.n.*, supplies the sensory knobs of the coxopodite. The main pedal nerve, consisting of two principal branches, supplies the muscles and sense organs of the appendage.

The Flabellum.—There are a few minor differences between the six pairs of pedal nerves; the most important is an enormous enlargement of the median entocoxal nerve of the sixth leg to form the nerve of the flabellum. (Fig. 80, flab.)

The flabellum is a large spatulate organ attached to the outer side of the coxal joint of the sixth leg. It is first seen in the embryos as a rounded knob, lateral to the sixth leg, and quite separate from it. Hence it has the same relation to the outer side of the appendage that the mandibular placode has to the inner. (Figs. 141–148.) There are indications of flabellar placodes on the other

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[1] For nerves of the prosencephalon see Chapters VIII to X.

thoracic segments, but they quickly disappear. The flabellar placode finally unites with the base of the sixth leg and then appears to be a part of it. The flabellum lies in the mouth of the channel leading to the gill chamber, and practically all the water going to the gills, either from the front or from the sides, must pass over its anterior surface. This surface is pigmented and very richly supplied with sense organs and nerves, and it undoubtedly serves to test the quality of water going to the gill chamber. (see p. 113.)

The flabellar placodes are probably represented in scorpion by the lateral coxal sense organs. (Figs. 15–16, *s.so.*)

The Cranial Ganglia.—The base of each pedal nerve, near its origin from the brain, enlarges to form an immense spindle-shaped ganglion. Similar ganglia are present in Branchipus, scorpions, and spiders, and they are also present on the pedal nerves of many other arachnids and phyllopods.

In Limulus they arise, at an early period, from large ectodermic thickenings between the base of the legs and the corresponding neuromere. How the connection between the ganglion and neuromere is established was not determined, but it is certain that the ganglion is not an outgrowth of the nerve cord. The body of the ganglion separates from the thickening, but retains its connection with the overlying ectoderm by ganglionated nerve strands. The latter become the gustatory nerves, and the ectodermic remnant of the thickening becomes the mandibles with their gustatory spines. The thick mass of slime buds on the inner face of the mandibles also arises from these thickenings.

In young Limuli, the ganglia are relatively large masses of cells, separated by clear fibrous stalks from the corresponding neuromere. (Figs. 36–39.) In the adult (Figs. 70 and 218) they are drawn a little closer to the brain, but are never completely merged with it.

In scorpion embryos, similar ectodermic thickenings appear at the base of the thoracic appendages, furnishing the anlage for the coxal ganglia. (Fig. 74, *D.*) The thickenings on the third and fourth appendages become greatly enlarged to form the four hypostomeal spurs that lie on either side of the mouth and rostrum. (Figs. 15–16.) The median face of these spurs is highly sensitive (gustatory?) and from them are developed enormous ganglia and thick masses of mucous glands or slime buds.

In the adult, the median face of the anterior pair of spurs is deeply grooved. The two grooves lie close together and thus form a thick chitenous tube, lined with sensory hairs. In feeding, the scorpion thrusts the spurs into its prey and sucks the blood and other fluids through this tube into the mouth. (Fig. 43, *mxl.*)

The independent origin of the flabellar and coxal spur placodes of Limulus and the scorpion suggests their homology with the inner and outer branches of an originally triramous appendage.

The coxal placodes represent the supra-branchial placodes of vertebrates. Their homology is indicated by their similarity in position, in function, in development, and, so far as may be determined, in number. In both cases, the pla-

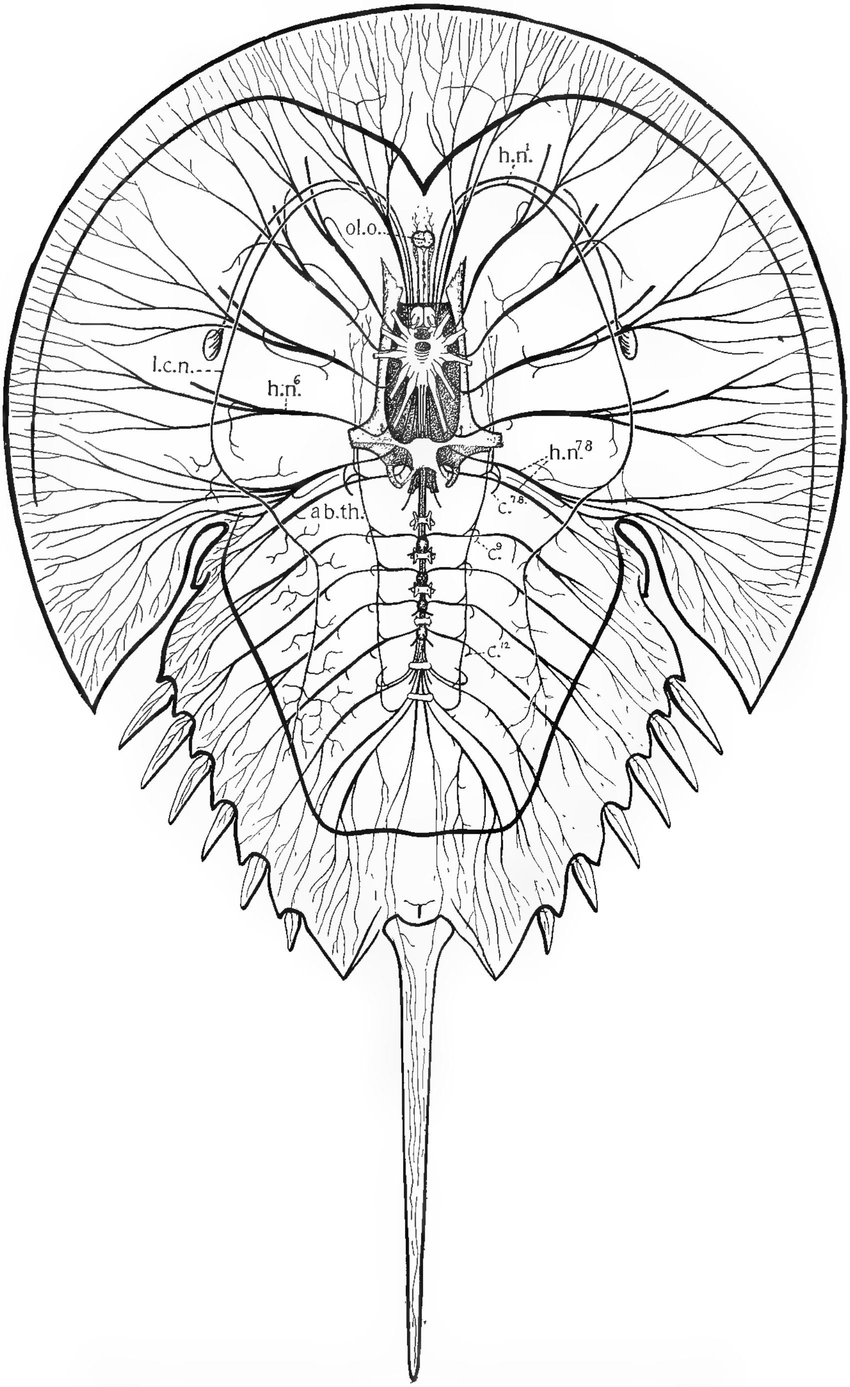

Fig. 70.—Nervous system, endocranium and endochondrites of an adult Limulus.

codes split into a special group of gustatory organs, and into a large cranial ganglion. (Figs. 27–34.)

The Ganglia of the Cord.—*Limulus.*—The roots of the neural nerves arising from the postcephalic neuromeres are also provided with ganglia, but they are not as large as those on the cranial nerves. They merge with the cord at an early period, and, in the adult form the large swellings on the roots of the branchial nerves. (Figs. 59–64.)

Scorpion.—In the scorpion the anterior pairs of nerves are much larger than the posterior ones, and spring from the outer or neural surface of the cord. In stage *H*, just before hatching, the root of the anterior nerve contains a large mass of cells, evidently arising independently of the nerve cords, just as the pedal ganglia do in the thorax. (Fig. 73, *D.*) In the later stages, just after hatching, the ganglion is drawn toward and partly merges with the cord. In the adult, ganglion cells are scattered for some distance over the root of the nerve. (Fig. 73, *C.*)

Meantime the two hæmal nerves move forward, and unite to form a single one with two roots, which in turn unite, a short distance from the cord, with the ganglionated neural nerve. There is no actual mingling of fibers, but the nerves run together, for a short distance, as a single nerve. (Fig. 72.)

The Hæmal Nerves.—*Limulus.*—A single pair of hæmal nerves arise from the anterior hæmal surface of each thoracic nueromere. (Fig. 70, *h.n.*) They are much smaller than the pedal nerves, without ganglia, contain motor and sensory fibers and are distributed mainly to the integument and other tissues of the thoracic shield. The sixth pair alone sends branches to the heart and intestine. Near the outer margin of the entacoxite, the nerves which are elsewhere round, become broad, flat bands; the parallel bundles of nerve fibers become interwoven in a complicated manner, and there is an increased number of neurilemma nuclei, but no ganglion cells. Beyond this swelling, the nerve divides into two main branches, *n* and *h*; one going to the neural surface of the carapace, and the other to the hæmal. After several subdivisions (see original memoir), the end branches of all these nerves form a continuous, subdermal plexus, distributed over the whole inner surface of the neural and hæmal integument, supplying the skin, glands, muscles and sensory hairs.

Lateral Line Nerve of Cheliceral Neuromere.—All these thoracic hæmal nerves are essentially alike, except the first one or that of the cheliceral neuromere. This remarkable nerve (Fig. 70, *l.c.n.*), at first extends forward, and then, bending backward in a broad curve, extends the whole length of the body. It runs close to the neural surface, just outside the bases of the appendages, and does not begin to branch till it reaches a large sclerite behind the base of the sixth leg. The main nerve continues beyond this point the whole length of the branchial chamber, sending one small branch toward the base of each of the five gills. This is a purely sensory nerve and supplies the skin lining the channel along which the water is carried to the gills. It is very remarkable that this nerve should cross the territory of so many other nerves of the same nature, in order to innervate a region so far removed from its origin. It is suggestive of the lateral line nerve of vertebrates, but its origin from the tween-brain region is strongly against such an interpretation. It resembles the large nerve in ganoids and teleosts, the ramus lateralis accessorius, which arises well forward in the head and is distributed to the taste buds of the head, back, tail, and fins.

The character of the sensory terminals to this nerve in Limulus is unknown.

III. The Nerves of the Metencephalon.

We have already shown that a certain number of abdominal metameres in arthropods move forward and unite with the thorax, and that there is a great reduction in their size and an obliteration of their external boundaries. The appendages and muscles show a similar reduction, but the corresponding nerves, neuromeres and heart segments are but little changed. In fact, the nerves and neuromeres may be relatively more voluminous or extensive than elsewhere. These metameres constitute the vagus zone and their neuromeres the metencephalon. Their nerves may be appropriately called vagus nerves, because, as in the vertebrates, they extend backward into regions to which they did not originally belong.

Limulus.

Neural Nerves.—In Limulus, this region contains two metameres, the chilarial and the opercular. The tergites of these metameres are still visible in the adult, the chilarial tergite forming a narrow band on the posterior margin of the thoracic shield, the opercular tergite, two wing-like segments on the anterior margin of the branchial shield. The hinge joint between the two shields lies between these two metameres. (Figs. 150–155.) The first entapophysis is formed between the chilarial tergites and the true thoracic metameres. (Fig. 193.)

The chilaria are without question true appendages. Their early development is like that of the other appendages, and they have separate nerves, muscles, mesoblastic somites, and gill bars. The chilarial and opercular neuromeres have all the typical nerve elements. They resemble the branchial neuromeres more than the thoracic, although in the adult they are intimately fused with the hindbrain and widely separated from the branchial neuromeres. Their nerves pass out of the occipital foramen of the endocranium together with the spinal cord. (Figs. 70–218.)

The chilarial nerves arise close together from the posterior neural surface of the accessory brain. They pass out of the endocranium just below the roof of the occipital ring, enter the chilaria and supply their muscles, the adjacent skin, and the numerous gustatory spines on their median side. (Fig. 81, *n.n*^{7}.)

The opercular nerve follows the same course, and on reaching the operculum

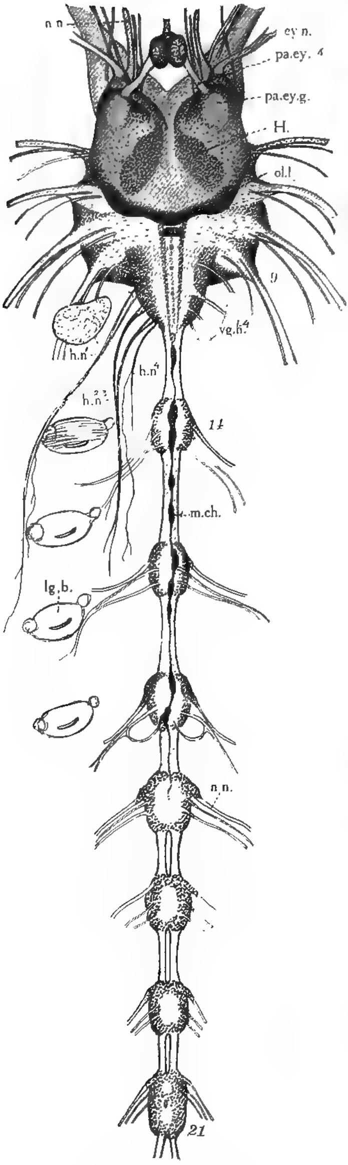

FIG. 71.—Brain and nerve cord of a new-born scorpion, seen from the hæmal surface.

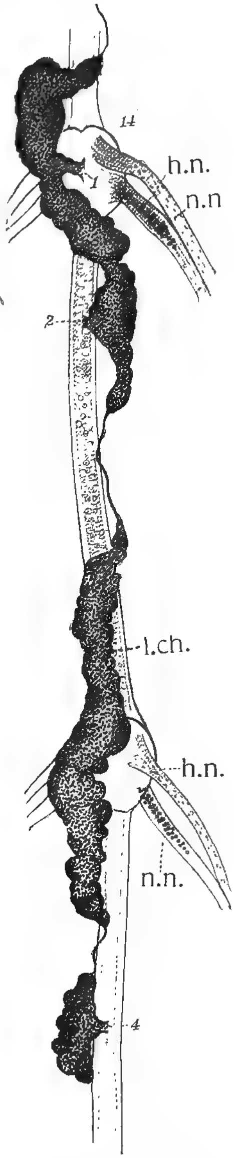

FIG. 72.—First two free branchial neuromeres, with the lemmatochord, spinal ganglia, and spinal nerves for an adult scorpion.

divides into three nerves which then subdivide into motor and sensory branches (for details, see original memoir, 1893).

The hæmal nerves (Fig. 70, *h.n*^{7} and *h.n*^{8}), pass out of the endocranium through the occipital ring and are distributed to the sides of the body, between the sixth pair of legs and the operculum. For the distribution of the intestinal and cardiac branches, see pp. 103, 200.

Scorpion.

In the scorpion, the vagus region consists of four metameres, two genital, one pectinal, and the first branchial, as I demonstrated in my first paper on this subject, 1889.

The tergite of the first metamere fuses with the thorax and cannot be detected in the adult. The other three tergites remain separate throughout life, the second or genital, and the third or pectinal, being much narrower than the fourth (Fig. 17). The fusion of these metameres is more strongly marked on the neural than on the hæmal surface.

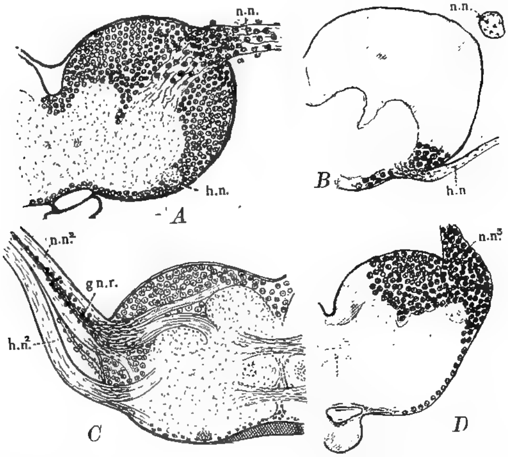

FIG. 73.—*A*, Section of an abdominal neuromere of a new-born scorpion, showing the ganglionated "dorsal," or neural, nerve root; *B*; same through the non-ganglionated hæmal nerve root; *C*, section of the second free branchial neuromere of an adult scorpion, showing both neural and hæmal nerve roots and the neural and hæmal transverse commissures; *D*, third branchial neuromere of an old embryo of a scorpion, showing the large ganglionic lobe at the root of the neural nerve.

During the early embryonic stages, one may recognize four distinct pairs of rudimentary, abdominal appendages (Figs. 15, 16). During the later stages, the first lung book appears in place of the last appendage. The third pair gives rise to the pectines; the first pair disappear altogether by the time of hatching; while the second pair finally unite in the median line in front of the pectines to form the genital cushion, or tubercles.

Before they unite, about stage G (Fig. 16, *B*), the genital openings may be recognized on the median margin of each appendage. About the time of hatching, the genital ducts are carried forward and unite to form an unpaired opening, between the remnants of the first pair of abdominal appendages and the second. During stage G, the brain may be dissected out, and the arrangement of neuromeres and some of the nerves observed (Fig. 54). The first two neuromeres are crowded forward and are overlapped by the posterior margin of the hindbrain. This produces a sharp hæmal flexure in the brain, at the dividing line between the thoracic and vagus region; the first two vagus neuromeres are thus partly concealed, in surface views, under the overlapping hindbrain. The vagus nerves, during these early stages, are small and cannot be followed with certainty. In the adult scorpion, they present an interesting condition. The nerves are now divided into two groups, one containing all the neural nerves, the other all the hæmal. (Fig. 42.) This is largely due to the constriction which is such a characteristic feature of the vagus region in arthropods. All the paired organs in this vicinity, such as genital ducts and appendages, are drawn toward a median position, hence in the adult the corresponding nerves take their origin from the neural surface of the cord, near the middle line.

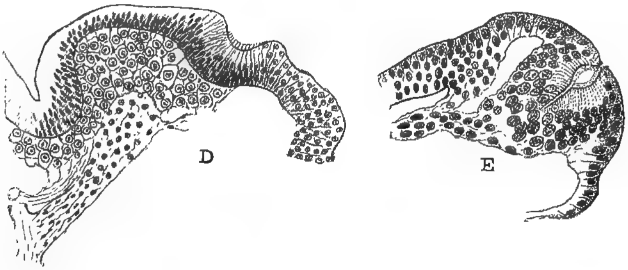

FIG. 74.—*D*, Section through the basal lobe of the third thoracic appendage of an embryo scorpion; *E*, section of one of the segmental sense organs on the outer margin of the thoracic appendages. See Figs. 15 and 16.

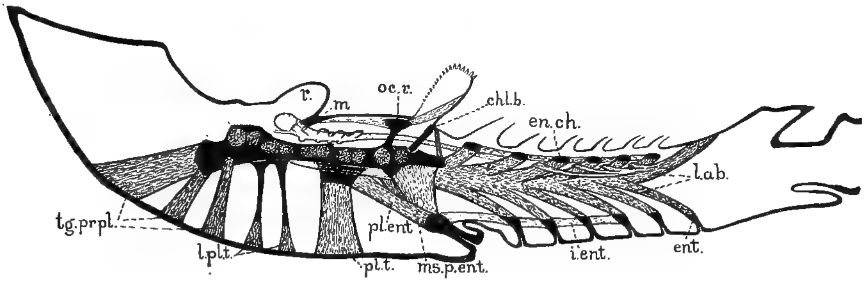

FIG. 75.—Side view of the endocranium, brain, neural arches, and associated muscles of an adult Limulus; semi-diagrammatic.

The Neural Nerves.—One small nerve, supplying the sexual ducts and papillæ, probably represents the nerve of the second pair of rudimentary appendages (Fig. 42, v^1). The nerve to the pectines has three roots, the first one *g.n.* forming an immense bilobed ganglion (ganglion nodosum) composed of ganglion cells and concentric lamminæ of medullary substance (*g.nd*).

It is united with its mate by two distinct bridges of nerve tissue that lie some distance above the surface of the neuromeres they thus form an imperfect roof to a deep, narrow canal between the two ganglia and the median sides of the underlying neuromeres (Fig. 40). The anterior ends of the ganglia may be traced in transverse sections a long distance forward, as two great longitudinal fasciculæ, just below the neural surface of the thoracic neuromeres. (Fig. 69, *v.g.l.* and *g.t.r.*)

The ganglion on the second root (ganglion fusiforme) is smaller, spindle-shaped, and as near as can be determined, appears to belong to the third neuromere. The third root is small, fibrous, and without any ganglionic enlargement.

The Hæmal Nerves.—The two hæmal nerves of the first neuromere remain separate, as in a typical thoracic neuromere. In each of the three following neuromeres, they unite to form a single nerve, each with a double root. (Fig. 42, *h.n.*$^{1-4}$.) A short distance from the brain all five hæmal nerves form a compact bundle that extends backward through the occipital foramen of the cartilaginous cranium. (Figs. 71 and 217.) The nerves to the third and fourth neuromeres, *h.n.*^{3} and *h.n.*^{4}, some distance from the brain, fuse to form a single nerve supplying the first and second lung books and the ventral surface of the body (Fig. 71). On its way to these organs, it passes over the ventral surface of the liver, to which it possibly gives branches. The anterior hæmal nerve of the first vagus neuromere, *h.n.*^{1} runs close to the coxal gland, and dividing into numerous branches, is lost on the surface of a thick, peritoneum-like membrane. The posterior nerve, *h.n.*^{2} extends along the arthroideal membrane, supplying numerous sense organs on the lateral and the hæmal surface of the abdomen. The fourth vagus nerve, *h. n.*^{4} supplies the skin and the longitudinal muscles on the ventral surface of the abdomen.

IV. Nerves of the Branchiencephalon.

The branchial neuromeres differ from those of the brain in that they remain separate through life. Their nerves are noteworthy for their association with the respiratory muscles, the heart, and the intestine.

Limulus.

The Branchial Nerves.—In Limulus, the branchial, or neural nerves, contain both motor and sensory fibers. They arise from large ganglia on the posterior neural surface of the neuromeres; on entering the gills they divide into three branches. (Fig. 82.) The external branch, *eb.n.* supplies the abductor muscles and the skin on the anterior lateral surface of the appendage. The median branch *g.n.* supplies the adductor muscles and the gill books. The internal branch *i.bn.* supplies the skin and muscles in the terminal portion of the appendage.

The Hæmal Nerves (Figs. 59 and 70), arise from the anterior margin of the neuromere and extend outward over the neural surface of the abdominal muscles. They divide into five principal branches; one goes to the enteron, one to the longitudinal abdominal muscles, one to the branchio-thoracic muscles, one to the heart, and one to the integument.

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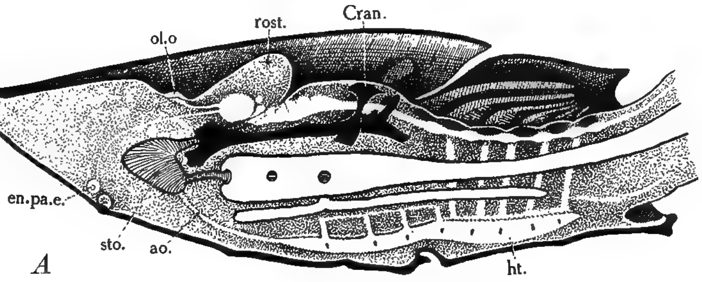

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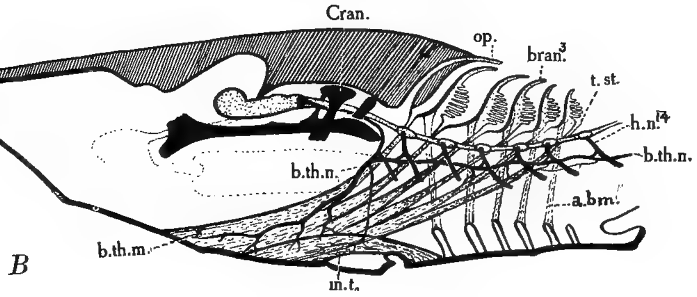

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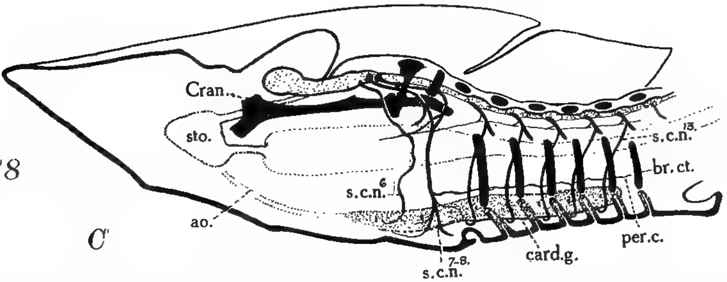

FIG. 76.—Side view of the brain, endocranium, alimentary canal, and principal vascular channels in Limulus; semi diagrammatic.

FIG. 77.—Same, showing the relation of the compound branchio-thoracic, or hypobranchial nerve to the hæmal nerves of the vagus and branchial-neuromeres. Semi-diagrammatic.

FIG. 78.—Same, showing the relation of the segmental cardiac nerves, *s.c.n.*$^{6-13}$, to the heart and to the vagus and branchial neuromeres. Semi-diagrammatic.

The Enteric Nerves.—In Limulus, the enteric nerves are intimately associated with the nerves to the longitudinal abdominal and hæmo-neural muscles. The enteric nerves form a plexus which covers the entire mesenteron and the plexus is united with the roots of all the hæmal nerves, from the sixth to the sixteenth, by paired rami communicantes. (Fig. 59 i^{7-14}.) Those from the sixth and seventh neuromeres pass through the foramina in the posterior lateral wall of the endocranium. (Figs. 59^{7-8} and 218.)

The rami from the sixth thoracic, the chilarial, and opercular neuromeres mingle with a plexus of nerves distributed over the longitudinal abdominal muscles; from there branches pass forward, ramifying over the surface of the mesenteron as far as the stomodæum.

In the branchial neuromeres, the nerves supplying the longitudinal abdominal muscles and the intestine are separate. The former arise from the anterior side of the hæmal nerve root (Fig. 60, *l.ab.*), and the latter from the posterior side. In the more posterior neuromeres, the intestinal branches gradually shift their point of origin from the root of the hæmal nerve to the median margin of the neuromere. In the branchial segments, the intestinal rami send a small branch to the corresponding hæmo-neural muscle.

The enteric nerves appear to represent the initial stages of the sympathetic system of vertebrates. It is a noteworthy fact that in Limulus the anterior cranial nerves are not directly united with the enteric plexus by segmental communicating branches. The most anterior connecting branch that is recognizable belongs to the ninth cranial neuromere, resembling, in this respect, the well known condition in vertebrates.

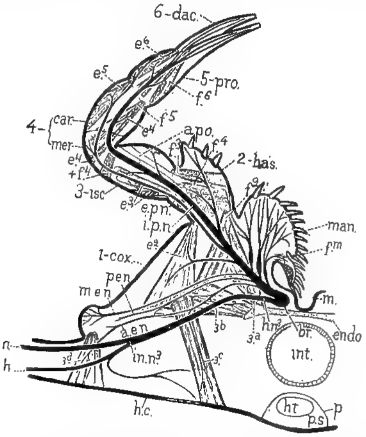

FIG. 79.—Muscles and distribution of nerves in the third leg of Limulus, from the anterior side. 1-*cox.*, Coxopodite, or first joint; 2-*bas.*, basipodite, or second joint; 3-*isc.*, ischiopodite, or third joint; 4-*car.*, *mer.*, fused carpopodite and meropodite, or fourth joint; 5-*pro.*, propodite, or fifth joint; 6-*dac.*, dactylopodite, or sixth joint; *apo.*, apodeme.

MUSCLES: 3^a and ^{b}, Plastro-coxal muscles inserted upon anterior side of entocoxite; 3^c and 3^d, tergo-coxal muscles inserted upon anterior side of entocoxite; $e.^{2-6}$, extensors of second to sixth joints; $f.^{2-6}$, flexors of second to sixth joints; *f.m*, flexor of inner manible.

NERVES: *a.e.n.*, Anterior ento-coxal nerve; *br.*, brain; *e.p.n.*, external pedal nerve; *h.*, hæmal branch of in tegumentary nerve; *h.n.*^{3}, hæmal nerve; *in.n.*^{3}, integumentary branch; *i.p.n.*, internal pedal nerve; *m.e.n.*, median encoxal nerve; *m.n.*, mandibular nerves; *n.*, neural branch of integumentary nerve; *n.n.*^{3}, neural nerve; *p.e.n.*, posterior ento-coxal nerve.

The Longitudinal Abdominal Muscles and Nerves.—The longitudinal abdominal muscles arise from the posterior hæmal side of the endocranium and pass backward, giving slips to each pair of the abdominal entapophases and to the abdominal endochondrites. (Fig. 75.)

The muscles are provided with a rich nerve plexus, extending their whole length.

(Figs. 57, 59, *l.ab.*) The fibers arise from small branches of the sixth to the sixteenth hæmal nerves. The branches are given off from the anterior side of the hæmal nerve, close to the cord. The neurones lie on the opposite side of the next anterior neuromere, with those that supplythe branchio-thoracic muscles. (Fig. 60, *D*, *l.ab.*) In the seventh and eighth metameres, the plexus appears to be continuous with that going to the intestine.

The General Cutaneous Nerves are largely, if not wholly, sensory. They extend over the surface of the branchial plastron, dividing into numerous branches on the margin. (Figs. 59, 70, *g.cut.*) The fibers that enter into these branches probably form the second root, *h.r.*^{2} (Fig. 61.)

Cardiacs.—For a description of the segmental cardiacs, see p. 200.

The Branchio-thoracic, or Hypo-branchial Muscles and Nerves.

The hypo-branchial muscle is a large compound muscle derived from the eighth to thirteenth metameres inclusive. The neural end of each component is separate and terminates in a tendinous infolding of the ectoderm at the base of its corresponding appendage. The hæmal ends form a single massive muscle which shifts its position a long ways forward into the hæmal region of the thorax, where it is attached to the inner surface of the shield, in front of the anterior end of the heart and the forebrain. (Fig. 78, *B*.)

The muscle aids in the performance of the complicated respiratory movements, drawing the bases of the gills forward and upward; it also aids in flexing the thorax on the branchial section of the body.

The hypo-branchial nerve[1] forms a great longitudinal trunk extending over the neural surface of the muscle. (Figs. 59 and 77, *b.th.n.*) It receives its fibers from the eighth to the fourteenth hæmal nerves, via short communicating branches. It is, therefore, to be regarded as a compound nerve formed by the united branches of at least seven segmental nerves. For the greater part of its course, it forms a compact longitudinal trunk, giving off at regular intervals branches to the proximal ends of the muscle slips, near their tendinous attachment to the base of the gills. At its anterior end, it breaks up into many branches that are distributed through the single muscle into which the six separate muscles merge. One nerve separates from the anterior end of the main trunk and supplies the inter-tergal, or arthro-tergal, muscle. (Fig. 77, *in.t.*)

The nerve fibers arise from clusters of large *D* neurones lying on the opposite side of the cord, on the posterior margin of the neuromere, in front of the one where the nerve enters the cord. (Fig. 60.) The very large axones cross in the posterior hæmal commissure and pass backward, as a conspicuous bundle of large nerve tubes, *h.r.*^{5}, to the hæmal nerve root. Some of the fibers go to the longitudinal abdominal nerves, but the main bundle passes on with the hæmal nerve, leaving it farther on, to enter the main hypobranchial.

The remarkable condition of the hypobranchial muscles and nerves of Limulus is, no doubt, one that has its counterpart in other arachnids. At present,

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[1] Lateral Sympathetic of Patten and Redenbaugh.

practically nothing is known about the anatomy of these muscles and nerves in other invertebrates.

In Limulus, the fact that is specially noteworthy is that the six originally vertical components of the branchio-thoracic muscle have been converted into a nearly horizontal, or longitudinal, compound muscle, thereby destroying all correspondence between the metamerism of the neural and hæmal surfaces as far as this muscle is concerned.

The hypo-branchial muscle, by this change in position, gains in effectiveness as a respiratory and flexor muscle, but it would be a mistake, I believe, to accept that as a primary cause of the change in position, or as an explanation for the existence of that particular function. The real reason lies deeper, and is to be seen in those changes that have gradually reduced the volume of the hæmal organs in the anterior head region. This atrophy or reduction of the hæmal surface of the head during the early embryonic periods, inevitably draws the hæmal structures of the post-cephalic metameres forward, and is the initial cause of that forward

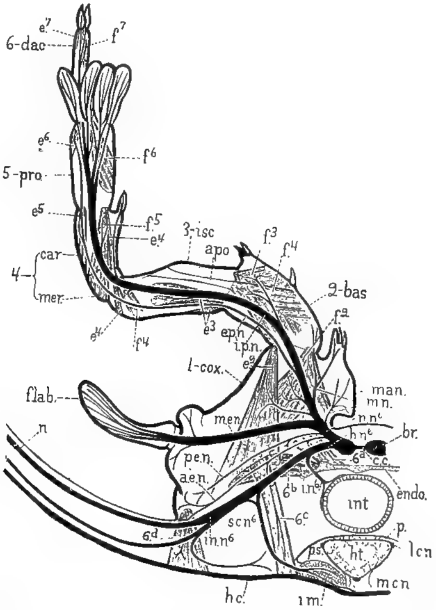


FIG. 80.—Muscles and distribution of the nerves in the sixth leg of Limulus, from the anterior side, 1-*cox.*, Coxopodite, or first joint; 2-*bas.*, basipodite, or second joint; 3-*isc.*, ischiopodite, or third joint; 4-*car.*, *mer.*, fused carpopodite and meropodite, or fourth joint; 5-*pro.*, propodite, or fifth joint; 6-*dac.*, dactylopodite, or sixth joint; *apo.*, apodeme; *br.*, brain.

MUSCLES: 6*a* and 6*b*, Plastro-coxal muscles inserted upon anterior side of entocoxite; 6*c* and 6*d*, tergo-coxal muscles inserted upon anterior side of entocoxite; $e.^{2-7}$, extensors of second to seventh joints; $f.^{2-7}$, flexors of second to seventh joints; *i.m.*, inter-tergal muscle.

NERVES: *a.e.n.*, Anterior entocoxal nerve; *e.p.n.*, external pedal nerve; *h.*, hæmal branch of integumentary nerve; $h.n._6$, hæmal nerve; $i.n.^6$, intestinal nerve; $in.n.^6$, integumentary branch of hæmal nerve; *i.p.n.*, internal pedal nerve; *l.c.n.*, lateral cardiac nerve; *m.c.n.*, median cardiac nerve; *m.e.n.*, median ento-coxal nerve or flabellar nerve; *m.n.*, mandibular nerve; *n.*, neural branch of integumentary nerve; $n.n..^6$, neural nerve; *p.*, pericardium; *p.e.n.*, posterior ento-coxal nerve; $s.c.n.^6$, segmental cardiac nerves.

displacement and condensation that we have just described in the hæmal ends of the hypo-branchial muscles.

This condition is a very ancient one, for these very muscles, in this position, no doubt cause that folding of the thorax onto the abdomen which is so common in trilobites. I have seen the same thing in Bunodes, very much to my astonishment. For sections of specimens that appeared to be headless, showed that the cephalo-thorax was present, but doubled over so as to lie with its neural surface flat against the neural surface of the branchial region.

The general trend of the branchio-thoracic nerves no doubt has been determined by these morphological changes in the muscles; but the union of these several nerves into a common trunk is to be regarded as an expression of the tendency to gain simplicity by the merging of several separate agents, performing the same function, into a single one.

V. RELATION OF THE VAGAL AND HYPO-BRANCHIAL NERVES IN ARACHNIDS TO THOSE IN VERTEBRATES.

The entire system of nerves belonging to the vagal and branchial regions in the arachnids, represents the initial stages in the evolution of the vagal and branchial complex in vertebrates. We can already distinguish in the arachnids the beginning of that remarkable segregation of similar components into compound nerves, that in the vertebrates has given rise to the branchial, hypoglossal, cardiac, visceral, and lateral line nerves; and the beginning of that readjustment in the position of the terminals that has given to each set of components their characteristic distribution and direction of growth. (Figs. 57, 58.)

The branchio-thoracic muscles and nerves of Limulus are clearly comparable with the hypoglossal nerves and muscles of vertebrates. In both vertebrates and arachnids, the nerves arise: *a.* from a large number of post-vagal neuromeres (five branchial and one opercular); *b.* they are either hæmal nerves (ventral roots) or branches of hæmal nerves; *c.* they are united to form a compound longitudinal trunk, terminating in an extensive plexus; *d.* the distal ends of both muscles and nerves migrate a long distance forward onto the anterior hæmal surface of the head, thus causing the nerves to follow their characteristic U-shaped course, and disguising the original relation between the metameric arrangement of organs on the neural and hæmal surfaces; *e.* the distribution of the neural nerves (branchial arch nerves) is not affected by these changes.

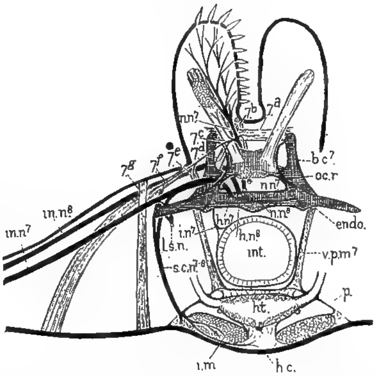


FIG. 81.—Muscles and nerves of the chilaria of Limulus, from anterior side. The appendages are revolved outward about 45°. *b.c.*7, Capsuliginous bar, or branchial cartilage of the chilaria.

MUSCLES: 7^{a-e}, Plastro-coxal; 7 *f* and *g*, tergo-coxal; *i.m.*, inter-tergal; *vp..m.*7, veno-pericardiac.

In the arachnids (scorpion), four abdominal neuromeres have migrated forward to unite with the hindbrain. Of these four, the last one is a true branchial neuromere.

In vertebrates, all the branchial neuromeres have fused with the hindbrain, probably in some such manner as that indicated in Fig. 68. The hypobranchial nerves united to form the hypoglossus, having the peculiar distribution indicated above, although in a more exaggerated form. The neural roots united with one another, and with the posterior neural roots of the vagus, as they have to a certain extent in the scorpion, to form the series of nerves supplying the gill arches. The nerves supplying the important sense organs in the group of modified vagal appendages, gave rise to the lateral line nerve; and the combined cardiac and intestinal components, that in the arachnids are confined to this region, gave rise to the corresponding elements in the vertebrates.

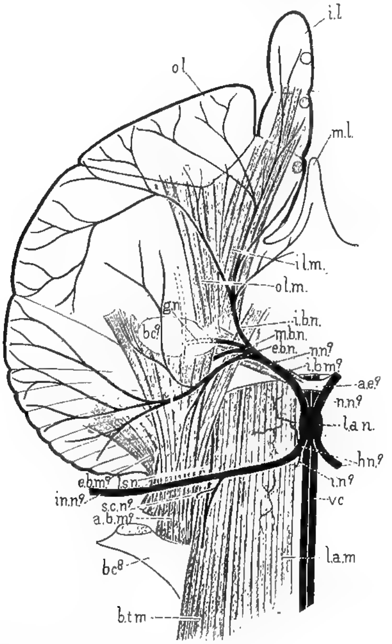


FIG. 82.—Muscles and distribution of nerves in the first gill of Limulus. The appendage is flexed upon the abdomen, and is seen from the neural side. *a.e.*9, Abdominal endochondrite; *b.c.*^{8} and *bc.*9, branchial cartilages of operculum and first gill; *i.l.*, inner lobe of gill; *m.l.* median lobe of gill *o.l.*, outer lobe of gill.

MUSCLES: *a.b.m.*9, Abductor muscle of gill; *b.t.m.*, branchio-thoracic muscles; *e.b.m.*9, external branchial muscle; *i.b.m.*9, internal branchial muscle; *i.l.m.*, inner lobe muscles; *l.a.m.*, longitudinal abdominal muscles; *o.l.m.*, outer lobe muscles.

NERVES: *a.g.*, First abdominal ganglion; *e.b.n.*, external branch of neural nerve; *g.n.*, branch of neural nerve supplying gill book; *h.n.*9, hæmal nerves; *i.b.n.*, internal branch of neural nerve; *i.n.*9, intestinal nerve (two branches are shown, a posterior and an anterior one); *in.n.*,9 integumentary branch of hæmal nerve; *l.s.n.*, hypo-branchial nerve; *m.b.n.*, median branch of neural nerve; *n.n.* 9, neural nerve; *s.c.n.*,9 segmental cardiac nerve; *v.c.*, ventral cord.

We need not carry this comparison any farther, for the conditions are extremely complicated, and there are many variations peculiar to each class. But that this entire region has undergone the same kind of changes in vertebrates that we now see taking place in the arachnids is, I believe, beyond question. The fact that the branchial appendages in arachnids, as nearly as we may determine, belong to the same group of metameres as in vertebrates, and the fact that the total number of branchial segments in Limulus and the merostomes is very nearly the same as in vertebrates, *i.e.*, seven appendages, four or five of which are gill bearing, as against five or seven gill bearing arches for vertebrates—is suggestive, but perhaps of less significance than the fact that in both cases, there is a much greater forward growth and concrescence of the structures on the hæmal surface than of those on the neural, thus producing that apparent lack of harmony in the serial arrangement of nerves, neuromeres, gill arches, and myotomes, so disturbing to the student of vertebrate cephalogenesis.

The conditions become still more significant when we recall that they are the inevitable results of very remote factors that are common to both types, such as the absence of lateral plates to the mesodermic segments in the anterior part of the head, the gradually increasing size of the yolk sphere, and the precocious development of the forebrain.

CHAPTER VII.

GENERAL AND SPECIAL CUTANEOUS SENSE ORGANS.

In the arachnids, we may recognize three main groups of sense organs; primitive segmental, special cutaneous, and general cutaneous.

a. The primitive segmental sense organs include the median and the lateral eyes, the olfactory and the auditory organs. With the exception of the last named, they are so highly developed and have been so long established that they and their nerve centers constitute the very foundations of the forehead and forebrain. *b.* The special cutaneous sense organs include the gustatory buds, slime buds, and other chemotactic, or tactile organs that have well defined nerves, ganglia, and central terminals, and that are located in definite fields, or areas, such as the coxal spurs, chilaria, pectines, flabellum, etc. They attain their highest development in the midbrain and hindbrain regions. *c.* The general cutaneous sense organs may be of the same nature as the special cutaneous, but they are irregularly distributed, and without separate, well defined nerves or ganglia; we also include in this category temperature organs and free nerve endings. They are supplied mainly by the subdermal plexus formed from the terminal branches of the neural, but especially of the hæmal nerves. These nerves may arise from all the main divisions of the neuron except the forebrain.

I. General Cutaneous Sense Organs.

Temperature Organs.—Reaction to changes in temperature in the lower animals is probably much more delicate and more generally exercised than has been suspected. The temperature sense is not dependent on the location of its organs in a particular part of the body, for changes of temperature are diffusely distributed, and are not likely to affect the animal at one point more than another. An effective response results in the transfer of the whole body to surroundings of a different temperature; thus the temperature organs primarily control them ovements of the animal as a whole, or its migrations, or distribution in space.

One would hardly suspect that such a heavily armored animal as Limulus would be very sensitive to changes in temperature, yet that such is the case may be easily demonstrated. When placed on its back and allowed to become perfectly quiet, it may be fanned, or the surface of the carapace, or the gills, or the legs, may be touched with an object the same temperature as the air, without causing any reflexes; but the instant any of these parts are touched ever so gently with the finger, or if water a little warmer or colder than the surrounding air falls on them, or even if one gently breathes on the gills and under surface of the body, the animal at once becomes greatly agitated.

The most sensitive areas are the margins of the carapace, and especially the margins of the gill chamber along which the main current of water passes to the gills, and the anterior surface of the branchial appendages themselves.

We cannot positively identify the temperature organs. They appear to be short, spike-like projections in which terminates a small tuft of sensory cells. They are distributed over all parts of the carapace and are supplied by the terminal plexus formed by the branching of the hæmal nerves.

They are seen to best advantage in the gills of young Limuli, 2–4 in. long. In those parts of the gills that are most sensitive to heat, *i.e.*, the outer surface of the terminal joints of the exopodites, one may see, in successful methylene blue preparation, a loose subdermal nerve plexus continuous with small clusters of spindle shaped sensory cells. From each cluster a very fine fiber extends outward, through a chitenous tubule, to a short spike situated on the outer surface of the gill. (Fig. 86, *A*, *t.s.*)

* * * * * * * * *

Free Nerve-Ends.—In the abdominal appendages that have been injected with methylene blue, large nerve branches may be seen going to the soft integument around the joints of the endopodites. Each branch ends in a group of bipolar or multipolar cells; from them arise many branching fibers that form a rich terminal meshwork, lying in or on the ectoderm, but without association with any specialized cells. (Figs. 86 *B*, 87.)

The hyphæ of a parasitic fungus sometimes ramify in all directions through or over the surface of the chiten. They usually take on an intensely blue stain, and at first sight might be mistaken for nerve fibers.

II. Special Cutaneous Sense Organs.

The Gustatory Organs of Limulus.—Gustatory organs are widely distributed over the neural surface of the head, but they are most highly developed in the appendages that come in frequent contact with the food. In other words, the principal aggregations of these organs are located around the mouth in segmentally arranged fields. This condition explains their remarkable distribution in vertebrates. There they are primarily arranged in several radiating series on the top of the head, an inconveniently long distance from the present vertebrate mouth, but close to the central areas where the old invertebrate mouth was located. (Fig. 89.)

The gustatory organs have been most carefully studied in Limulus, and they form the principal basis for my conclusions. They are abundant in the mandibles of the thoracic appendages, except the first and last pairs, and in the tips of the thoracic appendages. Their presence in the mandibles is indicated by a most beautiful series of reflexes, first described by me in 1892. Organs similar in structure to the ones we are about to describe occur in other parts of the head and trunk, but stimulation of them does not produce any recognizable reflex.

a. Reactions to Stimulation.—If an adult Limulus be placed on its back, it soon becomes quiet, except that after long intervals the gills are raised and lowered a few times. If, during the quiescent condition, the jaw-like spurs, or mandibles, at the base of the legs are gently rubbed with some hard object, such as a piece or wood, glass, or iron; or if water the temperature of the surrounding medium be gently poured over them; or if the animal be vigorously fanned, or loud noises be made near it, only slight, aimless movements of the legs or abdomen are produced; usually none at all. But if a very small piece of clam, not more than two or three millimeters long, is gently laid on the surface, say of the third mandible on the left side, care being taken not to touch any other parts, that leg will be repeatedly raised and the tip bent toward the mouth, while its mandible will move back and forth, alternating with the leg movement. Meantime all the other mandibles and appendages are motionless. One may start in this way one appendage after the other (except the first and last pairs), until all of them, first on one side and then on the other, are in action.

If all the jaws are stimulated with food at the same time the normal chewing reaction takes place as follows: The second and fourth pairs of mandibles move in unison inward toward the median plane, and downward toward the mouth; then back again in the reverse order. When they are farthest from the mouth the corresponding legs (except the second pair in both males and females) are quickly raised, flexed, and the tips carried toward the mouth, where they remain an instant, and then fall back on to the under side of the carapace; the corresponding jaw movement then begins again. The third and fifth pairs of appendages and the corresponding jaws work in unison in the same manner, but they alternate with those of the second and fourth. At intervals these movements cease, the abdomen is raised, and the stout crushing mandibles on the sixth pair of appendages, which have heretofore remained motionless, are slowly closed with great force, as though to crush some object too large to be swallowed whole, or to kill some struggling prey. These powerful jaws then slowly relax their convulsive grasp, and the chewing movements are resumed.

All these movements go on with the greatest precision and regularity, so that the food that was placed on the jaws is forced into the mouth and down the œsophagus.

A drop of clam water is sufficient to start the whole reaction, which is performed in the same manner as during the actual process of eating.

If wads of blotting paper are used, wet with ammonia or picric acid, the chewing movements are reversed, and the offensive object may be snapped up by the cheliceræ and rejected.

Strong smelling food held close to the mouth, or to the jaws, produces no effect, although chewing movements are instantly produced when the jaws are touched by it.

If the mandibles on one side are stimulated, the chelicera of that side, although not stimulated itself, extends rigidly backward, or waves aimlessly back and forth snapping its chelæ and thrusting the tip of the appendage into the mouth. If the jaws on the opposite side are now stimulated, the chelicera on that side begins to work also.

The chewing reactions can only be produced by stimulating the spines on the mandibles, or the smooth, under surface of the inner mandibular spur. Stimulating the skin around the mouth, or in it, does not produce the chewing reflexes. If the mandibles are amputated, no reaction in the leg so treated occurs. If the spines are shaved off, the reaction is produced only after strong stimulation, or by stimulating the under surface of the inner mandible.

It is thus evident that we are dealing with true taste organs, and that they must be located in the mandibular spines.

b. Structure of the Gustatory Organs.—The mandibular spines are thickly covered with minute pores arranged in vertical lines. (Fig. 83, *A*.) The pores lead into canals, each of which contains a long, slender chitenous tubule that terminates flush with the outer surface. The chitenous tubule contains an exceedingly fine, hair-like prolongation of a gustatory cell. Toward its inner end, the tubule expands into a peculiar spindle, beyond which lies the nucleated cell body. The gustatory cells are united into spindle-shaped clusters, each cluster corresponding to a single line of pores. The central ends of the cells are continued as nerve fibers into the main gustatory nerve, which extends over the surface of the pedal ganglia, through the gustatory tracts, to the common centers in the cheliceral lobes and hemispheres. (Figs. 65–114.)

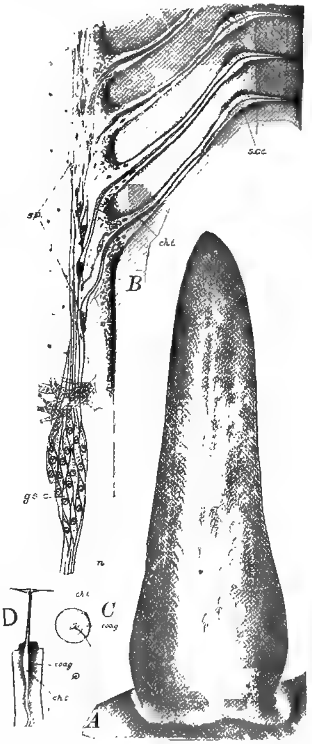


Fig. 83.—*A*, Gustatory coxal spine of Limulus, showing linear arrangement of the gustatory pores; *B*, longitudinal section of a gustatory spine, showing the gustatory cells, *g.s.c.*, spindles, *sp*, and chitenous end tubes, *sch.t.* highly magnified. *C.D*, Details of surface terminals.

* * * * * *

The flabellum is a large spatulate organ, one to one and one-half inches long, attached to the outer side of the coxal joint of the sixth leg. It lies in a channel leading into the respiratory chamber, so that the water going to the gills passes over its flat anterior surface. The latter is perforated with innumerable canals that afford an opening for the elements of the underlying sense organ, the most voluminous one in the whole body.

Each canal contains the outer end of a pear-shaped sense bud composed of eight to twelve, or more, sense cells. The buds are loosely united into small groups that are surrounded by an ill defined sheath and supplied by a single nerve. (Fig. 84.)

The slender outer ends of the sensory cells unite to form a dense, conical body, enclosed in a bulb-like enlargement at the base of a chitenous tubule. Before uniting, the cell ends become especially distinct and each one develops a minute, bead-like swelling.

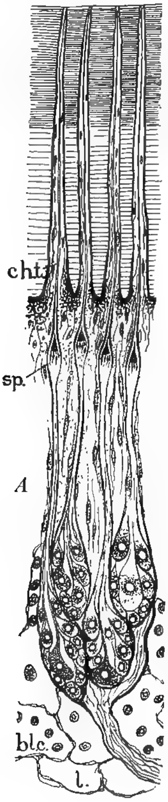


FIG. 84.

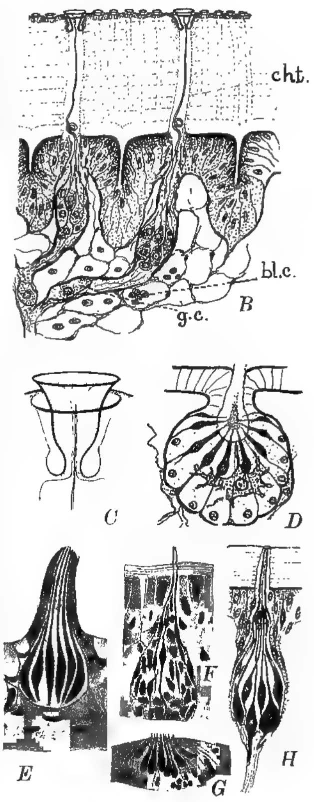


FIG. 85.

FIGS. 84 and 85.—*A*, Section through the anterior surface of the flabellum of an adult Limulus, showing four flabellar sense organs—von Rath's preparation; *B*, section throngh one of the gill warts of an adult Limulus, showing the peculiar bell-shaped terminal "hairs" and the associated cluster of sensory cells and chitenous tubules—von Rath's preparation; *C*, terminal hair of a gill wart, more highly magnified; *D*, diagram of a slime bud, Limulus; *E*, taste bud from the pharynx of an embryo Catastomus (*after Johnston*); *F*, a taste organ from the skin of an adult Lampetra (*after Johnston*); *G*, a neuromast from the skin of Catastomus (*after Johnston*); *H*, diagram of an arachnid sense bud.

The apex of the cone extends outward as an exceedingly minute fiber, through a small chitenous tubule, probably as far as the outer surface of the flabellum. Between the slender necks of the organs are a few elongated cells, and similar ones, but smaller, are seen in the canals through which the chitenous tubules pass to the exterior.

The thick epidermis is heavily pigmented, and pigment is frequently seen in the body of the sensory cells.

The sense buds are so numerous that their inner ends are crowded together several rows deep. The inner surface of the sensory field is very vascular, and the narrow crevices between the organs are often crowded with blood corpuscles.

The posterior wall of the flabellum, in marked contrast to the anterior, contains few or no sensory perforations, and the epidermis is thin, nearly colorless, and with few blood-vessels.

The flabellum is supplied by a very large nerve the root of which passes over the neural surface of the sixth pedal ganglion and joins the main gustatory tracts. It does not differ from the fascicles coming from the gustatory cells in the mandibles, except that it is larger. It appears to form the greater part of the conspicuous neuropile enlargements seen on the median face of each crus. (Fig. 65.)

The flabellum doubtless serves to test the quality of the water that is drawn into the gill chamber. I have not been able to detect any characteristic reactions when it is stimulated.

The flabellum probably represents the exopodite of the sixth pair of appendages. Traces of similar organs are seen for a short time at the base of the other appendages. (Fig. 141.)

* * * * * * * * *

The Branchial Warts.—The branchial warts are blister-like elevations about four mm. in diameter, located on the endopodites of the branchial appendages. They are covered by a soft, bluish chiten, and lie either folded over the margin, half on each side of the gill, or in pairs, one member on the anterior, the other opposite to it on the posterior surface of the appendage. (Fig. 82.)

The outer surface is thickly and uniformly covered with goblet, or bell-shaped hairs, deeply set in conical recesses. There are two distinct sizes, evenly distributed in about the proportion of five small ones to one large. The large bell-shaped hairs lie over the outer ends of large canals which contain spirally coiled, and very distinct chitenous tubules. (Fig. 85, *Br.* and *C.*)

The canals are colorless and, except for the tubule, appear to be empty. They do not contain blackened fibers or nuclei such as occur in the flabellar canals. The tubule springs from a small, fusiform cluster of sensory cells lying well below the surface. Thick nerve bundles, remarkable for the large ganglion cells scattered over them, leave the inner ends of the cell clusters and uniting with the other bundles form a loose nerve plexus, which is continuous with terminal branches of the branchial nerve.

The smaller goblet hairs are without visible tubules, and their faint, underlying canals do not perforate the outer chitenous layers. They do not appear to be connected with nerves.

The inner surface of the flexible chiten that covers the branchial warts extends inward in the form of thin, vertical walls that form a coarse, polygonal network when seen in surface views. They are covered with a thick epithelium, giving them in sections a false appearance of sensory infoldings.

Between two opposing organs is a loose, areolar tissue and a conspicuous venous chamber.

These organs are clearly of a very special kind. In addition to their unusual naked eye appearance, they are peculiar in the shape of the terminal goblet hairs; in the absence of cells or fibers in the underlying canals; in the thick walled, spiral, chitenous tubule; in the ganglionated nerve branches, and in their inflated elastic walls that lie on opposite sides of the appendage.

Their peculiar structure indicates that they may be provisionally regarded as a kind of pressure guage which aids in the control of the heart beat and the respiratory movements.

* * * * * * * * *

The Slime Buds.—Slime buds are spherical masses of glandular cells, mingled with nervous or sensory ones, and richly supplied with nerves.

They vary greatly in their grade of development, and in the relative number and size of their sensory and glandular cells. They are scattered over the whole surface of the body, but are especially abundant in certain regions, or areas, that are known to be highly sensitive.

While at first sight they appear to be merely integumentary glands, closer examination raises many important questions that are difficult to answer, as, for example, in regard to their function, minute structure, and development.

It is probable that they play an important part in the reactions toward certain kinds of stimuli, but whether their secretions serve to protect the adjacent nerve buds against excessive stimulation (which seems to me very improbable), or as absorbers and intensifiers of certain substances, has not been demonstrated.

A familiar illustration of a similar condition in vertebrates is the association of slime, or mucous cells with the sense organs of the lateral line. There is also an intimate association of mucous and sensory cells in many molluscs, *i.e.*, in Lima, Arca Noæ, and in the tentacles of Haliotis.

The facts that have special significance for our problems are as follows:

1. Secretion of mucus. When small Limuli are violently stimulated, the slime buds discharge an abundance of mucus, and, if the surface of the shell has been previously wiped dry, it may be seen to collect in small drops over each pore. When allowed to accumulate, it forms a thick slimy covering to the whole surface.

2. Distribution. The slime buds are very numerous in certain well defined areas which, from their location and abundant nerve supply, have every indication of being highly sensory, as, for example, in the olfactory organs, in the mandibular spurs of Limulus, and the maxillaria of the second and third pairs of thoracic appendages in the scorpion.

3. Innervation. These groups of slime buds are innervated by special nerves,

or by the same nerves that supply the adjacent gustatory organs. Those that are scattered over the general surface of the body are supplied by branches from a subcutaneous plexus, formed by the ramifications of the general cutaneous branches of the hæmal nerves. In the appendages, the subdermal plexus arises from the general cutaneous branches of the neural nerves.

4. Structure. Slime buds are found in many crustacea and arachnids, and, although but little is known about them, they appear to have a similar structure to those in Limulus.

The slime buds differ in appearance in different regions, and apparently at different times. They are generally spherical or oval, with a small central space from which a chitenous tubule leads to the exterior. (Fig. 88.) This tubule may or may not be convoluted near its origin, but it generally terminates in a straight delicate tubule that cannot be distinguished from those covering the outer ends of the gustatory and temperature-cells. All the tubules are shed with the old shell at ecdysis. They may be seen protruding a considerable distance from the inner surface of the cast off shell that have been cleaned with boiling potash.

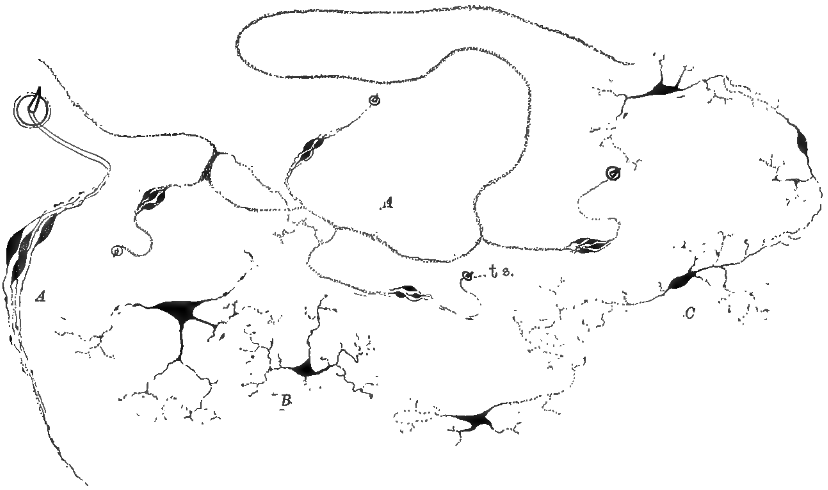


Fig. 86.—Anterior, or outer, surface of the branchial appendage of a young Limulus, two inches long. *A*, a portion of the subdermal plexus of nerve fibers, with clusters of bipolar sense cells whose outer ends terminate in minute chitenous spikes; *A*, one of the sense buds, more highly magnified, with its chitenous tubule, *ch.t.*, that conveys the terminal fibers to the surface; *B*, two apparently isolated multipolar ganglion cells, lying just below, or in, the surface ectoderm of the branchial appendage; *C*, four multipolar ganglion cells from the same region. Methylene blue.

The slime buds contain at least two different kinds of cells, namely, true slime cells, which may constitute the greater part of the organ, and one or more sensory cells. The slime cells vary greatly in appearance. In the typical olfactory and mandibular slime buds, they are irregularly conical or cylindrical, their walls are sharply defined, and they contain, at their pointed central ends, a mass of refractive colorless spherules. The enlarged peripheral ends of the cells, in which is located the small nucleus, may be finely granular, staining a dark gray or bluish-black in von Rath's fluid. (Fig. 88.)

Each slime bud contains a single ganglionic or sensory cell, distinguished from all the others by its large size, dark, finely granular protoplasm and indistinct outline. This cell appears to be larger and more distinct in the mandibular slime buds than it is in the olfactory buds.

Between the outer ends of the slime cells there are minute, rod-like bodies with a dilatation at their inner ends. They have the appearance, under some conditions, of being minute sensory cells, but I have not been able to fully satisfy myself that such is the case. In von Rath's fluid, they become very black, and in some cases hair-like processes appear to project from them into the cavity of the slime bud, where they unite to form a small star-like body. (Fig. 85, *D.*)

In some cases, the buds are greatly distended and the cells appear nearly colorless and empty, as though after a certain period of activity they were about to degenerate.

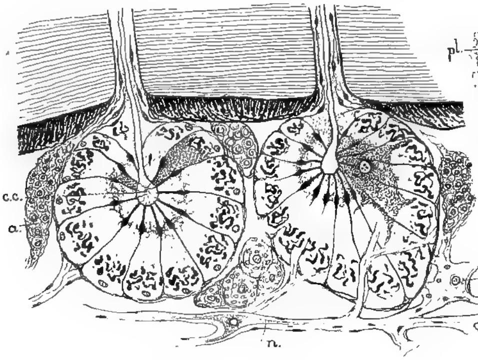


FIG. 88.

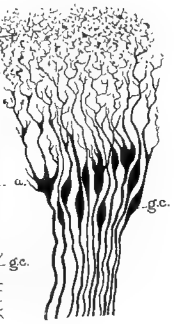


FIG. 87.

FIG. 87.—A cluster of ganglion cells terminating in a sub-dermal plexus of anastomosing fibers; from the soft skin between the joints of the endopodites of the branchial appendages of a young Limulus. Methylene blue.

FIG. 88.—Two slime buds grom the olfactory region of an adult Limulus—von Rath's prepration. *a.* Groups of cells of unknown significance; *c.c,* central coagulum resting on hair-like projections.

New slime buds, that have arisen de novo from the indifferent ectoderm, or by the division of the existing buds, appear in the older stages.

5. In the vertebrates, there is a similar association of sensory and mucous cells in the lateral line organs. For a long time it was assumed that the lateral line canals were primarily slime producing organs, and nothing more. When the sense organs in the canals were discovered, the associated mucous cells were apparently forgotten.

In the lower vertebrates, the typical taste organs form small clusters of sensory cells, resembling in structure and innervation the taste organs and the flabellar organs in Limulus. (Fig. 85, *E.*) The typical lateral line organs, or neuromasts, consist of short, hair-bearing sense cells, united with longer so-called "supporting," or indifferent cells, which may or may not secrete mucous (Maurer). This association of mucous cells and hair cells in one organ is comparable with the association of sensory and mucous cells in the slime buds of arachnids and in the olfactory organs of insects (Necrophorus, Dahlgren and Kepner). If the short, rod-like bodies in Limulus are true sensory cells, then the morphological resemblance between an arachnid slime bud and a vertebrate neuromast is very striking. (Figs. 85, *D–H*.)

According to Maurer, there are some cases in the vertebrates where the lateral line organs still remain in a condition approaching that in the arachnids, for he regards the slime buds in Myxine and Bdellostoma as probably representing modified lateral line organs of Petromyzon. In other words, in Myxine and Bdellostoma, the mucous sacs are sense buds, in which all or nearly all the cells secrete mucous.

In the vertebrates, however, the secreting function is usually relegated to separate cells in the adjacent ectoderm, the "supporting" cells apparently retaining their secreting function only in exceptional cases (Maurer). In reply to an inquiry on this point, Prof. C. Judson Herrick writes me that "the line organs of vertebrates are so exceedingly variable that I would not venture to generalize, with my present knowledge, on the relation between the sensory and the mucous cells; but certainly in some cases, and I think as a rule, they are closely associated. The mucous cells are I think generally absent in the non-sensory parts of the lining of the canals. As to the function of the mucus, I have hitherto regarded it as like the mucus of the general body surfaces, protective. But in view of Parker's work on the function of the lateral canal sense organs as receptors for slow vibrations, it may be that the mucus and the cilia of the hair cells both enter into the formation of the cupula which overlies the lateral line organs much as in the case of ampullæ of the internal ear and that the whole cupula assists in the stimulus of the sensory cells."

However, it is clear that we must go farther back than primitive vertebrates for our explanation. In Limulus, for example, we have the same kind of gland cells intimately associated with cutaneous sense organs, and it is extremely improbable that the abundant mucus there serves either to protect an already practically impervious covering, or to assist, by slow vibrations, in the stimulation of the sensory cells.

6. The function of the slime buds in Limulus is not apparent. The presence of the mucoid secretion is obvious enough in both vertebrates and arachnids, but a satisfactory explanation of its purpose is not available; and it is difficult to account for the rich innervation of these organs in Limulus, or for the presence of sensory or nerve cells in them, or for their association with other sense organs, on the ground that they are mucous glands and nothing more.

The only conclusion open to us at present is that first suggested by me in 1889, namely that in the arachnids and primitive vertebrates, the mucous secretion serves to absorb certain chemical substances held in solution, and to thus intensify their action on the nerve ends. This explanation would account for the abundance of mucous in the olfactory and gustatory organs, and for its absence in the tactile or auditory ones.

The mandibular slime buds are sufficiently numerous to suggest that they are in the nature of salivary glands. This, however, does not seem probable, since there is no way to get the secretions into the mouth with the food; and the membranes immediately within, or surrounding the mouth are entirely devoid of these organs. Moreover, it is certain that the precisely similar slime buds in the olfactory fields, and in the integument of the back or branchial chamber, cannot be regarded as salivary organs.

7. The slime buds of Limulus and other arachnids are found in segmentally arranged fields, or groups, that are supplied by special nerves, the most conspicuous groups being those in the olfactory organ, in the mandibles of the second to the fifth thoracic appendages, and in the rudimentary vagus appendages (scorpion). These organs appear at an early embryonic period as thickenings of the ectoderm and in close association with the cranial ganglia.

The Auditory Organ.—In my first contribution, 1889, I maintained that the large segmental sense organ, which in Limulus embryos lies opposite the fourth pair of legs, was the probable forerunner of the vertebrate ear. I see no reason to change my opinion on this point. Although the evidence in favor of this conclusion is not voluminous, it is sufficiently precise as far as it goes. In Limulus, the organ in question is a large discoidal placode, of a sensory nature (Figs. 131, 140 to 153), strikingly like the auditory placode of vertebrates in its general outward appearance, in its minute structure, and in the fact that it is located, as nearly as one may determine, on the same segment of the head, using as a guide either the history of the oral arches (Figs. 29–34), or the number of the corresponding brain neuromere. (Fig. 57.)

It is assumed that in the primitive vertebrates this particular placode, which lies at the head of the posterior division of the thorax, formed a simple, sac-like infolding, similar to the auditory sac in decapods, and that from this sac developed the inner ear of vertebrates.

The placode belongs to the same series as the visual and olfactory organs. (Figs. 140–148, *s.o*^{4}.) It increases in size up to the time of hatching. During the early trilobite stage, the cells become slightly pigmented, take on a sensory appearance, and a lens-like thickening of the overlying chiten is formed over it. (Fig. 131, *B.*) The organ disappears completely at the close of the trilobite stage.

That is as far as the evidence goes. There is no evidence that the placode in Limulus is auditory; or that it is serially homologous with the antennal auditory organs of decapods, although that is not improbable.

Gaskell regards the flabellum of Limulus, or the pectines of the scorpion, as the precursor of the vertebrate auditory organ; but they lie much too far back in the head to be compared with the ear of vertebrates. His description of the minute structure of the flabellum is very inaccurate, and his intimation that it is an auditory organ, possibly homologous with the pectines of scorpions, is contrary to well established facts.

Lateral Line Organs of Vertebrates. Summary and Comparison.— The lateral line organs of vertebrates consist of several distinct groups that arise at an early embryonic period from the neural surface of the head. Each line of organs makes its appearance as an oval thickening of the ectoderm, located between the dorsal extremity of a gill arch and the lateral margin of the medullary plate. (Figs. 26–34.) The thickening gradually extends in a peripheral direction, and as it does so it separates into a superficial linear series of sense buds and an accompanying underlying nerve and ganglion. Subsequently an infolding of the ectoderm may take place along the line of growth, forming first an open groove and then a canal, in which the organs are located at regular intervals. Finally the several canals may unite, forming a continuous system, but each part that was originally a distinct canal is innervated by a special cranial nerve. (Fig. 89.)

It has been suggested that the anlage of each canal represents a very ancient sense organ (the so-called branchial sense organ), but so far as I know, no explanation has been offered for the extraordinary fact that these ancient organs must have originated, not around or close to the vertebrate mouth, as one would naturally suppose, but from the opposite or aboral side of the head; and not from a single anlage, but from several.

This condition, however, is perfectly intelligible as soon as we recognize that the whole system of taste buds and lateral line organs of vertebrates represents the thoracic and vagal coxal sense organs of arachnids, which there lie on the neural surface of the head around the primitive mouth, the latter having closed up and disappeared in the vertebrates.

When the sense organs of the arachnids are projected on the neural surface of the cephalothorax, the principal groups, each one containing many organs, appear as oval or circular areas arranged around the mouth. (Fig. 89, *A*.) We may recognize three sets: the gustatory organs and slime buds located side by side in the thoracic and vagal appendages, and the chemotactic general cutaneous organs located on the neural flanks of the thoracic and branchial regions, and supplied by a great longitudinal nerve arising from one of the anterior thoracic neuromeres, *l.n.*

Taste buds predominate in the second, third, fourth, and fifth thoracic coxæ, *i.e.*, those immediately surrounding the mouth. Sense cells of the same general type are abundant in the flabellum and in the vagal appendages, but there they may serve as tactile organs, or for some other purpose.

The organs of the gustatory-tactile type and the slime buds may arise side by side from the same anlagen, and they may be supplied by the same nerve trunks and ganglia. Their later phylogenetic history appears to follow along the same lines in both cases, but there is apparently a tendency to separate, more and more, the two kinds of organs, so that each kind assembles in particular areas and is supplied with distinct nerves arising from distinct brain tracts. We shall here refer to the common anlagen of both sets of organs as coxal and vagal sense organs.

There is a sharp distinction morphologically between the anlagen of the thoracic organs and those of the vagal region. The thoracic anlagen are always directed forward and outward and are located well on the sides of the thorax. The vagal anlagen are always crowded close to the median line and are directed backward, approximately parallel with the nerve cord. (Fig. 89.) The location and direction of growth of these organs is determined by that of the appendages to which they belong and is prophetic of their condition in vertebrates.

When the oral appendages were transferred to the hæmal surface (see Chapter XV), it is probable that the anlagen of the coxal organs were drawn forward and outward into a narrow band, each one giving rise to a row, or linear series of taste organs, the general course or direction of the organs, and the accompanying nerves and ganglia, indicating the path of migration of the corresponding appendage.

The vagal appendages of the arachnids are always carried backward, relative to the other parts of the same segments, as shown by the invariable direction of their nerves and ganglia. The conditions that controlled their movements have no doubt continued to direct the line of growth of the vagal group of anlagen in the embryos of their vertebrate descendants.

There is nothing to indicate what conditions determined the backward growth of the immense longitudinal cutaneous nerve, which in Limulus arises from the first post-oral neuromere. (Figs. 70, 89, *l.n.*)

The embryological history of the lateral line organs in primitive vertebrates bears out this interpretation. We may recognize there two principal groups of organs, one lying in front of the auditory organ and belonging to the oral arches, the other lying behind the auditory organ and belonging to the branchial region and trunk. The former represent the coxal organs of the arachnid thorax, the latter, the organs of the vagal appendages. These two groups of organs grow in the same general direction in the vertebrates that they do in the arachnids, but they have extended very much farther in the former.

In the vertebrates the several pairs of anlagen tend to run together, and it is not clear just how many there are in either region, or which ones of those in the arachnids they represent.

The second, third, fourth, and to a less degree, the fifth pairs of coxal anlagen en the arachnids are probably in part retained in the vertebrates, forming the rudiments of lines of canal organs for their corresponding appendages, which have themselves furnished the basis of the premaxillary, maxillary, mandibular and hyoid arches. One or more groups of vagal sense organs gave rise to the lateral lines of the branchial region and the trunk.

* * * * * * * * *

Let us now consider the several lines of canal organs as they appear in ostracoderms and primitive vertebrates.

In the ostracoderms, they undoubtedly occur in the most primitive condition known in the adult of any vertebrate-like animal.

In Tremataspis (Fig. 236), the organs were apparently located in short, shallow surface grooves; in Bothriolepis (Fig. 247), in continuous open grooves. When expressed in a simple diagrammatic form, the sensory grooves of the ostracoderms appear to originate in the occipital region and to radiate from it in the following lines: There is a main suborbital (Fig. 89, *B.*), *i.o.l.*, continued forward as the rostral line, *r.l.*, in front of the olfactory organs. In Bothriolepis, a branch line arises from it and extends hæmally over the surface of the premaxillæ. A mandibular line is not recognized in any ostracoderm, probably owing to the small size of the mandibles. There is no true supra-orbital line, probably owing to the median location of the lateral eyes, although the short-post-orbital line of Tremataspis and the longer one in Bothriolepis possibly represent the proximal end of such a line, *s.o.l.*

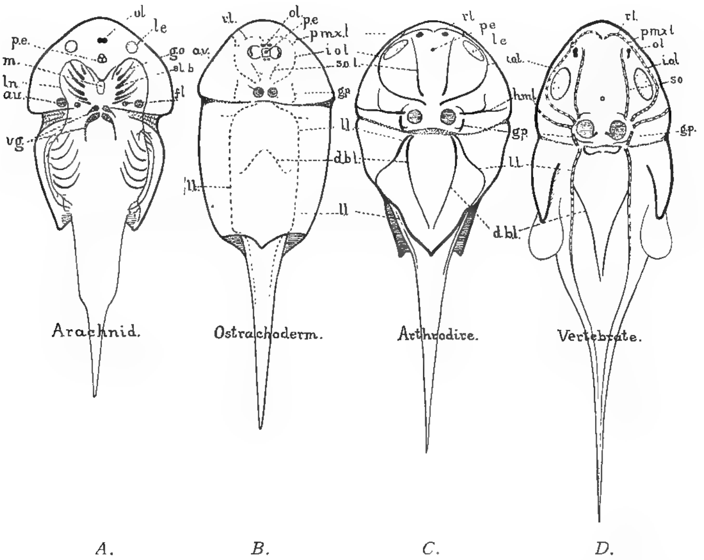


FIG. 89.—Schematic figures showing the location of the lateral and median eye, olfactory, auditory, gustatory, and canal organs, in the arachnids, ostracoderms, arthrodiri, and primitive vertebrates. All figures seen from the neural surface.

The orbital line appears to be continuous with the lateral line of the branchial region and of the trunk, by means of short glosso-pharyngeal sections, *g.p.* Judging from the embryological conditions in vertebrates, this section represents a separate line, supplied solely by the glosso-pharyngeal nerve. The main lateral line extends along the branchial region and in Bothriolepis may be traced for a short distance on to the trunk. There are two accessory dorso-branchial lines in Tremataspis and one in Bothriolepis.

In the *Arthrodira* (Fig. 89, *C*), the most important advance is in the appearance of a distinct supra-orbital line, *s.o.l.*, extending forward between the now widely separate lateral eyes; and a distinct hyomandibular line *h.ml.* extending toward, and probably onto, the greatly enlarged mandibles. In the arthrodira the neuromasts apparently never form a series of separate dots and dashes, but lie in continuous grooves of varying depth.

In true vertebrates, no important changes or new conditions arise. The several lines may be deeply infolded and joined at their proximal ends to form a united series of canals, with the sense organs located in them at regular intervals, suggesting the interrupted surface grooves of the ostracoderms. (Fig. 89, *B* and *D*.)

CHAPTER VIII.

LARVAL OCELLI AND THE PARIETAL EYE.

I. The Different Kinds of Eyes in Arthropods and Vertebrates.

Since the principal facts in their embryonic development became known, it has been generally assumed that the vertebrate eyes originated inside the brain chamber, and that the retina was a highly specialized part of the brain wall.

There are fundamental objections to this interpretation, namely: *a.* it reverses the usual order of histological development, for nerve cells are to be regarded as specialized sensory cells, not *vice versa;* and *b.* it fails to establish any connection or relation between the eyes of vertebrates and those that are almost universally present, and often highly developed, in the invertebrates. In fact, it neither explains how the eyes got into the brain chamber from without, nor under what conditions they developed "de novo" from within.

The arthropod theory is not open to these objections, for we shall show that the evolution of a cerebral eye has already taken place in the arachnids, and that the principal steps in the process are recorded there in great detail.

Eyes of Arthropods.

In the arthropods, we may recognize four types of eyes, namely: paired larval ocelli; parietal eyes; frontal ocelli, or stemmata; and the lateral or compound eyes.

The larval ocelli, of which there may be six pairs, two for each of the forebrain segments, are present in the active larvæ of most insects, but disappear during the metamorphosis (coleoptera, lepidoptera, neuroptera, hymenoptera). They are cup-like infoldings of the ectoderm, with upright or horizontal retinal cells or rods. In the insects, the retinal cells are never completely inverted, and the ocelli never form unpaired eyes enclosed in a common chamber or vesicle.

The Parietal Eye.—In the crustacea and arachnids, two pairs of ocelli unite to form an unpaired ocellar vesicle, or parietal eye. The ocellar placodes remain more or less distinct and form the side walls of the dilated anterior, or distal end of the vesicle. The proximal, or posterior end is generally tubular and may open on the outer surface of the head; or it may merge with the palial folds and open into the forebrain vesicle. The parietal eye usually persists through life, and it may be the largest and most important one functionally.

The frontal eyes or stemmata of insects consist of two pairs or placodes that form a median, tri-oculate group. They arise during the metamorphosis, or at any rate after the embryonic period, and are quite independent of the primitive ocelli. They are never involved in a palial fold or in a common vesicle, and the retinal cells are, apparently, always upright. They are functional eyes only in adult insects, or in the late larval stages.

In the arachnids and crustacea (phyllopods, entomostraca), the frontal ocelli are present in a highly modified form, as two sets of frontal organs two paired and one unpaired. In Limulus, they become the olfactory organs. In spiders and scorpions, they are apparently absent. Their nerve roots arise from the median anterior surface of the forebrain, or from the anterior surface of the optic ganglia and hemispheres (Limulus).

The lateral or compound eyes are found in adult insects, crustacea, and arachnids, including the trilobites and merostomes. Like the stemmata, their relation to the primary head segments cannot be easily determined, because at the time the cephalic lobes are most clearly segmented, as in the embryonic stages of Acilius and the scorpion, the lateral eyes are absent, and they do not appear, if at all, till near the close of larval life. In Limulus they belong to the cheliceral segment; in insects, they appear to belong to the antennal segment.

The development of the lateral eyes is essentially the same in all arthropods. They are derived from large crescentic placodes lying near the posterior lateral margin of the cephalic lobes close to the edge of the infolding for the optic ganglion; but they never lie inside the fold, and the visual cells are never inverted. The entire visual layer is formed from a single layer of primitive ectoderm.

The placodes are frequently divided, or may be entirely separated, into two distinct parts, which differ in their histological characters, and in function (hymenoptera, neuroptera, coleoptera). One part may be especially developed in males (ephemeridæ), or one may serve for vision under water, and the other for vision in air.

Cerebral Eyes of Vertebrates.

In vertebrates we recognize as belonging to the forebrain, the median or parietal eyes, the lateral eyes, and the olfactory organs. At an early embryonic period they lie on the outer margins of the open neural plate, in similar positions to the ones they occupy in arthropods.

The Parietal Eye.—There are probably two pairs of ocellar placodes that for a short time occupy this marginal position. Later, they are caught in the palial overgrowth and carried on the inner limb of the closing neural crests to the median line. There they form a group of one, or two, or three placodes lying in the membranous roof of the brain. During or after the closing of the cerebral vesicle, the brain roof is evaginated at the place where the ocelli are located, thus forming a sac or tube in the blind end of which the ocellar placodes lie.

The extraordinary way in which the vertebrate parietal eye develops is, therefore, essentially like that of the parietal eye in Limulus and the scorpion. This fact, and many others to be brought out later, demonstrates that the parietal eye of the crustacea and arachnids is a true cerebral eye in the vertebrate sense, and is identical with the parietal eye of vertebrates.

The lateral eyes of vertebrates represent the compound or convex eyes of arthropods that have been transferred to the interior of the cerebral vesicle. In the arthropods the lateral eyes lie near the margin of the cephalic lobes, on the outer edge of a deep ganglionic infolding. In vertebrates, they are first seen in a very similar position on the lateral margin of the open medullary plate. Later they are swept into the infolding brain, turning the retinas inside out. They then grow out laterally on the end of membranous tubes, in much the same manner as the median eyes. In arthropods, the lateral eyes usually have a crescentic, or kidney-shaped outline; in vertebrates, this shape is retained, giving the retinas their characteristic crescentic outline during the early stages. When the two limbs of the crescent unite, a circular retina is produced, giving rise to the choroid fissure and the centrally located optic nerve that, together with the inverted rods and cones, have long been such inexplicable features of the lateral eyes in vertebrates.

The olfactory organ in vertebrates arises from three placodes situated on the anterior margin of the cephalic lobes. They are not drawn into the brain chamber, but remain permanently in the surface ectoderm. They move forward along the median line followed by two pairs of olfactory nerves, that in the lower vertebrates may remain separate up to the adult stages. Its structure, development, and innervation is therefore similar to that of the frontal organs of the crustacea, and the olfactory organ of Limulus.

II. The Eyes as Segmental Sense Organs.

The larval ocelli, lateral eyes, auditory organs, stemmata and olfactory organs appear to be local modifications of a series of primitive sense organs belonging to the procephalic and first six thoracic metameres.

In insects and arachnids, the larval ocelli of the procephalic lobes present a clearly defined segmental arrangement. (Fig. 14.) In scorpion and Limulus, in addition to these ocelli, there is a transient series of segmental sense organs in the thorax, which appears to be a continuation of that in the forebrain. (Figs. 15, 16, 140–142.)

In Limulus, the first pair of the thoracic series are the lateral eye placodes, *l.e.* The fourth pair, $s.o^4$, are large, circular placodes, distinctly sensory in character, that are retained through the first larval or trilobite stage, after which they disappear. This organ is probably the forerunner of the auditory organ of vertebrates for it has the same shape and general appearance as the auditory placode in vertebrate embryos, and as nearly as may be determined, lies on the same segment. The other placodes are less distinct and are visible for a very short period only.

In scorpions, on the outer margins of each coxal joint (Figs. 15–16), there are two transitory sense organs which appear to represent the thoracic series of Limulus. They disappear before hatching, after contributing an important mass of ganglion cells to the pedal nerves.

The series of procephalic and thoracic sense organs just described should not be confused with the segmentally arranged gustatory organs, which belong to a different system, and which are always located on the median side of the base of the appendages.

After this preliminary survey, we may consider the several organs under discussion in more detail.

III. The Ocelli of Insects.

A very primitive and suggestive condition is seen in Acilius, where the early history of the ocelli is best known. Here the cephalic lobes are clearly divided into three segments, each one containing a segment of the brain, one of the optic ganglion, and one of the optic plate. (Fig. 14.) Three deep infoldings, *iv*, $^{1-3}$, form on the median side of the plate, carrying the three-lobed optic ganglion below the surface. The openings soon close, without the formation of a palial fold like that which covers the whole forebrain in the scorpion.

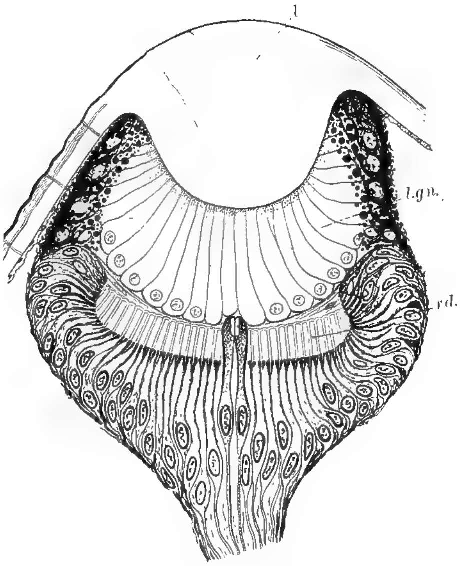


Fig. 90.—The ocellus of an insect larva, Acilius (eye *V*). This ocellus looks forward and outward.

The ocelli are formed by separate, pit-like infoldings of the optic plates, the retina forming from the bottom of the pits and the dioptric apparatus from the lips of the closed vesicles. (Figs. 90–91 and 102.)

At the close of larval life, the ocelli break away from the surface ectoderm and become lodged deep in the head, on the surface of the optic ganglia, where they degenerate.

The frontal ocelli are new formations, usually appearing at the beginning of the metamorphosis, and differing from the larval ocelli in their mode of development, time of appearance, and relation to the brain.

IV. The Parietal Eye.

Parietal Eye of the Scorpion.

The development of the parietal eye in the scorpion and spiders furnishes the best picture of the process by which ocelli are carried into the brain chamber to form a true parietal eye like that in vertebrates.

The evolution of the brain chamber and the parietal eye is essentially the same in scorpions and spiders. (Figs. 15, 20, 21.) I will describe the condition in the former.

The cephalic lobes soon divide into three segments that have a very constant and characteristic form in the arachnids. (Fig. 15.) One may distinguish the centrally located brain neuromeres, *br.*$^{1-3}$, two prominent optic ganglia, and a marginal plate, with deep infoldings between it and the ganglia.

The whole of the first segment forms a dark infolded band, extending across the anterior margin of the cephalic lobes. From it is formed the olfactory lobes (organ stratifié of St. Remy).

The lateral lobe of the second segment forms the optic ganglion of the median eyes, *p.e.g.*, and the one behind forms the ganglion of the lateral eyes, *l.e.g.*

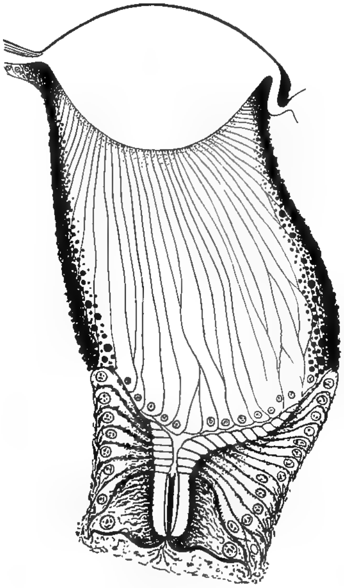


FIG. 91.—The ocellus of an insect larva, Acilius (eye *I*). This eye looks directly upward.

Between the two ganglia and the lateral margin of the cephalic lobes are two infoldings, the floor of which is formed by the lateral portions of the optic ganglia, iv^2–iv^3.

The median ocelli will develop from the extreme lateral margins of the cephalic lobes, opposite the second pair of infoldings, and the lateral ocelli opposite the third pair. The ocelli, however, are not visible till later.

The arachnid cephalic lobes are clearly comparable with those of Acilius, the principal differences lying in the union of the parts of the first segment to form the olfactory lobe, and the small size and late appearance of the ocellar placodes.

Another important difference lies in the method of closing the ganglionic infoldings, which is as follows: in the scorpion, the openings to the two pairs of marginal infoldings lengthen till they merge with each other and with the one in the olfactory lobes. A continuous groove, varying in depth, is thus formed around the sides and anterior margin of the cephalic lobes. The edge of the optic plates projects over the groove forming a thin-walled fold, which represents the beginning of the palial fold, its free margin being the neural crest.

The margin of the palial fold now advances inward and backward over the outer surface of the forebrain. At the same time the olfactory lobes sink below the surface, and slide backward, underneath the second segment, leaving only a small, median part visible from above.

As the palial fold advances, the optic plate is rolled inward, transferring the median eye placodes from the outer limb of the fold to the inner. When the placodes have been carried about half-way across the surface of the brain, pigment develops in them that may be seen, in surface views, through the overlying ectoderm. (Fig. 16, *A*.) As the edge of the palial fold moves still farther backward, the outline of the two eye sacs becomes distinctly visible. (Fig. 16, *B*.)

Finally both sacs merge into a single bi-lobed sac, with a narrow neck, or epiphysis, that opens to the exterior through a small pore, which we shall call the anterior neuropore. (Fig. 18, *a.n.p.*)

The neck to the eye sac elongates somewhat, its walls thicken and become lined with chiten. It is still open in young scorpions, and remnants of it may persist through life. (Fig. 43, *e.t.*)

The posterior edge of the completed palial fold extends straight across the posterior boundaries of the forebrain. (Fig. 18.) When the latter is bent backward onto the hæmal surface of the egg, the edge of the fold forms the anterior edge of the cephalo-thoracic shield. (Figs. 17, 43.)

By the time the eye tube and palial fold are completed, the anterior portion of the palium, that is the part overlying the hemispheres, and the part originally connected with the anterior wall of the inferior lobes, has thinned out and is no longer recognizable. The position it would have, if retained up to that period, is indicated in Fig. 43, *pl.*

It is clear that the anterior neuropore in the scorpion represents the point over the forebrain toward which the palial folds converge and finally unite. The pore leads, not only into the proximal end of the eye stalk, but also into the forebrain vesicle and into the olfactory lobes. Furthermore, it is clear that there is no real difference between this method of forming a parietal, or cerebral eye, and that in vertebrates. In the latter animals, the eye tube usually appears at a relatively later stage, as an outgrowth of the completed palium or roof of the brain, near the place where the anterior neuropore closed. In arthropods, the same final condition is shown, and in addition, all the preliminary steps by which the eyes were transferred from their original position to the brain roof.

The lateral ocelli lie for a considerable period on the external surface of the procephalic lobes, close to the margin of the palial fold, but, unlike the median ocelli, they are not swept into the infolding, and hence onto the brain roof. They develop into typical external eye-pits, which permanently remain in their original position as regards the procephalic lobes. But in the adult, after the forebrain has been folded back onto the hæmal surface, they lie on the anterior lateral margins of the cephalo-thoracic shield, on the hæmal surface of the body, instead of the neural. (Fig. 17.)

The Parietal Eye of Limulus.

In Limulus, the cephalic lobes, at first sight, bear no resemblance to those of the scorpion, or of Acilius, but a more careful examination will show that the essential features are the same in all of them.

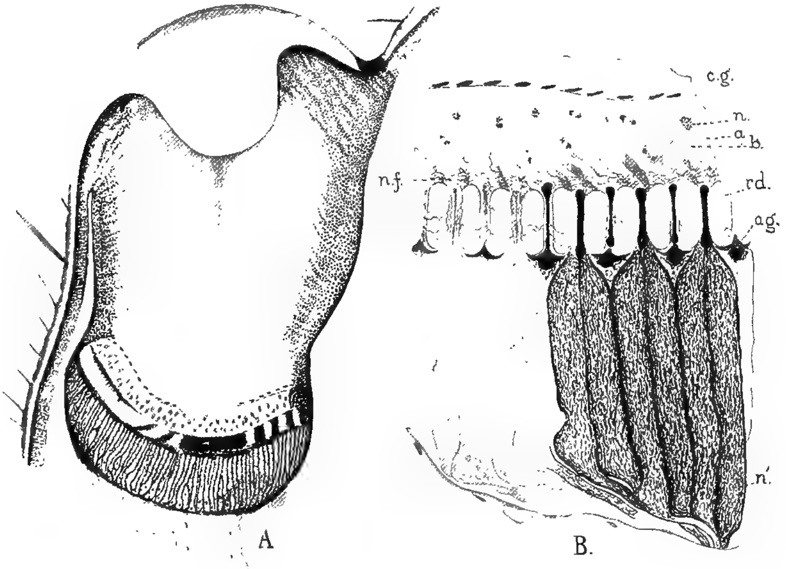


FIG. 92.—*A*, Ocellus of Lycosa (middle one of the three lateral ocelli); *B*, retinal portion of the same, more highly magnified, showing the retinal cells, each with a large outer nucleus, *n*, and a smaller inner one, n^1; the lateral rods, *rd*, are in parallel rows, fenced off by vertical walls of dense pigment; concave reflecting membranes underlie each double row of rods.

Development.—The cephalic lobes at first form two wing-like expansions of the neural plate, with the stomodæum on the extreme anterior margin and the chelicerae on the posterior one. (Fig. 140.) No division into segments is visible at this stage.

A little later (Fig. 141), one may recognize the various parts that belong to these segments, viz., two large infoldings in the olfactory lobes representing the first segment, *ol.l.*; two pairs of minute pores representing the marginal infoldings for the median ocelli on the second segment, *p.e.*; a large olfactory placode on the anterior edge of the lateral eye ganglion, representing the sense organ of the third segment, *ol. o.*; and the compound eye placode itself, about opposite the cheliceræ, and belonging to the fourth segment, *l.e.*

The compound eyes arise just behind the true cephalic lobes; apparently they are not represented in the scorpion or in spiders, or in the embryonic cephalic lobes of those insects that undergo a metamorphosis.

During the following stages, the two pairs of ocellar tubes unite in the median line in front of the olfactory lobes, forming a single median tube or epiphysis, directed forward, below the skin. (Fig. 142, *e.p.*) Its distal end is dilated and contains, as shown by its structure in the later stages, four ocellar placodes, two paired and two practically unpaired ones; its posterior end opens on the surface of the head by an oval pore situated just in front of the hemispheres, *an. p.*

Meantime the two paired olfactory placodes move mesially and a new unpaired olfactory placode appears just in front of the pore of the eye tube. The compound eyes migrate in the opposite direction, toward the posterior hæmolateral surface of the thorax.

We may harmonize these conditions with those in Acilius by assuming that the two pairs of ocelli of the second segment are the only larval ocelli of the acilius type retained in Limulus; and that the three olfactory placodes and the compound eyes represent respectively the three stemmata and the compound eyes of insects, which do not appear there till the close of the larval life. In other words, in Limulus the secondary, or imaginal, set of eyes, and the primary, or larval set, appear at the same period, the more recent organs being reflected back into the same embryonic period as the more ancient ones.

While these events are taking place, the palial fold is forming in separate sections, one being directed backward and inward over each lateral eye ganglion *op.g.*; another over each infolding for the olfactory lobes, *ol.l*, and a third over the ocellar plates, *an.p.*

The margins of all three folds gradually move toward the anterior margin of the hemispheres where they unite to form a common opening, the *anterior neuropore.* This pore appears to be merely the opening to the united ocellar tubes, but in reality it represents more than that. It is obviously comparable with the anterior neuropore of the scorpion, differing from it only in that it lies farther forward. In both cases, the main opening represents the point toward which all the epithelial overgrowths of the forebrain converge and the last point to be covered by them. This interpretation is no doubt the correct one, for it is clear that the opening offers access, as it does in the scorpion, not only to the eye tubes, but also to the cavities of the olfactory lobes, the spaces between the hemispheres and the palial wall, and the spaces between the under surface of the hemispheres and the floor of the forebrain. (Fig. 47, *B.*)

Change of Position.—The distal end of the ocellar tube is at first directed horizontally forward toward the ectoderm that forms the anterior margin of the procephalon. (Fig. 142.)

As the embryo develops, this layer of ectoderm extends forward, carrying the ocelli with it and drawing out the ocellar sac into a long epithelial tube or *epiphysis*. The procephalic ectoderm then forms a vertical wall covering the median anterior surface of the egg; still later it is bent backward onto the hæmal surface of the buckler, where it represents the exposed surface of the anterior end of the primitive head, or procephalon; the posterior end of the head, coincident with the forebrain, remaining on the neural surface. (Figs. 152, 153, *pc.c.*)

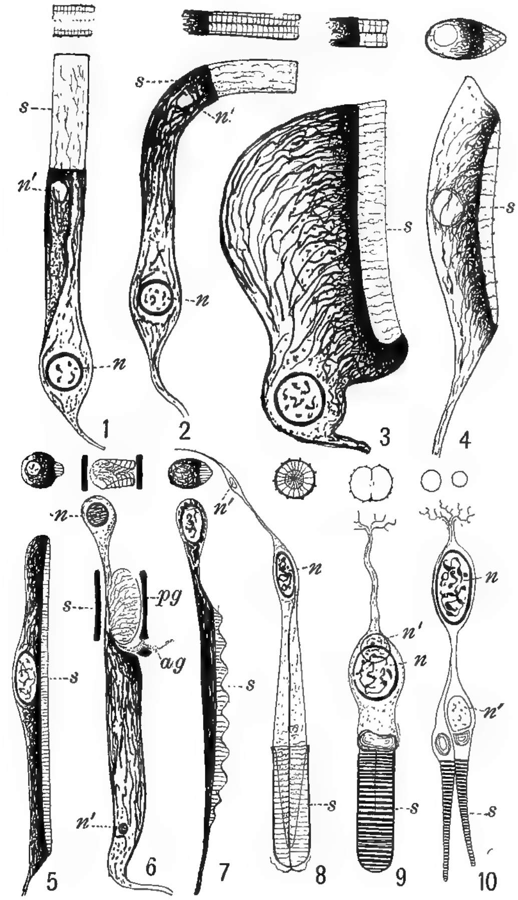


FIG. 93.—Various forms of retinophoræ, isolated by maceration and showing the position and shape of the retinal rods. Cross-sections of the rods are shown over each figure, the place where the section is taken being indicated by the letter *S*. 1. Upright terminal rod from ocellus *V* of Acilius; 2, horizontal terminal rod from sides of ocellus *II* of Acilius; 3, a giant retinal cell with short horizontal rod, from ocellus *II*; 4, retinal cell, with lateral rod from compound eye of Limulus; 5, retinula cell from the compound eye of Tabanus; 6, retinal cell from the ocellus of Lycosa; 7, retinula cell, with serrated rod, from the compound eye of Pinæus; 8, inverted retinal cell from the eye of Pecten; 9, rod cell from retina of an amphibian (species of Diemyctylus), showing two nuclei, *n'* and *n*, and indications of division of rod into two parts with either a canal or fiber running through a part of the rod; 10, cone cell from same animal, showing double nature of the cell as well as of the cone. The body corresponding to the second nucleus lies at *n'*

While this is taking place the ends of the anterior liver lobes unite in front of the cephalic lobes, thus apparently isolating that part of the head containing the ocelli, from the neural portion containing the olfactory organs and cephalic lobes. (Figs. 149, 151.)

At this stage, the surface contours of the forehead cannot be clearly distinguished. But during the early trilobite stages, after boiling in caustic potash, a distinct suture is visible on the cephalo-thoracic shield, marking the boundaries of the primitive procephalon. (Fig. 152, *pr.c.*)

This suture quickly disappears, and in all subsequent stages the only part of the primitive fore-head visible on the hæmal surface is a narrow patch bearing the ocelli. (Fig. 155.)

Appearance of the Placodes.—We may now confine our attention to the later stages of the parietal eye.

After the trilobite stage, one pair of ocellar placodes form the lateral walls of a terminal dilatation, that may be called the *ecto-parietal* eye. (Fig. 102, *D.*) Their cells become invested with black pigment and they take on the character of typical visual cells. (Fig. 94, *l.ec.p.e.*)

The other pair form the walls of a second median dilatation that we shall call the *endo-parietal* eye, *en.p.e.* It lies below the surface, and on the proximal side of the ecto-parietal eye. Its cells are unlike the usual retinal cells in shape, arrangement, and pigmentation; but they are provided, temporarily, with plate-like visual rods or rhabdoms.

Nerves.—In young Limuli, three to four inches long, four nerve fascicles may be seen at the distal end of the eye tube, one for each retina of the ecto-parietal eye, and two for the unpaired endo-parietal eye. (Figs. 94, 101, *A.*)

In the middle section of the tube, the four nerves unite to form a common layer of fibers outside the epithelial walls of the tube. Toward its proximal end, the nerve fibers separate from the epithelial walls of the tube and again divide into four fascicles, or two pairs of roots, the larger pair ending in two conical ganglia on the hæmal surface of the olfactory lobes, the smaller one in two smaller ganglia situated a little farther back. (Fig. 51, $ey.r^1$, $ey.r^2$.)

Thus the evidence afforded by the infoldings on the cephalic lobes, the structure of the terminal sac, of the eye tube and the four nerve roots, show that the "unpaired eye" of Limulus is formed by the partial fusion of two separate pairs of ocelli.

Structure of the Retinas.—From the earliest larval stages, the difference in structure between the endo- and ecto-parietal eyes is very striking. The ecto-parietal retinas contain, besides numerous indifferent cells, well defined ommatidia consisting of from five to seven cells with the visual rods arranged in star-shaped rhabdoms near their outer ends. (Fig. 94.) The visual cells contain a relatively small amount of reddish-brown pigment, and little, or none, of the white pigment. The endo-parietal eye, in young Limuli three to four inches long, is a thick-walled, pear-shaped vesicle lying well below the surface and almost inaccessible to light.

An unpaired tubercle, or a more transparent spot in the chiten, usually marks its location from the exterior. (Fig. 201.)

The thick inner wall of the vesicle, *en.p.e.*, now consists of irregular elongated cells with small nuclei. The cells may show an obscure arrangement into large groups, and are completely filled with minute granules, which are snow-white by reflected, and greenish-black by transmitted light.

The outer wall consists of a few prominent sensory cells, whose pointed outer ends terminate in nerve fibers. They are devoid of either white, or colored pigment, or of visual rods, rt^2.

This eye reaches the height of its development in the young animals from four to six inches long, and from that stage on it appears to undergo a slow histological degeneration, but without perceptible diminution in size.

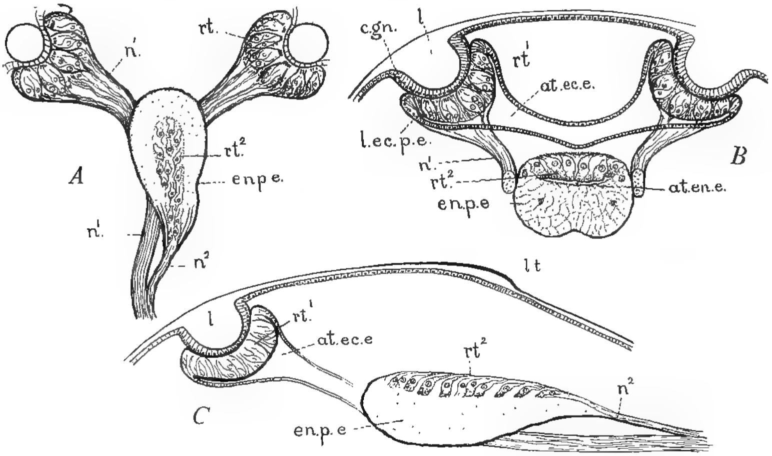


FIG. 94.—The three chambered parietal eye vesicle of Limulus. *A*, from above; *B*, in cross-section; *C*, in longitudinal section. Semi-diagrammatic.

In the older animals, the distinction between the inner and outer walls disappears, and the entire eye then consists of a solid mass of large vesicular cells, with minute nuclei, crowded with "white pigment."

After the early larval stages, all traces of the epithelial walls to the primitive eye sacs have disappeared; the eyes appear to be separate organs, except in so far as they are innervated by separate branches of a common nerve.

The development of the eyes has shown us that the epithelium of the eye tube merely represents the tract of ectoderm that separated the ocellar placodes from the brain, before they were enclosed in the brain chamber; along the inner surface of this tract the nerve fibers passed from one to the other. When the placodes were infolded, the connecting paths of ectoderm were infolded also, forming the walls of the eye tube or epiphysis. When the fibers of the optic nerve grew from the eye to the brain, or from the brain to the eye, they were compelled to follow the old paths, that is, the outer surface of the eye tube. When the nerve fibers separate from it, the tube is left as functionless epithelium, which may, in whole or in part, disappear.

The dilated proximal end of the eye tube, from which the nerve roots have separated, remains for a long time (up to three to four inches long), adhering to the anterior surface of the hemispheres, beneath the thick neurilemma sheath. In the adult all traces of it have disappeared. The distal end of the tube likewise disappears, so that finally the three ocelli are united to the brain by a single solid nerve with four terminal branches and two pairs of roots, each of the four roots ending in a distinct ganglion.

* * * * * * * * *

The parietal eye of Limulus differs from that of the scorpion in the great length of the eye tube, in the presence of the endo-parietal eye, and in the location of the ganglia on the hæmal surface of the brain, instead of the neural. These differences, although sufficiently striking, are not fundamental, but due merely to differences in the relative rate of growth of the adjacent organs in the two animals. One cause of the difference was the closing of the anterior neuropore in front of the hemispheres in Limulus, and behind them, in the scorpion. Moreover, as the parietal eye in the scorpion lies (morphologically) behind the hemispheres, and over the neural surface, the ocellar ganglia are drawn upward, toward the median neural side, as near to the eye as possible. In Limulus, the parietal eye has migrated forward, and then backward on the hæmal surface, drawing the nerves and ganglia forward and hæmally. (Fig. 47, *A* and *B*.)

The Parietal Eye of Branchipus.

The early stages in the development of the median ocellus of phyllopods and other crustacea are imperfectly known. But its structure in the adult indicates very clearly that it is the same kind of an eye as the median one in Limulus and other arachnids, and probably develops in a similar manner. That is, it consists of two pairs of ocelli enclosed in a median sac that opens to the exterior for a time at least by a short, median duct, or epiphysis. (Fig. 102, *A*.)

The parietal eye of Branchipus is probably typical of many crustacea. Its characteristic features appear in the nauplius at a very early period. In Branchipus it is a tri-lobed vesicle consisting of two communicating sacs. (Figs. 95 and 96.) The larger, outer one, or ecto-parietal eye, has thick, lateral walls representing two ocellar placodes or retinas. The distal ends of the retinal cells are directed inward and are capped with minute lateral rods, or plates. The cavity of the sac is coated with a layer of dense black pigment, apparently the product of two large cells whose nuclei are seen in the posterior lateral part, *pg.c.*

The inner sac, or endo-parietal eye *en.p.e.* is conical and with a minute central canal or crevice toward which the inner ends of the retinal cells converge from all sides. It is colorless, and doubtless represents one completely fused pair of ocelli, corresponding with the inner, colorless eye sac of Limulus.

In sagittal sections, the pigmented floor of the outer sac, in younger specimens, appears to be continuous with the outer ectoderm, leaving a narrow pore or crevice by which the cavity of the eye sac communicates with the exterior. (Fig. 102, *A*.) This opening is doubtless comparable with the eye tube of scorpion and Limulus. As the tube itself is very short the opening leads directly into the common eye chamber containing the three ocellar placodes.

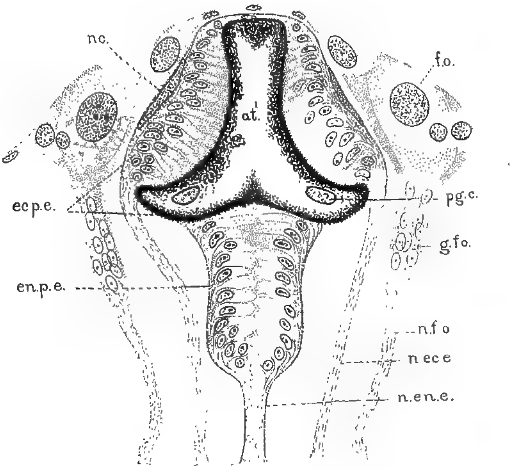


FIG. 95.—Parietal eye vesicle of a young Branchipus, with the adjacent frontal organs (or lateral olfactory organs). Composite frontal section. Camera outline.

There is no lens for any part of the eye, light having free access to the shallow retina of the outer sac from either side, and to the inner sac from all sides.

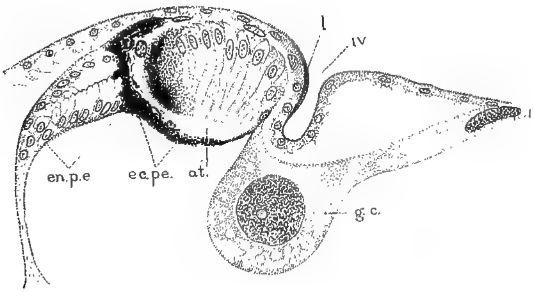


FIG. 96.—Sagittal section of the parietal eye of a young Branchipus. Camera outlines.

The ecto-parietal eye has two distinct nerves distributed over the outer surface of the retinas, *n.ec.e.* They arise from ganglionic enlargements of the anterior median portion of the brain. The endo-parietal eye has a single nerve, *n.en.e.*

The Parietal Eye of Apus.

In Apus, the conditions are a little more complicated. Here, as in many other phyllopods, there is a remarkable skin fold directed forward, forming a broad, shallow chamber over both the compound eyes and the ocelli. (Fig. 102, *B*.) It opens to the exterior by a narrow pore plugged with chiten. (Fig. 98, *O*.) This opening should not be confused with the epiphyseal pore of scorpion and Limulus. The parietal eye forms a closed chamber with a retinal placode on each side wall, and two unpaired placodes, one on its posterior, the other on its inner wall. (Figs. 97–99.)

Each placode consists of a single row of large, colorless, columnar cells. Their distal ends are buried in a dense mass of dark brown, or black pigment; their proximal ends are colorless.

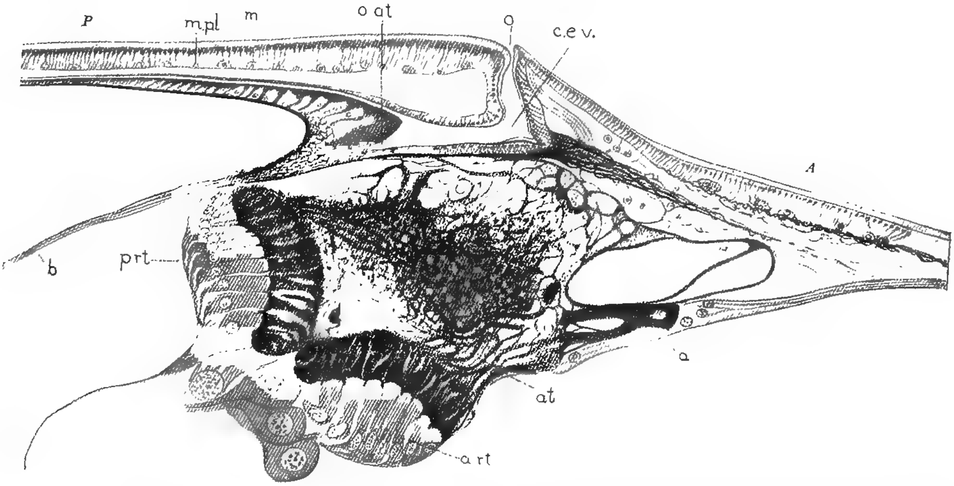


FIG. 97.—Sagittal section of the parietal eye vesicle of an adult Apus. *m*, Fold covering the lateral eyes; *O*, opening of the lateral eye vesicles, *c.e.v*; *o.at.*, remnants of canal leading into parietal eye vesicle; *a.t.*. cavity of the same; *p.rt.*, posterior retina; *a.rt.*, anterior ratina.

As in Branchipus, there are two large cells which appear to give rise to the greater part of the pigment that fills the cavity of the vesicle. (Fig. 98, *p.g.c.*)

When the pigment is partially dissolved, it is seen that each retinal cell is capped with a large brush-like mass of fine fibers (retinidium), apparently the free ends of nerve fibers passing through the interior of the cells, or over their outer surfaces. They are comparable with the nervous network described by me in the visual rods of Pecten, Acilius, Lycosa, etc., except that they are not regularly arranged, and are not imbedded in a dense, transparent matrix, which usually forms the most conspicuous part of a visual rod.

The parietal eye sac of Apus probably contains the retinas of four distinct ocelli, which during development migrated from the sides of the head toward the median line. There they became enclosed in a common sac, that opened to the exterior by a short duct or pore. The remnant of this duct is seen in the adult in the deep recess on the posterior outer margin of the eye sac. (Fig. 97, *o. at.*, and 102, *B.*)

The fold of skin that covers both lateral and median eyes was no doubt a later formation, having nothing to do with the original parietal eye infolding.

The parietal eye of Apus lies entirely below the surface. There are no overlying lenses, or thickenings of the adjacent ectoderm, to control the direction of the light. The latter may enter the paired retinas from the sides, and the unpaired ones from in front, or from behind.

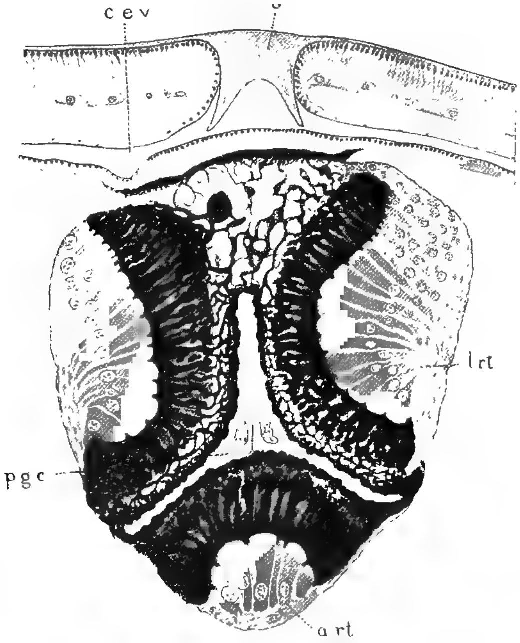


FIG. 98.—Parietal eye vesicle of Apus, in cross-section.

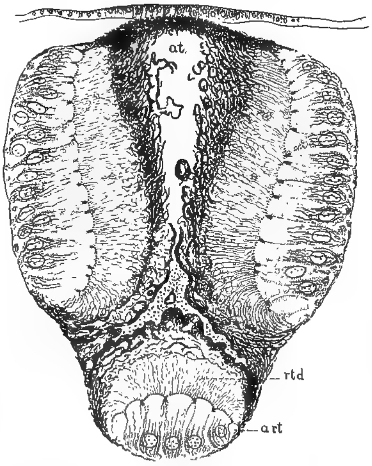


FIG. 99.—Same as preceding figure, with pigment removed, showing the coarsely fibrillated visual rods, *r.t.d.*, on the inner ends of the retinal cells.

There is no reason to doubt that the tri-oculate median eye of decapods, copepods, trilobites, and merostomes, in structure and development is essentially like that of Limulus, scorpions, spiders, Apus, and Branchipus. The evidence presented clearly indicates that this group of ocelli is very constant throughout the crustacea and arachnids, and that it has certain remarkable features which distinguish it from all other visual organs. There is no parallel to the way in which these ocelli develop except in the parietal eye of vertebrates, and there is no explanation available for the condition seen in vertebrates except the one offered by the arachnids.

The Parietal Eye of Vertebrates.

The parietal eye of vertebrates was long ago demonstrated to be a vestigial eye, although there are some authors who still refer to it as a mysterious organ of unknown function. It is difficult to understand how any one familiar with visual organs, could fail to recognize in the parietal eye of Petromyzon, or Hatteria, or Lacerta, a visual organ of some kind. The pigment, lens, retinal cells, and nerves, are unmistakably parts of an organ that served at one time as an eye, whatever its function may be now.

The conflicting accounts of the parietal eye are due in part to the various conditions in which it appears in different groups of vertebrates, but mainly to a fundamental misconception of the ground plan of the organ and how it happens to get inside the brain.

It has not been clearly recognized that the parietal eye is a paired organ arising originally outside and beyond the boundaries of the brain; that it contains several distinct sensory placodes; that there is a fundamental distinction between the sensory placodes and the non-sensory epithelial tube that connects them with the brain; and it has been very difficult to eliminate the idea that the paraphysis is an eye or a part of one, or that it produces some part of the parietal eye.

From our new point of view, the parietal eye of vertebrates is a most significant and illuminating organ. The best insight into its meaning may be obtained by studying its structure and development in the lamprey.

Petromyzon.—My observations on the development of the eyes of this animal in the main, agree with those of Sterzi, especially in regard to the nature of the early epyphysial outgrowth.

The Parietal Eye Vesicle.—In larvæ about 6 mm. long, a single median parietal eye tube is seen just in front of the superior commissure. The dilated end of this tube appears to divide into two lobes, the larger one lying outside of, and a little in front of the other. The inner one lies somewhat to the left of the median line, the outer one to the right; the displacement, however, is not enough to indicate that the two sacs are right and left lobes of a single pair.

I have no material representing the stages between 6 mm. and 30 mm. larvæ, and I do not know just what takes place at this critical period, but the next following stages seem to indicate clearly enough that, meantime, the inner sac has become separated from the main tube, giving rise to an endo-parietal, or "parapineal" eye; while the outer sac remains connected with the primitive eye tube, giving rise to the "pineal" or ecto-parietal eye. (Fig. 100, *ec.p.e.*and *en. p.e.*) The floor of each sac is now divided by a deep longitudinal groove, consisting of undifferentiated epithelium, into two symmetrically placed, concave discs, each disc probably representing a retinal placode. (Fig. 101.) Both sacs develop a small amount of brownish pigment, which is, however, masked by a large quantity of the characteristic white granules. The entire organ, when seen with the naked eye, is a glistening white spot that looks precisely like the endo-parietal eye of Limulus. In both Limulus and Petromyzon, the granules are soluble in weak acid.

The outer eye sac presents the most characteristic retinal structure. In six inch ammocœtes, the retinas consist of a layer of sensory cells, each bearing a long, fibrous, colorless rod suggestive of those seen in Apus. (Figs. 99 and 100.) A layer of nuclei and fibers is seen below the columnar cells. Its outer wall, in its central portion, consists of similar cells and rods. They have been regarded as forming an imperfect lens, but their histological structure indicates that they represent the remnants of visual cells, although they are not so well developed as those on the floor of the sac. The two sets of rods meet in the middle of the sac, their distorted ends forming a distinct cleavage band. On the periphery of the eye the walls consist of a single layer of short, columnar cells.

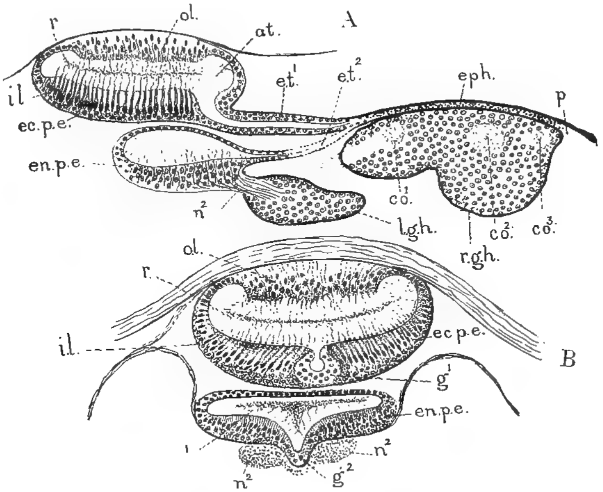


FIG. 100.—The parietal eye vesicle of a young lamprey, 6mm. long. *A*. Sagittal section; *B*. cross-section.

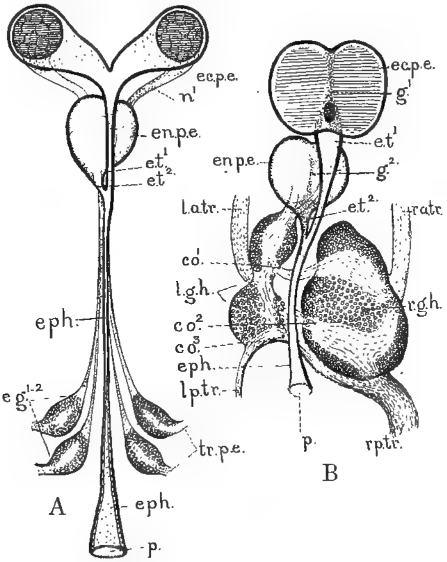


FIG. 101.—Plan of the parietal eye vesicle with its nerves, ganglia, and epiphysis, seen from the neural surface. *A*, Young Limulus; *B*, young lamprey.

The amount of pigment, and its distribution, varies greatly in different individuals and at different stages. In many cases, the cells of the outer walls are colorless, and the inner wall, and especially the two layers of rods, are densely crowded with pigment, a condition similar to that seen in Apus and Branchipus.

The inner sac *en.p.e.* resembles the outer one, except that its retinal cells are less highly specialized, and its outer wall consists of a thin layer of indifferent, columnar cells.

The groove on the floor of the outer sac is hardly recognizable anteriorly, but it gradually deepens toward the posterior margin, where it leads into the enlarged, distal end of the epithelial eye tube or epiphysis. This part of the tube persists in the adult as the conical "atrium" of Studniaka. The proximal part of the tube likewise persists as a small solid cord, extending over the outer surface of the ganglion habenula. A trace of its original opening may be seen as a conical recess, in front of the superior commissure. (Figs. 100 and 101, 141.)

A similar groove, leading into a short blind tube, is seen in the floor of the inner sac, et^2. This tube leads toward the base of the "atrium," but at this stage does not unite with it. It undoubtedly represents the remnants of the connection, existing during the early stages, between the inner sac and the main eye tube.

After the metamorphosis the parietal eye loses the clear cut histological details seen in the early stages, and is then undoubtedly of less importance functionally.

The Parietal Eye Ganglia, or *Ganglia Habenulæ*, consist of a main right and left ganglion, each consisting of an anterior and a posterior lobe. We may therefore, recognize four lobes, or two pairs of ganglia, for the parietal eye, a condition in complete harmony with the presence of two pairs of retinal placodes in the eye.

The left ganglion is smaller than the right and differs from it in minor, histological details. It gradually moves forward and mesially, till the anterior lobe lies close to the posterior, inner wall of the inner sac, with which it is connected by a large bundle of nerve fibers. This nerve divides into two, one passing on either side of the median groove. (Fig. 100, n^2.)

The larger, outer eye is said to be connected by nerve fibers with the larger, or right ganglion. I have not been able to satisfy myself that this was the case. In fact the nerves to the outer sac are small and very difficult either to identify, or to follow to their terminals.

The right and left ganglia are connected by at least two commissures that originate in two large cores of neuropile. (Fig. 101.) From the latter, two pairs of nerve tracts arise, the anterior pair, *a.tr.*, passing downward and forward to the median face of the olfactory lobes; the posterior pair, *p.tr.*, downward and backward to the floor of the midbrain.

It is a surprising fact that the two anterior bundles are of approximately equal dimensions, while of the posterior pair, the right is very much larger than the left.

The inner and outer sacs of Petromyzon and the two similar ones in teleosts have been regarded as right and left mates of a single pair, on the ground that they are, for a short time at least, somewhat asymmetrical in position, one being a little to the left, the other to the right of the median line; furthermore, it is claimed that in the lamprey the larger outer sac is innervated mainly from the right ganglion habenulæ, and the inner one from the smaller, left ganglion habenulæ.

The evidence however, is, by no means conclusive. My own observations lead me to the conclusion that the inner and outer parietal eyes are just what they appear to be, namely, two unpaired organs of slightly unequal value, one of which has been crowded away from the median line.

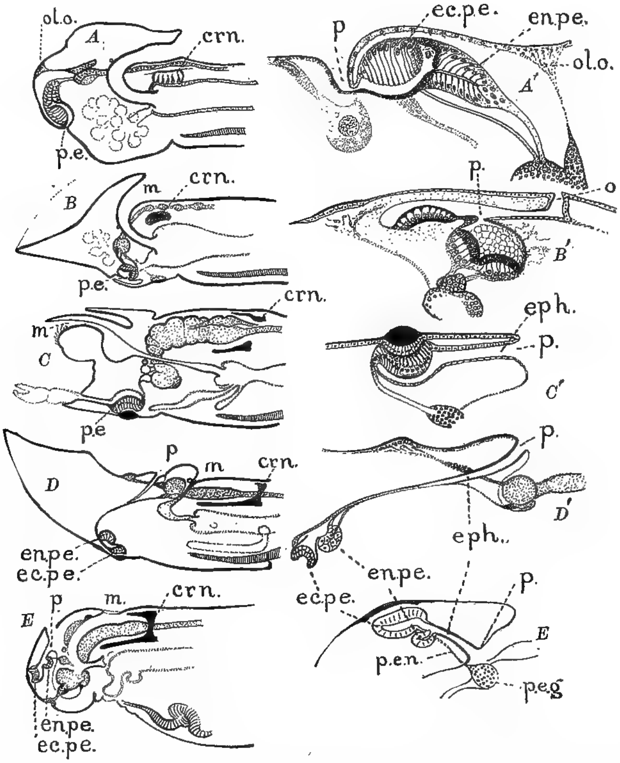


FIG. 102.—Semi-diagrammatic, sagittal sections of the head, showing the relative position and character of the parietal eye, the epiphysis, neuropore, etc., in *A*, Branchipus; *B*, Apus; *C*, scorpion; *D*, Limulus; *E*, vertebrate. On the right the eyes are shown on a larger scale.

Evidence for this conclusion is afforded by the parietal eye of the cyclostomes and less directly by the parietal eye of arachnids.

1. In the first place, in the lampreys, during the earliest stages, one sac lies directly behind the other, and there is nothing to indicate that one is the right or left mate of the other. Whatever asymmetry appears in the eye sacs is seen later, and is comparatively slight. The same condition appears to prevail in teleosts, according to Hill's observations, although he interprets them differently.

2. The two parietal eye sacs in the cyclostomes not only stand very nearly, in the median plane, but each sac contains a right sensory placode, or retina, separated from a left one by a median groove, or by an unspecialized band of tissue. Thus there are two symmetrical retinal placodes in each parietal eye.

3. In young lampreys about two inches long, each ganglion habenula is divided into a smaller anterior lobe, united by two nerves with the inner sac, and a larger posterior one, probably united in a similar manner with the outer sac. Thus there are apparently four ganglia corresponding to the four placodes, These facts are incompatible with the assumption that one sac is the right or left mate to the other.

4. The asymmetry of the ganglia is pronounced. The left anterior lobe ultimately takes up a central position below the inner sac, and remains comparatively small. The other three lobes become very large, especially the two on the right; but the reason for this unequal development is not apparent, since the nervous connection with the right sac is insignificant.

5. A comparison with the parietal eye of arachnids (Fig. 101), shows that the inner sac of petromyzon (parapineal eye) corresponds to the endo-parietal eye of Limulus, both sacs agreeing in position, in their lower grade of histological structure, in their innervation, and in their relation to the epiphysis. The outer sac of the lamprey corresponds with the outer one of Limulus, both sacs agreeing in relative position, in being symmetrically bi-lobed, and in the presence of the more highly specialized visual cells and rods.

The Lenses of the Parietal Eye.

It will be recalled that in the simple isolated ocelli of insects, the chitenous lens and the thick transparent ectoderm that serves as a vitreous body are parts of the optic cup, or of the lips of the cup. (Figs. 90, 91.)

When there are well defined lenses to the parietal eye, as in many arachnids, they are formed from isolated thickenings of the ectoderm and of the overlying chiten, wherever the distal end of the eye tube reaches the surface of the head, however remote that point may be from the one where the retinal placodes first appeared.

In the scorpions, the parietal eye has a highly developed vitreous body and two lenses. (Fig. 105.)

In Limulus, there are two well developed lenses, one for each retina of the outer sac (Fig. 94). But the inner sac never has over it a true chitenous lens, or any ectodermic thickening which may represent the remnants of a vitreous body, although there may be a tubercle like thickening of the chiten, or a semi-transparent spot. (Fig. 201.)

In the phyllopods, although the parietal eye is often very highly developed, it lies well below the surface, and there is no thickening whatever of the adjacent ectoderm, or of the chiten, to form a lens or vitreous body for them. The fre-

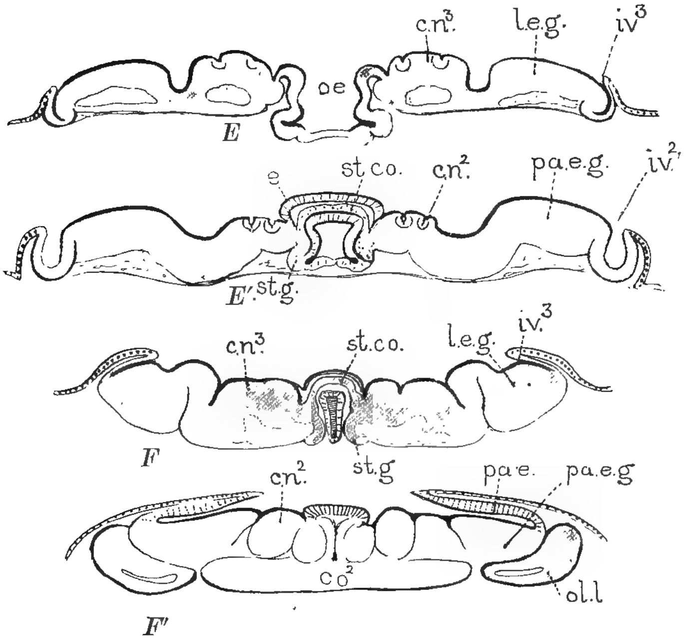


FIG. 103.—Cross-sections of the procephalic lobes of an embryo scorpion. *E*, Posterior part of stomodæal region, showing the third cephalic neuromere, *cn*³, the lateral eye ganglion, *l.e.g.*, and the corresponding invagination, and the posterior margin or the palial fold; *E'*, same stage farther forward, showing the stomodæal ganglion and its commissure, the second cerebral neuromere, the parietal eye ganglion and its corresponding infolding, *iv*². Compare Fig. 15, *B*. *F* and *F'* are corresponding sections in an older stage, Fig. 16, *A*, showing the crowding of the lateral eye ganglion over the cerebral neuromeres and the appearance of the parietal eye, *p.a.e.*, on the inner limb of the palial fold. Camera outlines.

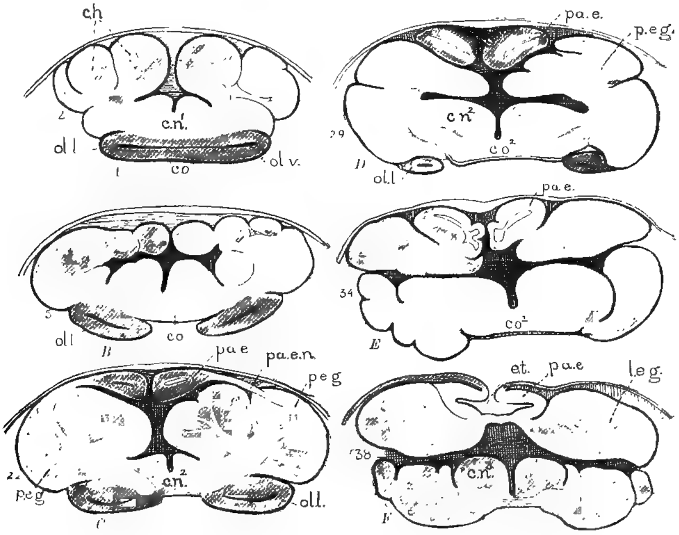
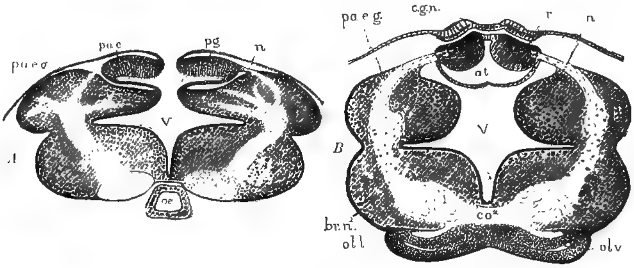


FIG. 104.—Selected sections from a continuous series through the procephalic lobes of an embryo scorpion, in stag *G* (Fig. 16, *B*). Camera outlines.

quent absence of a lens and vitreous body, in the otherwise well developed parietal eye of arthropods, is remarkable, since it does not occur in the other types of arthropod ocelli. The fact is all the more significant when we recall that in vertebrates true lenses to the parietal eye are never present. In place of them, we find a transparent spot, or tubercle, or a thin place in the overlying tissues. The thickening of the outer wall of the eye vesicle, which may possibly serve, in exceptional cases, as a lens (reptiles), is probably the remnant of a retinal placode.

Location of the Placodes.—The location of the retinal placodes in the parietal eye vesicle varies greatly. In the arthropods, they may lie in the side walls (Branchipus), or in the outer wall (scorpion and Limulus), or in the inner wall or floor, as in Apus. The prevailing position in arachnids is in the outer wall, thus inverting the cells, and turning the rod bearing end toward the cavity of the vesicle. But the retinal cells have a remarkable method of readjustment, so that in the later stages, they appear to be standing in an upright position.



A B

FIG. 105.—*A*, Section through the posterior margin of the parietal eye in stage *H*, showing the approaching union of the two retinas, and the palial folds; *B*, section through the parietal eye of a newly born scorpion, showing the parietal eye vesicles, and the ventricle, *V*, formed by the optic ganglia, the palial folds, and the forebrain neuromeres. The ventricle extends forward and downward, into the cavity of the olfactory lobes, *ol.v.*

In vertebrates, the placodes in general appear to occupy the floor of the vesicle, but they may develop on both walls, as in Petromyzon.

Minute Structure.—In the arthropods, there is nothing constant in the histological structure of the parietal eye retinas. The principal elements are columnar, sensory cells arranged either in a continuous layer, with terminal rods projecting into the eye chamber (Apus, Branchipus), or they may be arranged in definite groups, or ommatidia, consisting of from two to five or more cells with plate-like rods attached to the side walls of each cell (Limulus, scorpion, Phalangium, Lycosa).

Where the eye, to all appearances, has become functionless, *i.e.*. endo-parietal eye of adult Limulus, the cells form a confused mass, without any definite arrangement in layers, or in respect to the source of whatever light may reach them. The black pigment is then absent and the cells are filled with a dense mass of glistening white granules. Even in this degenerate condition, the visual rods may be retained as irregular plates, singly or in groups, attached to the side walls of the retinal cells.

In the scorpion and other arachnids (Limulus, Galeodes and Phalangium) a transformation takes place in the arrangement of the retinal cells, shortly after the eye assumes its definite form. In the scorpion, owing to the method of infolding, the retinal cells are inverted, the nerves being distributed over the outer surface of the sac, and the rods turned toward the lumen of the vesicle. Later, however, the nerves, entering from the side, appear to penetrate the retina about midway between the inner and outer surfaces. In the adult, the rods are located on the sides of the cells, near their outer ends, and the nerves then enter the opposite, or inner end. Just how this apparent, or actual, reversal of the retinal cells takes place, I have not been able to determine.

In the scorpion, Limulus and Phalangium, the rods lie in isolated groups, on the sides of the cells, just below the outer surface of the retina. But in the parietal eye of Galeodes and of spiders, where the same method of development prevails, the rods form in the adult a continuous layer outside the retinal cells, and there is no indication as to what was the nature of the of the post-embryonic transformation that brought the rods and nerve ends into that position.

I. Summary.

We may summarize our conclusions in regard to the parietal eye as follows:

1. All vertebrates possess remnants, more or less distinct, of a median or parietal eye which in some forms contains true retinal cells and visual rods, and is connected by several (4?) distinct nerves with as many ganglia.

2. There is but one median or parietal eye consisting, however, of several parts.

3. The eye proper consists of three or four sensory placodes, each one representing the retina of a simple ocellus of the arthropod type. The placodes form the walls of a sac on the end of a membranous tube projecting from the roof of the tween-brain.

4. The placodes have a paired arrangement and probably represent two pairs of ocelli, located originally in the ectoderm, just outside the lateral margins of the open medullary plate.

5. They were ultimately forced into, or carried into, the brain chamber by the same forces that produced the brain infolding. The placodes are carried on the crest of the brain infolding toward the median line, meantime shifting from the outer, to the inner, limb of the fold. When the crests unite, the four placodes form a compact group on the membranous roof of the brain. At that point a tubular outgrowth of varying length is formed which has a vesicle or dilatation at its distal end, in the walls of which the placodes lie. This vesicle with its four placodes is the parietal eye.

6. The primary vesicle may now be constricted, forming two unpaired lobes, or the lobes may separate, forming two separate sacs, a larger, anterior and outer one, the ecto-parietal eye, containing the two most highly developed placodes,

and an inner posterior one, or endo-parietal eye, containing the remaining two placodes, now completely united into one organ, and with greatly reduced structural details.

7. The membranous tube, or epiphysis may disappear in whole or in part, leaving the terminal eye sacs either isolated, or united by distinct nerves with the parietal eye ganglia, or the ganglia habenulæ.

8. The parietal eye of vertebrates is homologous with the parietal eye of such arthropods as Limulus, scorpion, spiders, phyllopods, copepods, trilobites, and merostomes, but not with the frontal stemmata or other ocelli of insects.

9. In the arthropods, various stages in the evolution of a cerebral eye are shown in detail, from functional eyes on the outer margin of the cephalic lobes, to a median group of ocelli enclosed within a tubular outgrowth of the brain roof.

The most primitive type of a parietal eye is seen in the nauplii of phyllopods and entomostraca, where the eye is a pear-shaped sac, opening by a median pore or tube on the outer surface of the head. (Fig. 272, 308.) In the higher arachnids, the process of forming an embryonic eye vesicle merged with the process of forming a cerebral vesicle, the external opening of the forebrain vesicle and that of the parietal eye tube, forming a common opening or anterior neuropore.

10. The parietal eye of arthropods is an important visual organ until the lateral eyes, which represent a later product, are fully developed. It may then diminish in size and activity, but it rarely, if ever, wholly disappears.

11. During the evolution of vertebrates from arachnids, there was a considerable period during which the lateral eyes were adjusting themselves to their new position inside the brain chamber, and when they were in functional abeyance. At this period, ancestral vertebrates were mon-oculate, that is they were dependent solely on the parietal eye, which had come to them from their arachnid ancestors as an efficient and completely formed organ.

When the lateral eyes again became functional, the parietal eye began to decrease in size and effectiveness.

The parietal eye is the only one now present in tunicates. In the oldest ostracoderms, like Pteraspis, Cyathaspis, Palæaspis, the lateral eyes are absent, or at least do not reach the surface of the head, the only functional one being the parietal eye, which is of unusual size.

In the lampreys we see the same conditions, the parietal eye being very well developed in the larvæ, while the lateral eyes are deeply buried in the tissues of the head, and useless. During the transformation, the lateral eyes again become functional, and the parietal begins to atrophy, finally losing many of its structural details and its function, although still retaining very nearly its original form.

CHAPTER IX.

THE COMPOUND EYES OF ARTHROPODS AND THE LATERAL EYES OF VERTEBRATES.

Froriep (Hertwig's Handbook of Embryology) states, quoting Kessler, 1877, that K. E. von Baer's discovery that the eye in the chick is a hollow outgrowth of the forebrain vesicle, is the most interesting fact in the development of the eye that could have been obtained, and is without a parallel. He also quotes with approval Gegenbaur's expression of astonishment that in the entire range of vertebrates there are no lower stages in the development of such a complex organ as the eye. The vertebrate eye, he says, Athene-like, makes its appearance completely formed, and comparative anatomy and embryology are powerless against it.

The problem, however, is not as hopeless as this, for we have shown that the parietal eye of arachnids furnishes a very striking parallel to the development of a vertebrate cerebral eye. The arachnid theory also provides a satisfactory explanation for the sudden appearance of lateral, cerebral eyes in vertebrates, and for their most striking peculiarities. It is clear, on the arachnid theory, that the lateral eye was delivered to the vertebrates in a high stage of perfection. There are no transitional stages between the external, convex eye of arthropods and the internal, concave eye of vertebrates, because there can be no half-way stages between an eye that stays outside the brain chamber, and one that during development is carried into the chamber. The eye must either get in early, before the brain closes, or stay out. Either position, at once and definitely, determines its character and the way it does its work. Whatever moulding influence the new environment had on the enclosed eye was felt immediately, and the necessary readjustments, no doubt, at first followed rapidly and then ceased, leaving the eye more stable than before, because enclosed in less variable surroundings.

* * * * * * * * *

I. Compound Eyes of Arthropods.

A. **Serial Location.**—The lateral eyes of arthropods are such essential and constant parts of the head that it is important to determine their origin, and to what metamere they belong. This, however, is a very difficult thing to do.

The view, often expressed, that the compound eyes are compact groups of larval ocelli is untenable, since the primitive larval ocelli (coleoptera and lepidoptera) degenerate and take no part in the formation of the lateral eyes. More over, in the very early larval stages of phyllopods, copepods, and many other crustacea the larval ocelli and compound eyes are present at the same time and clearly arise independently of each other.

In forms like Acilius, that give us a most detailed picture of ancestral conditions, not a trace of the lateral eyes appears till late in the larval stages, when it is impossible to certainly determine their relations to the cephalic lobes, or to other segmental structures. They are first seen on the hæmal side of the head of the oldest larvæ, median to the ocelli. The latter, during the metamorphosis, are torn away from the ectoderm, apparently by the relative shortening of the optic nerves, and are finally lodged on the surface of the optic ganglion, where they may be seen in a degenerate condition, long after the lateral eyes have become functional. In the early embryonic stages of insects that do not pass through a metamorphosis, and in many crustacea, the lateral eyes are seen on the posterior, lateral margins of the cephalic lobes, just lateral to an infolding that gives rise to the optic ganglion. Here also their relation to the metameres has not been determined.

Limulus is the only form in which the larval ocelli, frontal ocelli (olfactory organs), and the lateral eyes, are all present at the same time in an early embryonic stage. Here it is clear that the lateral eyes arise from the cheliceral or first thoracic segment. (Figs. 141 and 142.)

I see no serious objections to regarding the lateral eyes of insects as also belonging to the first appendage bearing segment, and if the "organ of Tömösvary," in the myriapods represents the rudiment of the lateral eyes, as I have suggested, 1892, then that also would have a similar position, since it is situated at the base of the antennæ, and its nerve is attached to the ganglion of the larval ocelli in the same way the compound eye-nerve is in Acilius. (See optic ganglion in Acilius.)

These facts indicate, therefore, that the lateral eyes of arthropods stand serially behind both the primitive cephalic lobes and the larval ocelli, and belong to the most anterior appendage-bearing segments of the primitive body or thorax. I can find no evidence in the structure or development of the lateral eyes to indicate that they are modified appendages.

B. **Development.**—Although the lateral eyes are often post-embryonic structures, they may, in some forms, arise during the embryonic stages.

In such cases, Vespa, Astacus, Limulus and others, the lateral eye placodes lie on the external margin of a deep infolding which gives rise to the optic ganglia, in the same manner that the infolding in Acilius gives rise to the ganglia of the larval ocelli. (Fig. 14.) The lateral eyes, however, are never involved in this infolding. It soon closes, and the placodes move away from the margin of the cephalic lobes onto the posterior hæmal surface of the cephalothorax (Limulus, many trilobites and merostomes), or in some cases, onto its anterior margin, or they may remain in their original position on the neural surface, (Cladocera). (Fig. 78.) The position of the lateral eyes in the adult, therefore, varies greatly, and is either determined by the prevailing position of the animal in relation to the source of light, or the location of the eyes determines the position of the animal.

In Vespa, after the ganglionic infolding has closed, the lateral eye placodes are themselves deeply infolded and partly covered by thin membranous folds, but the latter soon disappear and take no part in the formation of the eye.[1]

In insects, crustacea, and Limulus, the eye proper, or ommatæum, including the cyrstalline cone cells and retinulæ, is formed from the single layer of columnar, ectodermic cells that constitutes the lateral eye placode. The infolding described by Reichenbach and others, in the crayfish, as forming the deeper layers of the eye, is merely the infolding that produces the lateral eye ganglion.

II. Lateral Eyes of Vertebrates.

In my first contribution to the origin of vertebrates, 1889, I pointed out the remarkable resemblance between the early position of the eye placodes in vertebrates and arthropods, and the similar way in which the neural crests enclose the forebrain vesicle.

Many contributions have been made since that time, especially in regard to the vertebrates, that confirm my observations and my interpretations of them, yet no one appears to have clearly understood the facts or their significance. It is hoped that a fuller description, with numerous additional figures, will make these important data intelligible and convincing.

While the lateral eyes of arthropods are never caught in the infoldings of the embryonic forebrain, as the larval ocelli are, they lie very close to the edge of such folds, so that any marked deepening or extension of them, brought about by the increasing size and precocity of the brain and its ganglia, would be likely to include the lateral eye placodes in the infolding, and thus transfer them to the inner walls of the brain chamber. In this new position, they would be subject to entirely new conditions, and they would doubtless quickly undergo important structural changes.

The structure and development of the vertebrate eye indicate that, in some of the intermediate forms between vertebrates and arthropods, these events have actually taken place.

Location.—It has long been known that the lateral eye placodes of vertebrates are visible at a very early stage on the outer margin of the open medullary plate, (selachians, amphibia, birds). (Figs. 34 and 35.)

As the neural crests advance toward the median line, the placodes are transferred to the inner limb of the fold, and finally come to lie in the walls of the brain chamber, in precisely the same manner that the parietal eye placodes reach a similar position.

Origin of the Choroid Fissure and the Blind Spot.—After they are thus enclosed in the brain walls, they assume the shape and position which is so characteristic of vertebrates, and which becomes so significant when compared with the same features in the lateral eyes of arthropods.

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[1] See the peculiar, hood-like fold over the lateral eyes of Apus and other phyllopods.

It will be recalled that in arthropods the compound eye is rarely circular in outline. It is usually crescentic or kidney-shaped, the convex margin being turned toward the source of light. A characteristic condition is seen in forms like Limulus, trilobites and merostomes, where the eyes are located on the sloping hæmal surface of the bucklers, the light coming from above, when the animal is in its normal crawling position. Here the eyes take the form of convex crescents, or some slight modification of them, because such a form distributes the maximum number of ommatidia to best advantage in reference to the direction and the intensity of light. For similar reasons of economy, the optic nerve reaches the eye at its topographical center, that is, near the middle of its neural or concave margin, and all the fibers are distributed from that point by the shortest paths to their respective terminals. (Fig. 106, *A*.)

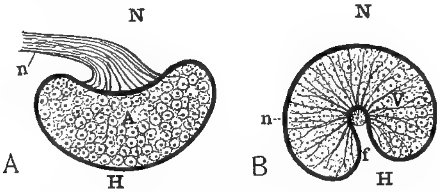


FIG. 106.—Diagram to explain the origin of the choroid fissure in the lateral eye of vertebrates. *A*. The extra cerebral, kidney-shaped compound eye of a marine arachnid; *B*, the same eye, as is appears seen through the walls of the head in vertebrate embryos. In its transfer to the wall of the cerebral vesicle, the eye is turned upside down and inside out. The arms of the horseshoe-shaped retina then unite, forming a choroid fissure, while the optic nerve, entering near the middle of the retina, distributes its fibers over what is now its outer surface.

If such a kidney-shaped eye, lying during the early stages near the margins of the cephalic lobes, were actually involved in the brain folds, as the larval ocelli are, it would still tend to retain the same shape and to occupy the same position that it did while on the outer surface of the body, that is, the eye would eventually grow out from the brain wall, on the end of a tube directed backward toward the original position of the eye.

But the kidney-shaped eye, owing to its inversion during the infolding, would now form a kidney-shaped retina, or sensory placode, with its convex surface directed inward, instead of outward, and its concave margin directed hæmally, instead of neurally. (Compare Figs. 32 to 34 and 106.) In other words, the inverted compound eye would have the same peculiar shape and position that the vertebrate retina has at an early embryonic period. But in its new position and under the new conditions prevailing within the head, the open crescentic form of the placode would probably not be retained. It would be likely to follow its original method of growth unchecked, till a new position of equilibrium was attained; that is, it would continue to grow more rapidly on one margin than on the other, till the two limbs of the crescent unite, forming a concave, circular retina, with a "choroid fissure" directed hæmally, and with a centrally located nerve at the apex of the fissure, distributing its fibers radially over the concave surface of the retina. (Figs. 107 and 108.)

The Retinal Cell Pattern.—In Limulus, and no doubt similar conditions prevail in trilobites and merostomes, the lateral eyes consist of numerous chitenous lenses, under each of which is an "ommatidium," consisting of a circle of fifteen or twenty rod bearing cells, surrounding a central one that appears to be more highly specialized and to have a richer nerve supply than the others.

The ommatidia are separated from one another by circles of unspecialized columnar epithelial cells. The crystalline cone cells and the corneagen cells of other arthropods are absent.

When such a simple kind of facetted eye was enclosed in the brain walls of vertebrates, not only was the primitive shape of the whole eye retained, but the characteristic pattern in the arrangement of the two different kinds of cells was also retained. That is, the circles of rod-bearing cells surrounding a single central one, is probably represented in vertebrates by the circles of rod cells surrounding a cone cell. (Fig. 106.)

The histological changes involved in this transformation are comparatively small, the most important one being a transfer of the retinular rods from a lateral to a terminal position. Such changes as this frequently occur in the arthropods. Compare, for example, the striking differences in the structure of the retinal cells in the parietal eye of Apus, Branchipus, Buthus, Galeodes, and Limulus.

The Retinal Ganglion.—In Limulus, there is a loose layer of ganglion cells lying just beneath the inner surface of the lateral eye; and a similar one is present in the eyes of many other arthropods, *e.g.*, retinal ganglion of insects and crustacea. When the lateral eye of vertebrates was involved in the palial fold, this layer went with it, forming the nerve cells that lie outside the stratum of rod and cone cells. (Figs. 107 and 108, *r.g.*)

* * * * * * * * *

The Lens.—A striking feature of the lateral eye is the development of a lens vesicle from the surface ectoderm and its union with a retinal placode which grows out from the brain walls to meet it.

The origin of the image forming organ at a remote time and place from that of the sensory receptive surface, has led many writers to the conclusion that they represent two originally different classes of organs, secondarily united into one. Thus the lens vesicle has been interpreted as a specialized gill pocket, or as a segmental sense organ serially homologous with those of the hindbrain region. These views are untenable because they are not called for by the facts as we now understand them. In Limulus and scorpion, we have shown that the cuticular lens and the lentiginous ectoderm of the parietal eye are formed wherever the vesicle reaches the surface ectoderm, no matter how remote that point may be from the original position of the retinal placode. (Figs. 101 and 102.) It is clear enough, in these cases, that the lens cups are an original part of the eye, and cannot be thought of as existing apart from it. Precisely the same condition, it seems to me, prevails in the lateral eye of vertebrates. We would therefore eliminate the lens vesicle from the category of organs foreign to the eye. It may be comparable with the thick-walled ectodermic cup that secretes the chitenous lenses for the parietal eyes of arthropods. (Fig. 108.) When the chitenous exoskeleton atrophied, the old lens cup probably remained to form the new lens of the vertebrate eye.

Origin of the "Imperfections" in the Vertebrate Eye. –Thus the compound eye of arachnids, which lies on the outer surface of the head, is represented in vertebrates by the retinal placode which there lies in the walls of the brain chamber. The vertebrate retinal placode still retains essentially the same contour, surface curvature, and arrangement of visual cells and nerve cells as that of its arachnid prototype, but owing to the inversion of the placode, which took place when it was transferred to the brain chamber, the concave surface and the concave margin of the retinal placode face in nearly opposite directions in vertebrates from what they do in the arachnids.

Thus arose those extraordinary imperfections of the vertebrate eye, which have so often excited the comments of the physicist, anatomist, and philosopher. The inverted retina, the choroid fissure, and the blind spot caused by the awkward entrance of the optic nerve, are the inevitable result of a combination of conditions, some of which, originally, had no relation whatever to the eye. These conditions were established in the arthropods long before the vertebrate stock appeared, and it was a purely incidental, or accidental, result of these conditions that the eye was swept into the brain chamber, where it did not originally belong. In other words, the fate of the lateral eye was not decided by what was best for the eye, as an instrument, or by any selective action, in which the eye itself played a part. The eye was a purely passive victim of its location, and of its more powerful neighbor, the brain. But it survived, in spite of its unfortunate location, although it will forever bear the marks of a displaced and made over organ.

III. THE OPTIC GANGLIA.

In reconstructing the history of the vertebrate brain, the structure and position of the optic ganglia of arthropods is no less significant than that of the eyes.

Location.—We have already shown that in the embryos of Acilius the optic ganglia consist of three lobes lying on the lateral margins of the neural plate, each lobe lying opposite a forebrain neuromere. (Fig. 14.)

When the larval ocelli of insects degenerate, the ocellar ganglia, without noticeable transformation, become the ganglia of the lateral eyes. But in Limulus and in the arachnids generally, the ganglia of the parietal eye and those of the lateral eyes are separate. In most insects and crustacea, the ganglia retain their lateral position through life. This is also the condition in young Limuli, but later the great overlapping lobes of the hemispheres crowd the lateral eye ganglia toward the hæmal surface. (Figs. 36–39.) Limulus is the only arthropod, to my knowledge, in which the ganglia occupy this position.

In the phyllopods and arachnids, they are generally drawn upward, so that they lie on, or over, the neural surface of the brain.

Sections and surface views of scorpion embryos show how this is done. (Figs. 15, 16, 18, 41, 103, 104.) It will be seen that as the palial folds advance, the optic ganglia move upward and inward till they lie on the neural surface of the forebrain neuromeres, the parietal eye ganglion lying in front of the lateral eye ganglion. In this position they give us the clue to the interpretation of the optic centers in vertebrates for, clearly, one represents the ganglion habenula, the other the tectum opticum, or the roof of the midbrain. (Figs. 43, 44.)

Parietal Eye Ganglia.—We have already shown that the two pairs of ganglia, from which the roots of the parietal eye nerves arise, are represented in petromyzon by a four lobed ganglion habenula. (Fig. 104, *B*.) The latter occupies the same relative position as in the scorpion, but a very different one from that in Limulus. However, the difference is more apparent than real, because the anterior roots of the ganglia habenulæ are directed downward and forward toward the olfactory lobes, showing not only the direction in which the ganglia have been shifted, but that their original point of union with the brain is the same as it is in Limulus. (Compare Fig. 47, *A*, *B*, and *C*.)

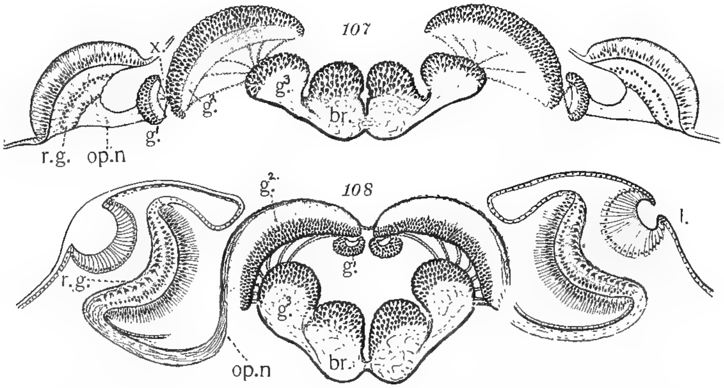
The difference in position of the parietal eye ganglia, in scorpion and Limulus, is due to the fact that in Limulus the eye is drawn forward and hæmally by the extraordinary size of the cephalic shield, and by the rapid growth of the hemispheres, which have grown up behind the epiphysis, instead of in front of it as in all other arthropods. (Compare Figs. 43, 44, 46, and 47.)

Lateral Eye Ganglia.—The characteristic shape of the optic ganglia is well seen in large-eyed insects, as Vespa, where they consist of three principal lobes. (Fig. 107, *A*.) 1. A proximal one, that is roughly spherical; 2. a median one, consisting of an immense concave crescentic disc, and 3. a long narrow one, extending around the distal margin of the middle lobe. Each lobe contains a mass of felted fibers of the same general shape as the lobe, and is covered, on its outer surface, by a thick layer of ganglion cells.

The hemispherical middle lobe is the most conspicuous one, and the one which, by its contour and dimensions, reflects most accurately the variations in the eye to which it belongs. This significant fact has also been observed in the ocelli of Acilius, where each one of the six pairs of eyes has a special shape, or some peculiarity in the arrangement of retinal cells, which is accurately repeated in the size, form, and structure of the neuropile core of the corresponding ganglion.

Minute Structure in Limulus.—In Limulus, the ganglia have a similar configuration to those of insects. (Figs. 37–39, 51, 66.) The inner lobes (Figs. 51 and 52) contain large association neurites, *op.g.*^{3} and *op.g.*^{4}; the two outer ones, the central ends of the optic nerve fibers, *op.f.*, and two relays of optic neurones, *op.g.*^{1} and *op.g.*^{2}

Each of the two outer lobes is a disc-shaped mass of fibers, one surface covered with a thick layer of nerve cells, the other bare. In certain cases, successfully impregnated with methylene blue, only the terminals of the optic nerves are stained. They are then seen as small bundles passing in definite order through the ganglion, between the medullary core and the nerve cell layer. (Fig. 51.) Each bundle of fibers, *op.f.*, probably represents the terminals of a definite ommatidium. On reaching the proximal edge of the lobe, two delicate fibers are given off, one on each side, that penetrate the first core and end there in a few straggling branches. (Fig. 51, *A*, *op.f.*) Just beyond them, a compact tuft of varicose fibers is formed on the proximal outer surface of the core. The main fiber then passes to the under surface of the second core, forming with other fibers a characteristic chiasma, *x.*, and then, bending upward, ends in widely distributed dendrites.



FIGS. 107–108.—Diagrams to illustrate the relation between the brain, optic ganglia and lateral eyes of an arthropod and a vertebrate. In both cases the parts are projected onto the same transverse plane. FIG. 107.—arthropod. FIG. 108.—vertebrate, where the same parts, by the infolding of the medullary plate, have been transferred to the walls of the cerebral vesicles. The optic ganglia are inverted, forming the roof of the midbrain; the compound eye, with its visual cells and underlying ganglionic cells, *r.l.*, forms the inverted retina.

Many other fibers, like the one just described, enter on the opposite side of the first core and extend along its inner face, giving off the varicose dendrites; they then pass to the outer face of the second, ending in the double set of dendrites on its proximal margin. (Fig. 52.) In figure 51, these fibers are seen as dotted strands running diagonally across the inner face of the first lobe, and appearing as continuous strands on the outer surface of the second. On passing from one lobe to the other, the two sets of fibers form the well known chiasma (Fig. 52, *X.*) When seen from the surface, the whole effect is that of a single lobe that has been twisted, through about one revolution, into two lobes.

The surface neurones of each lobe send their fibers into the other medullary core. For example, the fiber from cell *a* (Fig. 52), extends along the outer surface of the second core, parallel with the optic nerve fibers, to the under surface of the first and then upward, ending in the central part of the distal margin of the core. Neurones *b* take the reverse course. The remaining ones take intermediate courses.

The proximal lobe consists of two parts; an anterior one, composed of large neurones, sending their main fibers into the olfactory lobes, and collaterals into the second lobe of the optic ganglion. (Figs. 51 and 52, *op.g.*^{4}); and a posterior part consisting of a spherical mass of somewhat smaller neurones, sending their main fibers backward into the longitudinal tract of the brain (*op. f.*^{3}), and their collateral branches into the second lobe of the ganglion (*op.g.*^{3}).

The optic ganglia are united with other parts of the brain by the following tracts: *a*, a distinct bundle of fine fibers that passes without interruption through the optic ganglion into the crura, and run the whole length of the brain (Figs. 51 and 66 *op.tr.*); *b*. a tract uniting the ocellar ganglia with the second lobe of the lateral eye ganglia (*oc.tr.*); *c*. a commissural tract through the olfactory lobe, formed by the neurones of the fourth lobe (*op.f.*^{4}); *d*. a longitudinal tract formed by the neurones of the third optic lobe, and which extend backward the whole length of the crura (*op.f.*^{3}); *e*. and finally, an important tract, the source of whose fibers is unknown extending from the second lobe of the optic ganglion into the cerebral hemispheres (Fig. 52, *op. tr. H.*).

* * * * * * * * *

IV. Comparison With Vertebrates.

We have already shown that the four ganglia of the parietal eye in Limulus are comparable with the four lobed ganglia habenulæ of the cyclostomes. There is also a striking resemblance between the lateral eye ganglia of arachnids and the optic lobes of vertebrates, especially when we make due allowance for certain peculiarities of position and structure.

We may best explain the origin of the optic lobes of vertebrates on the assumption that the optic ganglia of some form like Limulus have been bent backward and upward onto the neural surface of the brain, in the manner shown in Figs. 44, 57, 58, and 108. In this position, which is similar to the one they occupy in the scorpion and other arachnids, they have the same general form and the same relation to the rest of the brain that the optic lobes have in vertebrates; the three lobes of the optic ganglia corresponding respectively to the colliculus, the tectum, and the torus.

It will be observed that in this new position (Fig. 108, *B*), the general contour of each of the ganglia is retained, but the general appearance of the whole series is greatly disguised, owing to the change of curvature of the second and third lobes, and to the diagonal movement of the ganglia in a caudad and neurad direction. (Fig. 46.) Both the distal and proximal ends of the series are fixed at the optic commissure, the original point of attachment of the ganglia to the basal lobes of the forebrain. The convergence of the fiber tracts of the optic lobes toward the optic chiasma shows that the optic lobes belong primarily to the hemisphere neuromeres, and that their position in vertebrates is a secondary one.

It is clear that, as regards compactness and economy of space, the change is an advantageous one.

The optic lobes of vertebrates have been forced into their present position by the general trend of several growth forces which appear at an early embryonic period in the arthropod head. We have already referred to some of these conditions. Those that are most persistent and which most affect the position of the optic ganglia are: 1. the overgrowth of the neural crests, which tend to carry the ganglia from the margins of the medullary plate toward the median line; 2. the central location of the eyes on the neural surface of the head in many free swimming arthropods and in ostrocoderms; 3. the tendency of the entire brain to move forward beneath the integument, while the rostrum and other superficial neural structures move backward. (Compare Fig. 46.)

When the optic ganglia are once established in a median neural position behind the hemispheres, the increasing size of the latter, and of the optic lobes themselves, exaggerates still more the backward movement of the neural portion of the ganglia and of the primitive cerebellar commissure.

Thus the roof and sides of the mesencephalon represent the ganglia of the compound eyes of arthropods that have worked back into the territory behind the hemispheres by that struggle for space between growing organs which adjusts and readjusts, till each part falls into the place of least resistance.

Whether the optic lobes helped in the closure of the old mouth, or the disappearing mouth and rostrum made a place for the lobes, cannot be determined. Doubtless these events are part of a general movement, where it becomes impossible to distinguish cause from effect.

Dr. L. Griggs, working at Dartmouth, has been able to locate the optic lobes on the margins of the forebrain region, in the open neural plate stage of Amblystoma, and has followed their course backward and upward till they reach their permanent position. The movements of the lobes, as he describes them, afford a striking confirmation of the interpretation given above.

Conclusion.

1. The lateral eyes are homologous throughout the insects, crustacea, arachnids, and vertebrates.

2. In the arthropods they develop historically later than the larval ocelli, and from a more posterior segment, namely the first appendage bearing segment behind the primitive cephalic lobes.

3. In the arthropods the lateral eye placodes lie for a time on the lateral margins of the cephalic lobes, close to the deep infoldings that form a part of the brain. In vertebrates, the eyes at first have a similar position, but a precocious enlargement of the cephalic lobes and the neural crests leads to the enclosure of the compound eye placodes in the brain chamber, so that they appear to form a part of the brain.

4. The characteristic shape of the arthropod eye and the arrangement of its retinal cells is retained in an exaggerated form in the vertebrate retina, and affords us the only satisfactory explanation of its inversion, its contour and mode of growth, its choroid fissure, its arrangement of rod and cone cells, and its centrally located optic nerve.

5. The parietal eyes of vertebrates belong to the second forebrain neuromere, the lateral eyes to the third or fourth.

6. The optic lobes of primitive vertebrates represent the compound eye ganglia inverted and transferred to a position overlying the mesencephalic neuromeres. Their genetic relations, as well as their most intimate functional and anatomical relations, are with the procephalic neuromeres.

7. The ganglia habenulæ of vertebrates represent the ganglia of the parietal eyes of arachnids, united in the middle line over the region of the diencephalon. They were primarily associated with the olfactory lobes.

CHAPTER X.

THE OLFACTORY ORGANS AND THE OLFACTORY LOBES.

The agreement between the olfactory organ of Limulus and that of vertebrates may be traced in respect to so many different characters that the existence of a genetic relationship between the marine arachnids and the vertebrates is placed beyond a reasonable doubt. Indeed there is a greater difference in respect to this organ, between Limulus and other invertebrates than there is between Limulus and vertebrates.

The olfactory organ of Limulus, in certain respects, stands in a class by itself. Nevertheless it represents a modification of organs very widely distributed in the arthropods, and known in insects as the frontal ocelli, or stemmata, and in the phyllopods and other crustacea, as the frontal sense organs.

The history of these organs is an important lesson in evolution. It affords an impressive illustration of the essentially unalterable character of the procephalic sense organs, and it distinctly sharpens our perspective of the long series of intermediate forms that connect the most primitive segmented animals with the modern ones.

I. The Olfactory Organ of Limulus.

Structure in Adult Limulus.—*Gross Structure.*—In an adult Limulus, the olfactory organ (subfrontal schlerite of Lankester) is a bi-lobed, wart-like thickening of the cuticula, from 5–8 mm. wide, situated in the median line, 30–40 mm. in front of the mouth. (Figs. 38, 39, 70, *ol.o.*) It is innervated by three large nerves, a median and two lateral ones.

The olfactory cuticula is provided with a central cluster of sensory spines and is perforated by many sensory and glandular openings. (Fig. 109, *A.*) The under-lying ectoderm is pigmented, and just beneath it are many branching nerve fibers, together with ganglionic or sensory cells, and a large number, about 1500, flask shaped, or spherical, slime buds.

The most conspicuous parts of the olfactory organ are the slime buds, which are, with few exceptions, sharply confined within the area of the olfactory schlerite. They have the usual form and structure, as described in the chapter on the gustatory organs (p. 116), the only noticeable peculiarity being the clusters of small ganglionic or sensory cells lying near, or on, their outer surface. (Fig. 88, a.)

Minute Structure. –The minute structure of the olfactory organ has not been satisfactorily determined, especially the character of the nerve terminals. So far as I have been able to discover without a thorough application of either the methylene blue or the Golgi method, there are three ways in which the nerves may terminate in the region of the olfactory organ. The median nerve, before reaching the organ, breaks up into numerous small branches which are distributed in the central portion of the organ. (Fig. 109, *m.ol.n.*) The two lateral nerves terminate in oblong masses of very large ganglion cells, just beneath the lateral margin of the organ. From these ganglia numerous branches arise that are distributed to the olfactory organ and to a considerable area of the surrounding epidermis.

The finer branches from both sources form a sub-epithelial plexus, from which still smaller branches are distributed over the surface of the slime buds. Others, possibly derived exclusively from the lateral olfactory nerves, end in peculiar ill defined masses of cells that are either wedged in between the slime buds, or lie against the epidermis. (Fig. 88.) They may possibly be connected with slender sensory cells, similar to those in the gustatory organs, that extend into the hollow spines and into the narrow canals leading to the outer surface.

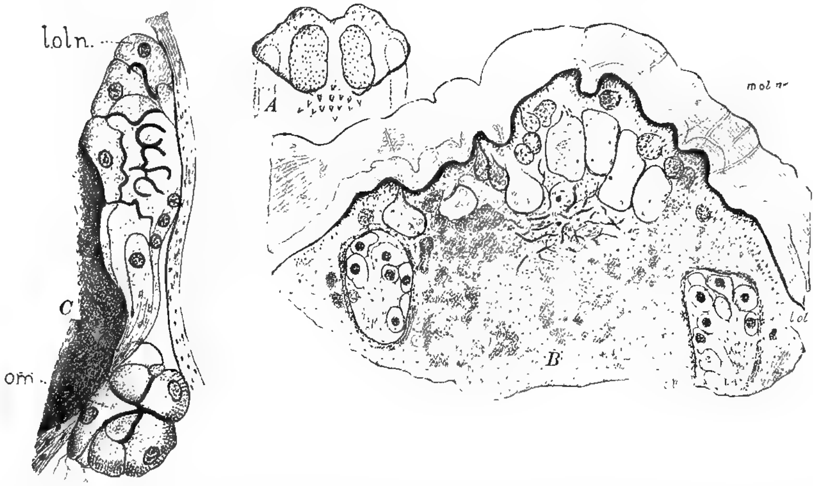


FIG. 109.—The olfactory organ of Limulus. *A*, Olfactory organ of the adult, seen from the outer surface; *B*, cross-section through the olfactory organ of a young Limulus, about seven inches long (*Flemming's solution*); *C*, longitudinal section through the root of the lateral olfactory nerve of a young Limulus, showing the ommatidia-like clusters of large cells with rod-like enclosures, derived from the primitive segmental sense organs.

Finally there appears to be a system of fine nerve strands that penetrate the soft chitenous exoskeleton surrounding the olfactory organ, where they form loose meshworks in superimposed layers. These fibers resemble those seen in the cornea of mammals, and although of very uniform caliber they appear to differ from the branching hyphæ of the parasitic fungus (Macrocystis) that is frequently seen in this region. The hyphæ take up the methylene blue in a similar manner to nerve fibers, and at first sight might be easily mistaken for them. However, recent preparations in von Rath's fluid show, in addition to the hyphæ above mentioned, branching fibers that appear to be true nerve-fibers.

Although the minute structure and the function of this organ need further study, there is no question that it is a true sense organ of great morphological significance.

The Development of the Olfactory Organ and Nerves.—*The Olfactory Placodes.*—The primary olfactory organ of Limulus represents a segmental sense organ serially homologous with the lateral eyes and the ocelli. It is first seen as a pair of sensory thickenings on the anterior margin of the lateral eye ganglion, behind the median eye tubes. (Fig. 141, *ol.o.*) It is connected with the middle lobe of this ganglion by the lateral olfactory nerve. (Figs. 36–39.)

Each organ soon separates bodily from the ectoderm. Although there is no visible infolding, the cells which have the appearance of visual cells, are inverted in the process and become filled with a dense mass of white pigment (guanin?). (Fig. 37, *A.*) At the same time certain cells filled with the same kind of pigment migrate forward from each placode, forming a gradually widening, sub-epithelial plexus of branching pigment cells connected with the anterior margin of the placode by a short thick stalk. (Fig. 36, *p.st.*) During the early embryonic stages the placodes move toward the remnants of the anterior neuropore and there unite in the median line, meantime acquiring a connection with the anterior surface of the cerebral hemispheres and the olfactory lobes. (Fig. 142.)

Lateral Olfactory Nerve.—In the following stages, the united placodes move forward beneath the integument toward their position in the adult. During this process, the lateral olfactory nerves become greatly elongated and the cells of the original placodes are now scattered as ganglion cells along the nerve, but forming a special enlargement at either end. These terminal masses consist of irregular clusters of five or six large pear-shaped cells which greatly resemble the ommatidial cells of the paired ocelli, not only in their shape and arrangement, but in the presence of the clear refractive rods, or rhabdoms, on their side walls. (Fig. 109, *C.*)

In young Limuli (2–3 in.), the peripheral end of the lateral olfactories still terminates in a compact, club-shaped mass of metamorphosed visual cells. (109, *B.l.ol.n.*) It also sends out several fine nerve branches which ramify widely under the skin, in the region surrounding the main olfactory organ. (Fig. 70.) At the same time the terminal group of cells breaks up into irregular clusters scattered among the branches of the nerve. In the ordinary methods of preparation, each cluster has the appearance of an isolated ommatidium composed of large pear-shaped ganglion cells, whose proximal ends form coarse nerve tubes. There is another group of cells, similar to those just described, scattered along the proximal end of the main nerve, some of them outside the brain sheath, but the majority within it, on the root of the nerve as it passes over the surface of the hemispheres. (Figs. 39, 48, 51, 66, 109, *ol.l.n.* and gc^1 and gc^2.)

Both these cell groups, which contain granules that have a glistening white appearance in reflected light, are the modified descendants of the cells constituting the original visual placode. Even in the adult, they still show traces of the white pigment, of the refractive visual rods or rhabdoms, and of their primitive grouping into ommatidia.

In young Limuli, the roots of the lateral olfactories become less compact, and as they were seldom seen in methylene blue preparations, it was very difficult to follow them. They appear to shift their point of attachment from the second optic ganglion, toward the inner face of the olfactory lobes, near the tract uniting the median and lateral eye centers (Fig. 51, *oc.tr.*) Whether they passed through this tract to the olfactory lobes could not be determined. In a few cases (methylene blue) a small strand of fibers was seen to leave the main root and pass mesially toward the horns of the olfactory lobes. (Fig. 51, *z.*)

Median Olfactory Nerve.—When the united olfactory placodes move forward away from the brain, a new outgrowth from the hemispheres and olfactory lobes appears which follows the placodes forward, or is drawn out by them, to form the median olfactory nerve. (Figs. 38, 39, 41, 48, 66, *ol.m.n.*) It consists of large globular masses of minute ganglion cells, each lobule containing a central core of medullary substance, similar to that in the hemispheres.

In young Limuli (2 to 3 inches long) there are four distinct roots to the median nerve, two hæmal ones continuous with the horns of the olfactory lobes, and two neural ones, continuous with the anterior median lobes of the cerebral hemispheres. (Fig. 48.) Each root contains a medullary core of neuropile surrounded by a cortex of "granule cells," the cortex and neuropile passing without perceptible change into the cortex and the neuropile of the cerebral hemispheres and the olfactory lobes. (Figs. 48, 51.)

In the adult, the two hæmal stalks disappear, while the two neural ones unite and shift their attachment in a neuro-posterior direction, so that they are ultimately widely separated from the apices of the olfactory lobes.

In larvæ about two inches long the distal ends of the three olfactory nerves form a rich plexus of nerves terminating in a small patch of ectoderm that may then be recognized as the definitive olfactory organ.

Summary.—The lateral olfactory nerves, then, are characterized as follows: The "ganglion cells" are large and pear-shaped, and arranged in small ommatidia-like clusters. Granule cells and neuropile are never present. The fibers are coarse tubes, with distinct sheaths. The nerves terminate in the lateral portion of the olfactory organ and in the surrounding integument. The ganglion cells of the lateral olfactories are the metamorphosed visual cells of the initial olfactory organ.

The median olfactory nerve represents a later, or secondary, outgrowth of the hemispheres and of the olfactory lobes. Its ganglion consists of lobular masses of granule cells and neuropile, and never contains large cells of a sensory nature. Its end branches are bundles of naked fibers, or at least they have no visible sheath. They terminate in the central region of the olfactory organ.

II. The Olfactory Lobes of Arachnids.

Development.—The olfactory lobes (organe stratifie, St. Remy) are probably present in all arthropods. They always form a conspicuous part of the forebrain in arachnids, but their functions and their relations to other parts of the procephalon are unknown, except in Limulus where they are associated with the olfactory nerves; their function is thus definitely indicated. It is singular that Limulus is also the only form in which the lobes come into close morphological relation with the nerve roots to the median ocelli.

In the *scorpion* and in *spiders*, the olfactory lobes arise from the walls of a deep transverse groove extending across the anterior end of the medullary plate. The groove probably represents the whole of the first neuromere, hence they represent the very anterior margin of the primitive nerve axis. (Figs. 15, 16, 20, 46.)

In the later stages, the groove closes and its walls form a conspicuous crescentic band of small, deeply stainable cells, on the anterior hæmal aspect of the forebrain, Figs. 41, 42 *ol.l.*

The Olfactory Lobes of Limulus.

Development.—In Limulus, the olfactory lobes appear as two separate infoldings. (Figs. 141, 142, *ol.l.*) Later the lobes unite and migrate backward over the hæmal surface of the brain, gradually changing from a thick, bi-lobed transverse bar extending across the very anterior end of the brain, to an elongated U-shaped disc lying on its hæmal surface. (Fig. 36.) In the adult, the posterior margin of the bow extends backward, well below the middle of the cheliceral segment, farther back than its position in the half grown specimens shown in Figs 47, *B*, 48, 51.

The lobe is formed from the posterior wall of the original infolding, the membranous anterior wall disappearing during the later stages.

The entire margin of the lobes consists of very small, closely packed cells resembling the granule cells of the cerebral cortex. As they freely absorb all kinds of nuclear stains, the outlines of the lobes can usually be seen with great distinctness.

In young Limuli the anterior arms of the bow-shaped lobes are drawn together, forming two slender horns which up to the late larval stages, are continuous with the lips of the anterior neuropore. (Fig. 36, *A* and *B*.) At about the time the neuropore closes (after the trilobite stage) there is a vigorous forward outgrowth at this point, apparently originating in the hemispheres. This forward outgrowth carries with it the pointed ends of the olfactory lobes and the peculiar tissue of the hemispheres, giving rise to the median olfactory nerve and its ganglion. Thus the stalk of the median olfactory is continuous with both hemispheres and with both horns of the olfactory lobes.

Structure.—As the crabs grow older, the cells on the median portions of the lobes become very large, and divide into several distinct clusters. All the marginal cells, however, remain very small, and of uniform size from one end of the lobe to the other; toward the center of the lobes, the cells gradually increase in size. (Figs. 51 and 66.)

The small marginal cells send their neurites into two sharply defined bands of very dense neuropile extending round the lobes. (Fig. 48, *ol.np.*) In the anterior horns, these bands become smaller, and unite to form a single band. The latter extends to the apex of the horns, and is continued into the neuropile axis of the median nerve. (Fig. 51.)

In methylene blue, either one or both of the bands often stand out very clearly, with only a single regular row of nerve cells visible over each band. The dendrites of these cells are very minute, show a longitudinal trend, and are confined to their respective bands. See the posterior median part of the olfactory lobes in Fig. 51.

On the inner face of the deeper band (Fig. 48, $ol.c^{1-4}$) are two small bundles of longitudinal fibers, derived in part from medium sized cells on the inner margin of the lobes. (Fig. 51, $ol.c^{2}$.) These bundles are continuous with the tracts arising from the median eye centers. One or two bundles of heavier fibers lie below and concentric with the ones just described. They arise from the cells of the fourth optic lobe, $op.f^{4}$. On reaching the opposite side, they turn outward and backward, and join the main longitudinal, hæmo-lateral tracts, $c.op.f^{4}$.

Of the larger central cells of the olfactory lobes, we may recognize special clusters of medium size cells sending neurites into the neuropile terminals of the two pairs of median eye nerves, and hence to the circular bundles and to the tract connecting them with the lateral eyes. (Fig. 51, $ey.r^{3}$.)

Farther back is a large cluster of cells, generally very conspicuous, sending richly branched neurites outward and backward, underneath (on the neural side), the main marginal bands of the olfactory lobes, into the longitudinal hæmo-lateral tracts of the same side, or in wide curves to the same tracts of the opposite side. (Fig. 51, $ol.c^{1}$.)

Finally in the posterior bend of the olfactory lobes there are some very large deep lying median cells that send their enormous branching neurites backward into the median neuropile mass of the cheliceral ganglion and hence right and left along the median hæmal side of each crus $ol.\ c^{3}$.

In the older crabs, the horns of the olfactory lobes gradually withdraw in a posterior hæmal direction and finally lose their connection with the median olfactory nerve root. Thus the main center of the olfactory lobes becomes relatively isolated, unless, as it appears probable, the lateral nerves ultimately establish a connection with them, through the median and lateral eye tracts.

III. The Olfactory Organs in Phyllopods. Frontal Organs.

The olfactory organ of Limulus undoubtedly represents a highly specialized condition of the characteristic "frontal sense organs" of the phyllopods. Each resembles the other in location, innervation, origin, and histological structure.

We may recognize two sets of organs in the phyllopods, the paired dorsal ones and the unpaired ventral ones. They probably correspond to the stemmata, or frontal ocelli of insects.

Branchipus.

In Branchipus the dorsal or paired frontal-organs consist of a compact mass of small ganglion cells, with one or two large ones situated on either side of the ocelli. (Figs. 95, 110, *B*.) The terminal cells are in contact with the unthickened epidermis in the center of a faint rounded elevation. They are connected with a small compact nerve, that runs parallel with the ocellar nerves, and that arises from the anterior surface of the brain near the root of the lateral eye ganglion.

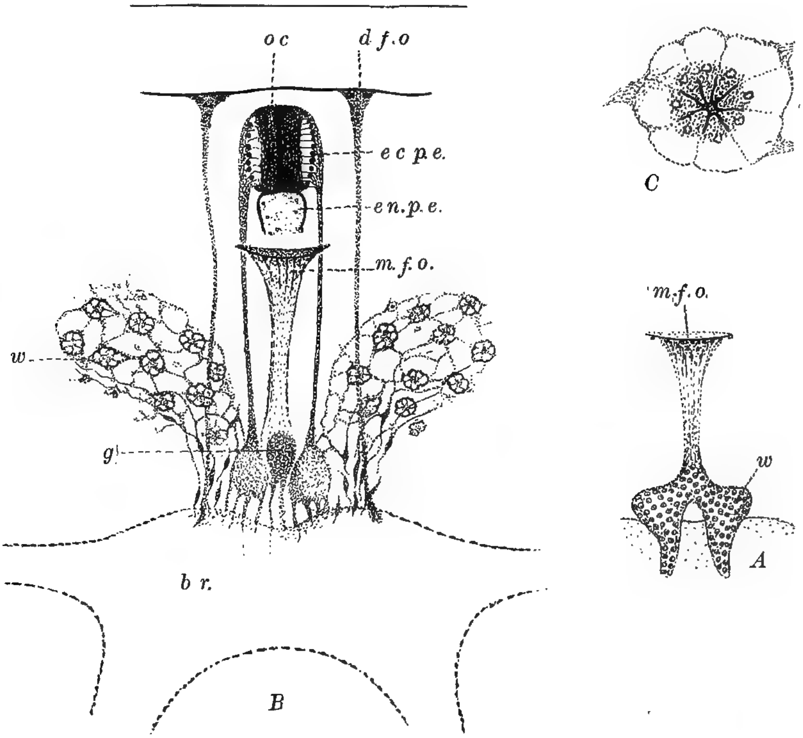


FIG. 110.—The parietal eye and olfactory organs, or frontal organs, of Branchipus. *A*, The median olfactory nerve of a young larva, showing at the base of the nerve, the ganglionic enlargement, *w*, formed on the anterior surface of the forebrain; *B*, a more mature specimen, showing the breaking up of the lobes into a nerve plexus containing ommatidia-like clusters of cells; *C*, one of the cell clusters more highly magnified.

The embryonic organ is formed by the separation, from the base of the lateral eye ganglion, of a small patch of neuro-epithelium, which then migrates under the epidermis toward the anterior median line of the head.

The history of this organ, therefore, is practically identical with that of the lateral, or primary olfactory placode of Limulus.

The ventral frontal-organ is unpaired and lies just in front of the ocelli. In larvæ about 10 mm. long, the organ is merely a rounded area, without any local thickening of the chiten or epidermis, in which terminate a great many fine nerve fibers, *B*, *m.f.o.* In very young larvæ the latter arise from the united anterior ends of two thick ridges, or lobes, on the anterior surface of the forebrain. (Fig. 110, *A*, *w.*) These lobes are solid masses of cells like those in the forebrain and undoubtedly arise as an outgrowth from it. In the later stages, therefore long after the ocelli are fully formed, they increase greatly in size, expanding laterally and forward, thus forming two wing-like plates, which still later break up into many scattered sensory buds united by a nerve plexus, *B*, *w*.

Each sensory bud contains several radiating cells; the latter are clear on the periphery, and their pointed inner ends are granular and capped by refractive plates or rods, like those on the retinal cells. (Fig. 110, *C*.) These buds, therefore, resemble the isolated ommatidia arising from the lateral olfactory nerves in Limulus.

In the adult Branchipus, the buds are united with the brain by loose nerve strands containing dark colored bipolar cells, the remnants of the stalk by which the median olfactory lobes were connected with the brain. A small cluster of nuclei, *g.*, at the base of the median nerve represents the remnant of the unpaired portion of the lobes.

Nowikoff, '05, also recognizes the resemblance of these cell clusters (in Limnadia) to groups of retinal cells, as I had previously done for Limulus in 1893. He regards them as detached retinal cells belonging to the median ocellus. But the development of these cells in Branchipus, long after the ocelli are formed, and the development of the lateral olfactory organ in Limulus, show clearly enough that the isolated ommatidia are formed from the breaking up of independent sense organs, quite distinct from the median eye.

The median frontal organ of Branchipus clearly corresponds to the median olfactory organ of Limulus, not only in its position, but in its development as a ganglionic outgrowth of the forebrain. There is, however, this difference, that in Branchipus there are no recognizable hemispheres, and the sensory buds are formed from the median olfactory outgrowth, while in Limulus they are formed from the lateral one.

Apus.

In Apus (Fig. 111), the frontal organ is represented by a thick oval sclerite behind the eyes. Here the underlying ectoderm is thickened and contains vertical fibers crossed by several layers of horizontal ones. Between these coarse fibers is a network of large ganglion-like cells, that appear to be connected with the branches of two large nerves *l.f.n.* (lateral olfactories), containing numerous scattered ganglion cells. These nerves arise from the base of the lateral eye ganglia and are distributed over a wide area, behind and between the lateral eyes, including the thickened ectoderm beneath the sclerite.

Similar conditions to those in Branchipus and Apus prevail in other phyllopods, but we need not consider them here. It is enough to show that the remarkable olfactory organ of Limulus becomes more intelligible when compared with the condition of the frontal organs in phyllopods. In both cases we may witness important steps in the transformation of primitive segmental sense organs into a very special condition preparatory for, and in part realizing, a new function.

The causes lying back of this transformation are remote and probably inaccessible. I formerly supposed that the unfavorable position of the organs in Limulus might have had something to do with their loss of visual functions, but I now regard this as merely a coincidence, since their position in the free swimming phyllopods is not unfavorable to their use as eyes, and yet they have suffered a similar transformation.

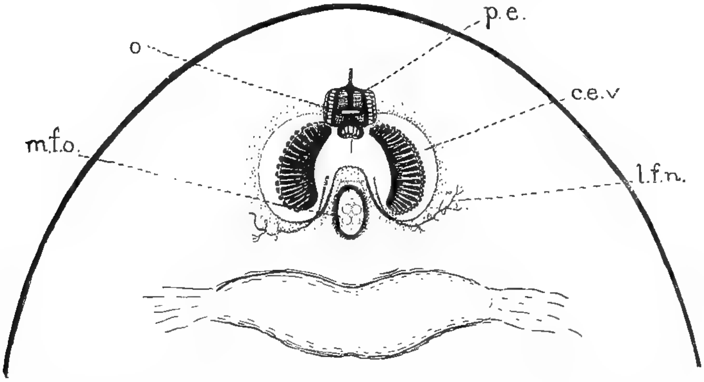


FIG. 111.—Head of Apus, showing the eye chamber *c.e.v.* and its external opening, *o*, the median frontal organ, *m.f.o*, and the course of the lateral, frontal nerve, *l.f.n.*

III. COMPARISON OF OLFACTORY ORGANS IN VERTEBRATES AND ARTHROPODS.

1. **Number of Placodes.**—In arthropods the olfactory organ arises from two pairs of sensory placodes that still retain structures characteristic of visual cells. According to the amount of median fusion that has taken place, the adult organ may be regarded as a single unpaired one, (Limulus); or as three, a paired and unpaired one, (Apus); or as two pairs, (Branchipus and other phyllopods.)

In vertebrates the primitive olfactory organ has been regarded by various authors as single, paired, or multiple. The first view has been widely entertained, especially by the older anatomists, and was based largely on the condition in the cyclostomes and in Amphioxus. Of more recent authors, Burckhart, 1908, is inclined to regard the vertebrate olfactory organ as formed by the fusion of two pairs of placodes. Kuppfer distinguishes three parts in Petromyzon, an unpaired one at the point where the neuron last closes and one on either side.

These conflicting views are intelligible on the assumption that the vertebrate organ is derived from three or four separated anlagen, as it is in Limulus and the phyllopods, and that in both classes it may undergo varying degrees of fusion, or of unequal development of its constituent parts.

2. **Number of Nerves.**—In the arthropods, the olfactory organ always shows traces of two pairs of nerves, even when the organ itself is practically unpaired. I pointed out in 1893 that the two pairs of olfactory nerves, then known in but a few vertebrates, were comparable with the two pairs in Limulus, but not with any other cranial nerves known elsewhere, either in vertebrates or invertebrates; I stated that: "It is now known that each olfactory nerve of the higher vertebrates is represented in amphibia by two distinct nerves, which have been likened to the dorsal and ventral roots of a spinal nerve. But if this were so they would differ from all other spinal nerves in that both dorsal and ventral branches supply sense organs. Moreover, on any supposition they are entirely different from those belonging to the other sense organs of the forebrain, such as the lateral and parietal eye, and the auditory organ. This condition is quite inexplicable on any theory founded on vertebrate anatomy. But this very thing occurs in the olfactory organ of Limulus, although the meaning of it cannot be explained there any more than in vertebrates."

It is interesting to recall the statements made at that time, since they have been in some respects so fully confirmed by the subsequent discovery of two pairs of olfactory nerves by Pinkus 1894, in Protopterus; by Allis 1897, in Amia; by Locy 1899, in the elasmobranchs; and by Zewertzoff 1902, in the embryos of Ceradotus. If the condition in Limulus had received more serious consideration, it is very possible that the little "foot note" to the ancestral history of the vertebrate brain, which according to Locy, is furnished by the development of the nervus terminalis, might have expanded into a chapter.

3. **Structure and Termination of the Nerves.**—Arthropods. Both pairs of nerves, while supplying the same organs, are widely different in their histological characters, and in their central termination. Both pairs are ganglionated. The lateral nerves contain very coarse nerve fibers with distinct sheaths, and scattered clusters of gigantic ganglion cells; they terminate in the base of the brain, near the roots of the optic tracts. The median nerve contains fine sheathless fibers, dense masses of neuropile and small ganglion cells; it has its roots in the olfactory lobes and in the hemispheres.

The olfactory nerves are "sui generis" and are only remotely comparable with any other cranial nerves, such as the optic nerves, the segmental gustatory nerves, or with the components of less specialized peripheral nerves.

Verebrates. According to Locy, both pairs of olfactory nerves are ganglionated, and although closely associated in their peripheral termination, have separate central origins, hence they are considered to be separate nerves, not as separate parts of one nerve.

What Pinkus says of the nervus terminalis, viz., "Eine kolbige Anschwellung dieses Nerven, welche durch die Einlagerung grosskerniger, von allen anderen nervosen Zellen des Protopterus anscheinend verschiedenen Zellen bedingt ist, macht es wahrscheinlich dass wir es hier mit einem neuen Organ zu thun haben" applies equally well to the lateral olfactory nerve of Limulus.

The nervus terminalis in elasmobranchs may have either a neural or a hæmal origin, but it is generally closely connected with the lamina terminalis (Locy); or according to Pinkus in Protopterus, it "Am vorderende des recessus præopticus das Zweischenhirn verlast," thus indicating its probable origin near the root of the lateral eye ganglion, as opposed to the origin of the main olfactory from the dorsal anterior surface of the hemispheres.

4. **Origin of Olfactory Ganglia.**—Arthropods. The lateral placode is a primitive visual organ which becomes bodily converted into the giant ganglion cells of the lateral nerves. The median placode is retained to form the epithelial area in or near which all the nerves terminate. Its ganglion cells are very minute and arise as outgrowths of the hemispheres and of the olfactory lobes.

Vertebrates. The difference between the development of the median and general placodes is unknown.

5. **Position of Placode Cells.**—Arthropods. The olfactory placodes arise from the anterior lateral margin of the open medullary plate, but unlike the adjacent visual placodes they are not swept into the neurocœle by the overgrowth of the palial fold; consequently the sensory epithelium is upright, and does not form the wall of a closed sac.

Vertebrates. The same.

6. **Serial Location of the Placodes and their Migration.**—In arthropods (Limulus), the lateral olfactory placodes are originally located on the margins of the medullary plate (procephalic lobes), between the median ocelli and the lateral eyes; they therefore appear to form the second set of cranial sense organs and nerves; the median ocelli forming the first set, and the lateral eyes, the third (Fig. 142). The lateral olfactory placodes first move toward the anterior median margin of the palial fold (edge of the neuropore) and then forward, taking up a position in the adult either on the neural surface (Limulus), the apex (Branchipus), or the hæmal surface of the head (many phyllopods), its position in each case being determined by local variations in the growth of the forebrain and the external surface of the forehead. The arrangement of ocelli, olfactory organs, and lateral eyes in the fully formed head, may, or may not, agree with their primitive serial arrangement on the margins of the cephalic lobes. The olfactory organs may stand alone in the adult (Limulus) or they may unite with the ocelli and lateral eyes to form a compact median group (Apus, Limnadia etc.). (Figs. 8 and 111.)

In vertebrates the same conditions are indicated, but the serial order of the ocellar, olfactory, and lateral eye placodes cannot be certainly determined in vertebrates without locating their positions on the margins of the open neural plate more accurately than has yet been done. Their serial order on the surface of the head in the later stages is not decisive.

During the closing of the medullary plate, the olfactory organs may or may not unite in the median line; but they invariably move forward either to the median neural surface (cyclostomes), or still farther forward onto the anterior hæmal side of the forehead. (Fig. 4.)

In most ostracoderms (Bothriolepis, Tremataspis, Cephalaspis), the olfactory organs and the median and lateral eyes unite to form a very compact group on the neural surface of the head, very similar to the grouping in Apus and other phyllopods, where they may be located on either the neural or hæmal surface. (Figs. 5, 8, 12 and 111.)

In the cyclostomes, all the pro-cephalic sense organs are on the neural surface, but they are not so compactly arranged as in the ostracoderms or in the phyllopods.

7. **The Olfactory Lobes.**—Arthropods. In the arachnids, the olfactory lobes make their appearance as a deep transverse infolding on the very anterior margin of the medullary plate. They soon sink below the surface and move backward onto the hæmal side of the forebrain. The posterior wall of the infolding gives rise to the olfactory neurones; the anterior wall is membranous, and later disappears. The cavity of the infolding, as long as it can be recognized, communicates with the spaces between the hemispheres, and with those under the palium, *i.e.*, with the potential first and second ventricles. (Figs. 46 and 47.) The roots of the median olfactory nerve and the parietal eye nerves may be located in the olfactory lobes.

Vertebrates. The olfactory lobes arise as deep transverse infoldings across the anterior margin of the open medullary plate (frog), (Figs. 25 and 26), therefore from precisely the same location and in the same manner as in the arachnids. The lobes are finally located on the anterior hæmal margin of the forebrain, and their cavities communicate as in Limulus. They are the only brain lobes that have a conspicuous connection with both the olfactory organ and with the parietal eyes. (Figs. 43, 44.)

8. **Function.**—The olfactory organ of fishes is recognized to be an olfactory organ largely on morphological evidence. Whether or no it actually has what is commonly understood to be an olfactory function, whatever that may be, rests on surmise. Nevertheless, it would still be proper to speak of it as an olfactory organ, even if it were experimentally demonstrated that it reacted to sound or to light, because we know that it is the true homologue of the olfactory organ in the mammals.

It is well to bear this in mind in comparing the olfactory organ of arthropods with that of vertebrates. Although our case rests primarily on morphological evidence, the evidence afforded by function, while meager, is confirmatory. Stimulation of the olfactory organ of Limulus with various kinds of food, with acids and with ammonia, does not usually produce any characteristic reflexes. Even drops of rather strong hydrochloric acid, or ammonia, have no more effect than when applied to other parts of the body; they cause a slight start, nothing more.

In order to test its glandular nature, the olfactory organ was cut out, its outer surface wiped dry, and then the attached nerves stimulated with electricity; no traces of a secretion appeared. But electrical stimulation of the olfactory region in uninjured male crabs in some instances at once produced very remarkable leg movements, rarely seen under any other circumstances.

When the electrodes are applied to the olfactory organs of the male, if the experiment is successful, rapid chewing movements of the mandibles are produced, accompanied by vigorous snapping of the cheliceræ, which may finally become rigid and stretched out backward at full length. At the same time the second pair of legs (the ones used to seize the females) which during all our preceding experiments on the gustatory organs have remained motionless, are now quickly and repeatedly flexed, as though trying to hug or grasp some object and force it toward the mouth; all the other legs remain motionless. Stimulation of the region about the olfactory organ, or along the median line between the olfactory organ and the brain, or above the brain, may produce the same effect.

These experiments indicate that the olfactory organ is a chemotactic organ, whose activities are associated with the process of eating, although it is difficult to explain why the chewing movements are not produced by direct stimulation of the olfactory organ with food. On the other hand, the extraordinary hugging and grasping movements aroused in the second pair of legs of the males, when the organ is electrically stimulated, indicate that it is used in finding the females during the mating season. That an organ for this purpose must be present seems certain, for the males during the breeding season seek out the females and attach themselves to them with great precision. In confinement, the males usually attach themselves to the abdomen of the females, but males whose olfactory organ had been cut out did not do so. Smearing the olfactory organs of males with the ova or secretions of oviducts produces no effect.

In primitive vertebrates, the olfactory organ was doubtless of great importance in mating, as indeed it is through the whole series of vertebrates. It is of special interest that they were intimately associated with sexual activities in such remote ancestors of the vertebrates as the arachnids. In this connection, the olfactory function of the antennæ of insects, and its relation to sexual reproduction will be recalled.

Summary and Conclusion.

The gustatory organs play an important part throughout the entire range of arthropods, and they have done so ever since the appendages have been used as aids to nutrition. In Limulus, they form the most voluminous nerve tracts and nerve centers of any single set of organs, and the great size of the hemispheres is largely due to important gustatory centers that are located in them.

The olfactory apparatus and the olfactory function arose in the higher arachnids through the secondary modifications of preexisting organs that had some other function or meaning.

The primary sensory functions of the marine arachnids were, therefore, visual and gustatory, and the main centers for these functions lie respectively in the optic ganglia and the primitive cerebral hemispheres.

In the higher marine arachnids, and toward the beginning of the ostracoderm, or primitive vertebrate stage in phylogeny, the olfactory function, as a secondary aid to nutritive and sexual activities, became definitely localized, and the most anterior section of the forebrain was successfully preempted as the main olfactory center.

The auditory function was definitely localized at a much later period than any of the three preceding ones, and it has probably for that reason never succeeded in creating for itself a definite, sharply circumscribed, brain region.

CHAPTER XI.

FUNCTIONS OF THE BRAIN.

PART I.

Introduction.—In the preceding chapters, we have shown that there is a far reaching resemblance in structure and development between the brains of vertebrates and arachnids. In this chapter, we shall show that they agree in function, and in their physiological relations to other parts of the body.

In the arachnids, the location of several important cerebral centers is already clearly indicated by the peripheral termination of the associated nerves, as for example, the visual, gustatory, cardiac, and respiratory centers. Nevertheless, it seemed highly desirable, indeed imperative, that there should be some experimental evidence to demonstrate the course of the principal nerve impulses, and to locate by experiment the centers that control a group of similar activities, or that bring them into coordinate relation with other activities.

Although Limulus has the largest forebrain, or hemispheres, of any invertebrate known, it does not approach such animals as the hymenoptera, the cephalopods, the crayfish, or the lobsters, in alertness, or in the variety of its responses to visual, tactile, or other stimuli. When compared with the members of its own class, such as the spiders and scorpions, it appears stupid and quite unaffected by the events going on in the world about it. Limulus, no doubt, appears to lead a sluggish life in the muddy bottoms of deep waters; but we should be greatly in error if we were to estimate the probable volume and complexity of its coordinating centers, or of what corresponds to the hemispheres of vertebrates, by its so-called "manifestation of intelligence." Indeed Limulus would furnish very little material that could be used for experimentation or observation along these lines. But, for the study of some of the simpler reflexes, Limulus is not excelled by any other animal.

The following experiments were made in the summer of 1897, at Woods Hole. In the summer of 1898, Mr. Raymond Pearl, then a student at Dartmouth, working under my direction, repeated many of my experiments, and the following year added others of his own. More than seventy different operations were performed, mostly on adult animals. They generally involved the transecting, or the removing, of various parts of the brain, or cord, in order to determine the path of nerve impulses, or to locate the centers of control.

We shall describe a few of the more important experiments, and summarize the results of the others that bear on the main problems here under discussion.

* * * * * * * * *

The principal method of obtaining the normal reflexes was to place healthy crabs on their backs on some convenient table, allowing the posterior end of the abdomen to hang over the edge. After a few minutes their muscles relax, and unless disturbed, they remain perfectly quiet for a long time. Meantime, local stimuli may be applied which, if a little care is exercised, usually produce very definite reflexes without arousing the animal from its comatose condition.

The usual stimuli for the chewing reflexes, were drops of clam juice, or pieces of clam, or the like, of the same temperature as the air; and a breath of warm air, or the gentle touch of the finger tips, for the crossed thoracic, the abdomino-thoracic, or other temperature reflexes. Various other stimuli were also used from time to time, as indicated in the description of results. Having familiarized myself with the normal reflexes, the brain or cord was sectioned in various ways. After the recovery from the shock, which lasts from five minutes to an hour or two, the crab was tested as before and the difference in behavior noted.

The operations were performed in various ways, the principal difficulty being to avoid the great loss of blood following any puncture of the skin near the brain or cord.

When the section had to be accurately located, there was no way but to thoroughly bleed the animal, expose the parts, and section as desired at leisure. This was the method followed in transecting one-half of the abdominal cord at a given point, and in cutting it in halves lengthwise.

In transecting the collar, the animal was tied down and the legs fixed in a convenient position; a quick cut was then made across the collar, care being used to keep the opening in the skin as small as possible. To prevent the loss of blood, that spurts with great force from the opening, the wound was instantly plugged with a tight fitting wad of absorbent cotton smeared with vaseline. If the operation is successful, very little blood is lost, the animal quickly recovers, and may live for six or eight weeks, or longer.

The principal errors to be guarded against arise from the difficulty of making the sections in the desired place, and from the degeneration of the wounded or isolated parts of the brain. In some cases, an isolated segment of the nerve collar would degenerate and completely disappear in a few days after the operation; or the degeneration may extend into other parts of the brain and vitiate the results. In some of the most successful cases, the cut surfaces of the brain, after a lapse of several weeks, were covered with an incrustation which, if removed, left the surfaces almost as clean and sharply defined as when the wounds were first made.

To check these sources of error, we have made careful post-mortem examinations and have excluded all those experiments in which there is any doubt about the location of the wound, or the extent of the degeneration.

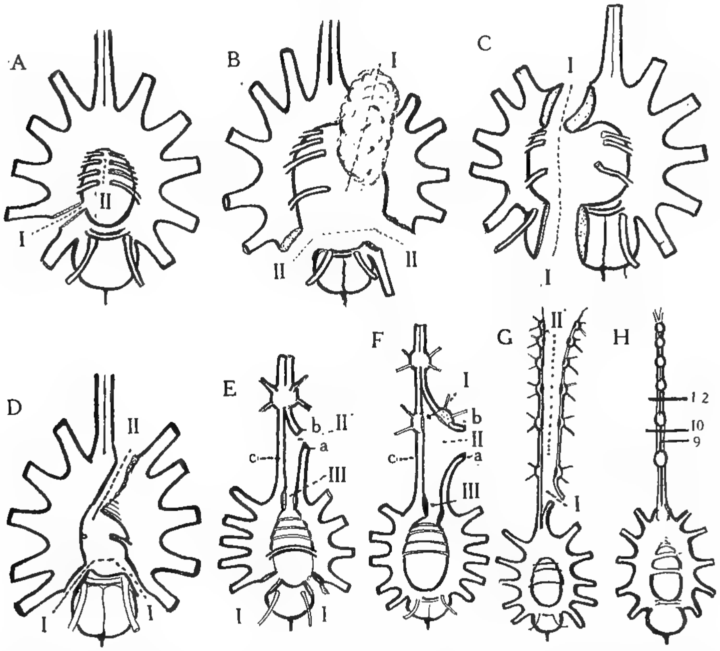
Experiment I—A.

August 16. Sectioned anterior end of left crus. (Fig. 113, A.I.) Before the operation, it was found that if the crab came to rest on its back, and the margin of the abdomen was gently touched with the fingers, the legs on the opposite side would always be raised a fraction of a second before the legs of the same side. When the movements are once started, they become general.

After the operation, the left chelicera is very restless, snapping and moving aimlessly back and forth. The second left leg is also restless, and usually elevated higher than the others.

I. Thoracic Reflexes.—Fifteen minutes later.

a. Hand, placed on left side of thorax, causes a slight start of left legs and left gills. Reverse experiment gives corresponding results.



FIGS. 112–113.—Brains of adult Limuli, that have been cut in various ways in order to determine the function of the principal brain regions and the course of the nerve impulses. All the figures show the brains from the neural surface, with the right side toward the reader's right hand. The roman numerals indicate different operations performed at different times on the same brain.

b. A little later the results are somewhat varied. The right legs are less readily induced to make reflex movements by stimulation of either side than are the left.

c. Hand placed on the left side of thorax caused a slight stirring of the legs of both sides, or a raising of the right or left legs, but no purposeful movements on either side. But placing the hand on the right margin causes well marked, thrusting away movements of the right legs.

d. Twenty-four hours later, repeated *c.* with same results.

II. Abdomino-thoracic Reflexes.—*a.* Fifteen minutes after the operation. Hand placed on left margin of the abdomen causes sudden depression of the gills of both sides and raising of the right legs. Reverse experiment gives corresponding results.

The gills on the side stimulated contract a little before those of the opposite side. This is in marked contrast with the fact that the *thoracic* appendages of the *opposite* side always move first when one side of tne abdomen is stimulated, showing that the abdominal reflexes are mainly uncrossed, and the abdomino-thoracic are mainly crossed.

b. Twenty-four hours later. The right legs frequently perform spontaneous movements, as in a normal crab, but the left are quiet unless stimulated.

c. Hand placed on the right margin of the abdomen causes very vigorous thrusting away movements of left legs, more vigorous than can be produced in any other way. The right legs may be raised and flexed in a sort of spasm, or may not; but they never thrash about as the left legs do. The movements of the left legs are governed entirely by the stimulation, and cease when the fingers are removed from the margin of the abdomen.

d. When the hand is placed on the left margin of the abdomen the right legs immediately move back and forth in the usual manner, the left legs either remaining quiet, or spasmodically flexed. If the crossed reflexes of the right legs are violent they may not cease on removing the stimulus, and the animal may attempt to regain its upright position.

There is a marked difference between the movements of the right legs, in *d*, and of the left ones in *c*. The movements of the right legs are those of a normal crab when stimulated. The left legs may move more vigorously, in response to a crossed abdominal impulse, than the right, but their movements are aimless, and cease with the cessation of the stimulus.

These experiments show conclusively the controlling and directing effect of the cerebral hemispheres.

Experiment I—B.

Same animal. Thirty-six hours later. Cut all the free, post-oral cross commissures of the thorax, leaving the vagus commissures intact. (Fig. 113, *A. II.*)

I. Thoracic Reflexes.—*a.* Ten minutes after the operation. Hand on either margin of the thorax causes slight movements of the legs on the same side, but none whatever on the opposite one; except that when the right side was stimulated, the second leg on the left made vigorous movements.

These experiments were repeated at intervals of one or two hours, with the same results, except that the uncrossed reflexes gradually became more pronounced.

The experiment shows that there are crossed and uncrossed thoracic reflexes, and that the crossed ones pass to the opposite side through the thoracic and the forebrain commissures.

II. Abdomino-thoracic Reflexes.—*a.* Fifteen minutes after the second operation, hand placed on the margin of the abdomen produced only faint movements of the legs of the same side. On repeating the experiment, at intervals of an hour, the *crossed*, abdomino-thoracic reflexes gradually appeared, and three or four hours later became well marked.

III. Gustatory Reflexes.—*a.* After cutting the left crus, the normal chewing movements could be readily produced, except that the second left leg was spasmodic and irregular in its movements.

b. After cutting the cross commissures, the chewing movements that could be induced on the right were very feeble; none at all could be induced on the left. These negative results were probably due to the feeble condition of the animal.

IV. Olfactory Reflexes.—On stimulating the olfactory organ with the electrodes, movements of all the right thoracic appendages and the first two on the left are produced.

Experiment II—A.

August 6 Female. Sectioned thoracic cross commissures and the right crus back of sixth leg. (Fig. 113, *B*, *I.*)

August 14. Crab is very restless when taken from the water. The thoracic appendages are in almost constant motion, waving about in an aimless manner.

I. Thoracic Reflexes.—August 14. Uncrossed reflexes well marked; crossed, indistinct or absent.

II. Abdomino-thoracic.—August 14. *a.* Hand placed on right side of abdomen causes raising of the abdomen and flexing of left legs. Hand placed on left margin of abdomen, no result; or if the fingers cover considerable area, a slight raising of abdomen may be produced.

b. August 25. Crab is vigorous. Hand, or even the tip of a finger, placed lightly on the right margin of the abdomen causes raising of the left legs, followed shortly afterward by the right, and then by general movements of both sides. Hand placed on the left margin of the abdomen, and on the left gills, produces at first no effect; but if the stimulus is increased, then the left legs are raised, followed by general movements, including movements of the right legs. Experiment repeated many times, with same results.

III. Gustatory Reflexes.—*a.* August 7. Stimulation of jaws caused normal chewing movements on either side, but movements of one side do not harmonize with those of the other. *b.* August 25. Same.

IV. Respiratory Reflexes.—August 24. *a.* When at rest, the left abdominal appendages are more elevated than the right.

b. Stimulation of the gill warts with clam causes twitching of the stimulated endopodites, then several lateral movements, the members of each pair stimulated alternately crossing and uncrossing over the median line, and finally a full, rhythmical, up and down, respiratory movement of all the abdominal appendages.

Experiment II—B.

August 25. Cut both crura back of the cheliceræ. Subsequent examination showed that the cut was made in front of the second neuromere on the left, and behind it on the right. (Fig. 113, *B.II.*) General movements of the legs and respiratory movements of the gills followed, but they lasted only a short time.

I. Gustatory Reflexes.—*a.* Immediately after operation, washed away the blood and stimulated the jaws with clam, producing marked leg movement, as in chewing, but very feeble jaw movement. *b.* Repeated the experiment after five minutes with same results. *c.* Again, two days later, stimulation of jaws with food produces chewing reflexes, consisting of leg movement only on the left; on the right, no reflexes.

II. Respiration.—*a.* On removing the crab from the water, all the left gills pulsate a few times, the right remain motionless.

b. When returned to the water after long exposure to the air, the respiration becomes nearly normal. The left legs are very restless and move back and forth in a lateral direction. The right legs are relaxed and motionless, except the sixth, which is directed backward and moving slightly.

c. Respiratory movements may now be induced by rubbing the gills with clam. The same premonitory twitching and lateral movements as in experiment 1. Repeated frequently with same results. When the movements are well under way, the left gills are raised higher than the right.

III. Purposeful Movements of Sixth Leg.—When the fingers were placed on the left abdominal appendages, the left, sixth leg was thrust repeatedly backward over the median surfaces of the gills, with the very evident purpose of thrusting away the stimulating object. The other appendages moved very slightly, but did not in any way make purposeful movements on stimulation of thorax.

Experiment III—A.

July 29 Female. Cut the nerves to the endopodites of all the left abdominal appendages about half way up the appendages. No other effects were observed than the loss of sensibility of the left abdominal endopodites.

This animal was then used for the following successful experiment. At the time the second operation was made, the crab was in such good condition and its normal action had been so little altered that it was not felt that confusion might result from this attempt to economize material.

Experiment III—B.

The second operation was performed August 6, 5 P. M. The autopsy, three weeks later, showed that the left crus was sectioned close to the spinal cord, and all the thoracic cross commissures severed. (Fig. 113, *C.I.*) At the anterior end, the left crus was cut so that a small piece of the left cerebral hemisphere remained attached to it. But only a very few cerebral cells, if any, could have been connected with the crus.

I. Gustatory Reflexes.—*a.* Immediately after the operation, the chewing reflexes were inhibited. Five minutes later, excellent reflexes, including the cheliceræ, were obtained on both sides; but the two sides were not coordinated.

b. August 7, 9 A. M. On stimulating right jaws with clam, obtain prompt and vigorous chewing movements of the jaws, but with moderate, or normal chewing movements of the legs.

On stimulating left jaws, obtain at first the same results, but the leg movement gradually grows more energetic till it is absurdly exaggerated in rapidity and range, and finally becomes much confused, the legs moving wildly back and forth, and often clashing with one another. This rapid movement may be followed by a spasmodic bending of the tips of two or three appendages into the mouth, where they are held in a trembling tetanus or rigor. All the left legs are involved in this movement, except the left chelicera, whose nerve was cut a short distance from the brain.

Repeated these experiments several times on August 10, 14, and 26, obtaining in each case essentially the same results.

II. Thoracic Reflexes.—*a.* August 7. On placing the fingers on the left side of the thorax, there is no response, and if the left legs happen to be making the chewing movements, the latter are not in the least disturbed.

b. Later. Fingers placed on the posterior, ventral surface of the left side cause no movement beyond a slight start when the contact is made, and uneasy opening of the chelæ. But on touching the anterior quarter of the ventral surface, rapid movements of the second and third left legs are produced. These movements at first do not last long, and are inconspicuous when compared with the movements that may be produced on the opposite side. But on the following days they became distinctly purposeful, repelling movements.

c. August 7. On placing the hand on the right ventral side of the thorax, all the right legs move furiously back and forth in unison, while the left continue their chewing movements as before.

d. August 10. Hand placed on the right side of thorax causes active, purposeful thrusting away movements of the right legs.

e. August 25 and 27. Repeated *a*, *b*, and *d*, with same results.

III. Abdomino-thoracic Reflexes.—*a.* Placing the fingers on right margin of abdomen caused back and forward movements of all the right legs (except chelicera) and with very marked thrusting away movements of the sixth leg. No movements of the left legs.

b. Hand placed on the left margin caused obscure movements of the right legs.

c. Hand placed on either side of the margin of the abdomen caused faint, rhythmical contractions of the gills of both sides, but movements of the right gills are the strongest.

d. August 26. Repeated *a*, *b*, and *c*, with same results.

IV. Temperature Reflexes.—*a.* August 25. On breathing gently on the ventral surface of the quiescent crab, that had been lying on its back in the air for some time, a general muscular spasm is instantly produced. All the legs are waved about, but the left legs are thrown into prolonged violent movements during which they are convulsively flexed, and the tips thrown repeatedly toward the mouth. The right legs, meantime, becoming quiet.

b. As soon as the crab had quieted down, the experiment was repeated, but with the utmost care not to produce too violent a stimulus. The little puffs of warm air could be so regulated as to cause the left legs to move, while the right remained motionless. The experiment was repeated many times with the same results, showing that the left side reacted much more readily than the right.

V. Respiration.—*a*. August 7. When at rest in the air, the gills are twisted toward the left, the left gills tightly compressed, the right ones slightly elevated. At first there was a tendency for the left gills to move spontaneously in rhythmical respiratory movements. A week or two later, the right gills frequently performed the normal yawning movements, or the normal respiratory movements, the left gills remaining motionless.

b. Placed in water, normal respiratory movements begin at once, except that the left gills are raised higher than the right.

c. August 26. Crab still vigorous. Repeat *a* and *b* with same results.

d. August 27. Stimulation of gills with clam, or finger tips, does not induce respiratory movements.

VI. Equilibrium; Locomotion.—*a*. August 7. Crab rights itself repeatedly when placed on its back in the aquarium. When righted, it constantly moves in a circle toward the left with right side raised high on the legs, the left side depressed. The caudal spine turned to the right, at an angle of about 20°. The crab, when righted, circulates to the left, because the right legs alone make the motor movements. The circular movement continues for hours at a time. August 27, condition same as *a*.

b. August 7. On removing the crab from the water and placing it on its back, the left legs move restlessly and aimlessly, often bending the tips into or toward the mouth. Movement continues for more than an hour. Right legs remain quiet, but may move vigorously if properly stimulated.

c. At certain intervals, when in the air, all the right legs swing in unison forward, and then with a vigorous stroke backward. The forward and backward movements are repeated many times with great regularity, precisely as in swimming, except that the gills did not join in the movement. The left legs never made these characteristic movements.

d. August 19. In water the crab sometimes fails to right itself. In such cases, the swimming movement of the right legs may continue for hours with great regularity, but without sufficient force to move the animal about. The left legs are meantime passive.

e. August 25, same conditions described in *c* and *d* are retained.

VII. Autopsy.—August 27. Three weeks after the hemisection of the brain the crab was alive and vigorous. On removing the brain, it was found that all the parts about the wound were thickly incrusted with a granulated matter, which when removed showed the cut surfaces of the commissures and of the crura to be very little changed. There was no indication of degeneration, or regeneration of the surrounding parts. There was a thick deposit of sepia colored pigment about the wound in the forebrain. The cotton plugs were incrusted with a granular matter, and they apparently had not interfered by pressure or otherwise with the action of the nervous system.

Experiment IV—A.

August 25. Large female. Cut both crura in front of the second thoracic appendage. (Fig. 113, *D.I.*) Immediately after the operation, the left legs moved restlessly, the right remained quiet.

I. Thoracic Reflexes.—*a*. Immediately after the operation, no definite crossed or uncrossed thoracic reflexes could be obtained by warming the sides of the thorax in the usual way.

b. Several hours later. There was, in no case, any raising of the legs, or purposeful thrusting away movements of the legs on either side, although faint movements of the opposite legs followed a stimulation of the sides of the thorax.

c. If the hands were placed on the margin of the thorax while the chewing movements were going on, the movements on the stimulated side were inhibited.

II. Abdomino-thoracic Reflexes.—The following results are in marked contrast with the above:

a. Hand placed on the margin of the *abdomen* causes raising of the legs of the opposite side, where they are held in a sort of tetanus, as long as the stimulus is applied. When the fingers are removed, they instantly drop back on the carapace. There is no purpose in the movements and it is difficult to understand their meaning. The legs of both sides may be affected, but those on the side opposite to the stimulus are flexed first and to the greater extent.

III. Leg-gill Reflexes.—If the surface of the gills and operculum is touched, the sixth legs at once make vigorous and well directed movements to rub the stimulated spot. If the stimulation is on one side only, the sixth leg of the opposite side moves first and most vigorously. The fifth and fourth legs may be, to some extent, involved in the movements.

The movements of the sixth legs, under these conditions, are remarkable. The ends of the legs are rubbed against each other, and over the surface of the gills, something like the "washing" movements of the posterior pair of legs in a common house fly.

IV. Gustatory Reflexes.—*a*. Immediately after the operation, stimulation of the jaws with food caused chewing movements of both legs and jaws on the left side, but none on the right Three hours later, however, vigorous chewing movements were produced on both sides. The coxal chewing movements were vigorous and normal, the leg movements greatly exaggerated.

V. Respiratory Reflexes.—Stimulating the gills with clam produced no effect.

Experiment IV—B.

Twenty-four hours later. Crab still shows remarkable vitality and spontaneity. Made a sagittal cut through the cross commissures of the thorax and right crus, *D,II*. For a few minutes after the operation, the left legs are very restless and the right are quiet.

I. Thoracic Reflexes.—*a*. Hand placed on the right margin of thorax produces no reflexes. On left margin, retraction of the left legs.

II. Abdomino-thoracic Reflexes.—*a*. Hand placed on right margin of abdomen causes slight movements of left legs, none of right.

b. Hand placed on left margin causes stronger movements than before of the left legs, none of right.

c. Hand placed on the gills causes violent movement of left legs, none of right.

III. Gustatory Reflexes.—*a*. Immediately after the operation, no chewing movements could be induced by stimulating the jaws with food. Applying the electrodes to the left jaws caused movements of the corresponding legs, but no movements followed when they were applied to the right jaws. The right legs would not respond to any change of temperature, whether applied directly or indirectly.

b. One hour later, obtained a faint chewing movement on the left side, on stimulating the jaws with clam; none on the right.

IV. Respiratory Reflexes.—After the second operation, respiratory movements of the gills ceased, and for twenty-four hours no rhythmical movements of the gills could be produced, either by stimulation with clam, or by placing the crab in sea water. But the next morning the following curious facts were observed. The crab was found on its back in the aquarium, just as it had been left the previous day. No respiration had apparently taken place during the night, as the gills were covered with a light sediment.

a. On removing the apparently dead crab from the water and stimulating the gills with the electrodes, peculiar rhythmical contractions followed. The movements stopped in a few moments.

b. On rubbing very gently a small piece of clam on the gills, the movements began again, but more vigorous than before. On returning the crab to the water, the movements, which had meantime ceased, began again and continued with some interruption, for purposes of experimentation, for several hours. These movements were as follows: 1. The abdominal appendages remained well elevated, pulsating in short strokes, once about every one and one-half second, for twenty-five seconds. 2. Two full vertical pulsations then follow, each one being a vigorous flattening of the appendages against the abdomen, followed by an elevation of the same to their full height. 3. They move repeatedly back and forth across the median line, rubbing the posterior surface of one appendage over the anterior surface of its mate, as though rubbing or washing the gills. They may remain crossed and motionless for several seconds, but finally return to their first position. 4. One full pulsation followed by 5. a long pause of twenty-five seconds, and then the whole begins again. One whole series of movements takes place in about seventy seconds, but this period may be gradually prolonged till all the movements cease.

c. When the crab was taken from the water and placed on its back, the movements gradually ceased.

d. Breathing on the gills produced only a slight contraction of the same. A drop of water produced two or three faint pulsations. Scratching the abdominal appendages with the fingers, or with a stick produced no result, but on rubbing them with a small bit of clam, the complicated series of rhythmical movements described in *b* began at once.

Experiment V—A.

10.30 A. M. Large female. Sectioned both crura back of cheliceræ. All spontaneous movements cease. (Fig. 113, *E.I.*)

I. Thoracic Reflexes.—*a.* Hand placed on either margin of the thorax causes contraction of the gills of the same side, and later the raising of the legs of the opposite side. In both cases, the legs on the side stimulated start slightly, but are not raised. No purposeful movements of the legs are made to remove the irritation.

II. Gustatory Reflexes.—Three hours after the operation no chewing movements could be produced by stimulating the jaws.

Experiment V—B.

3 P. M. Sectioned the right half of the ventral cord, in front of the first abdominal ganglion, *E.II.*

I. Abdominal-thoracic Reflexes.—*a.* Hand placed on the left margin of the abdomen caused raising of the right legs, first to sixth. Hand placed on the right margin, caused movement of the fifth and sixth legs on the opposite side.

These two experiments show that impulses cross both above, and below, the cut, *II.*

Experiment V—C.

3.30 P. M. Made a sagittal cut through the vagus neuromeres, but without cutting the free, thoracic cross commissures, *E.III.*

I. Abdomino-thoracic Reflexes.—At first all crossed abdomino-thoracic reflexes ceased.

a. A few minutes later, placing hand on *right* margin of *abdomen* causes the fourth, fifth, and sixth legs of *left* side to be raised.

b. Hand placed on left side of abdomen causes fifth and sixth legs of *same side* to be raised, but these movements are not so strong as when the right side of the abdomen is stimulated.

Crab died after about twenty-four hours.

Experiment VI—A.

August 11, 11 A. M. Exposed the spinal cord, and made a longitudinal median section through the first abdominal ganglion. *F.I.* Rhythmical contractions of the gills followed, lasting a short time.

Experiment VI—B.

The right cord was then cut across about midway between the brain and the first abdominal ganglion. *F.II.*

I. Respiratory Reflexes.—*a.* At first no reflexes followed the section, but after one or two minutes respiratory movements began. The left gills were raised much higher than the right, the latter being apparently dragged up by the left gills, rather than by their own action. When respiratory movements ceased, the left gills remained in a higher position than the right.

b. When placed in the water, the respiration was at first about normal, but in a few minutes it almost ceased, leaving the left gills moving slowly, the right motionless. After about an hour, respiration ceased, leaving the left gills raised, and the right closely pressed against the abdomen.

II. Abdomino-thoracic Reflexes.—*a.* On placing the hand on the right margin of the abdomen, all the left legs are promptly raised, remaining in that position till the hand is removed, when they again fall back slowly into the thorax. The right legs are also raised, but after the left.

b. Hand placed on the left margin of the abdomen causes raising of the right legs (but the response is not as prompt and vigorous as that of the left legs in the previous experiment). The left legs are not raised, but their chelæ stir uneasily.

c. Repeated *a* and *b* two hours later with the same results.

d. Stimulating with a weak electric current at *b*, causes contractions of the right gills, also slight movements of the left gills (see below); at *c*, causes contractions of the left legs and the gills on both sides; at *a*, causes contractions of the right legs.

e. 2.30 P. M. Applying electrodes at *a*, the right gills are slightly raised, and then moved back and forth faintly as in respiration. Left gills move much less than right.

f. Stimulating at *c*, obtain movements of left gills and partial ones of the right, and with vigorous and immediate movements of the left legs.

g. Stimulation at *a*, causes immediate movements of the right legs only.

We thus see that stimuli applied directly to the spinal cord produce uncrossed reflexes of the appendages anterior to the cut, and both crossed and uncrossed below the cut.

But temperature impulses, starting on the sides of the abdomen and traveling centripetally, produce both crossed and uncrossed reflexes in the thorax. It is not clear why direct stimulation of the spinal cord should produce only uncrossed impulses above the point of stimulation.

Experiment VI—C.

3.30 P. M. Made an accurate sagittal cut through the vagus neuromeres, care being taken not to cut the first three or four post-oral commissures. *F.III*

a. Stimulating at *a* or *c*, produced leg movements of the corresponding side, as before.

b. But stimulation of the margin of the abdomen and gills, with the hand, produced no leg reflexes, although breathing on the legs, or dropping tepid water on them, produced prompt movements of the same.

It would thus appear that all the uncrossed temperature impulses started in the abdomen cross in the vagus neuromeres.

Experiment VII—A.

Adult male. Sectioned right cord (Fig. 113, *G.I*). Twitching of the right operculum and first right gill followed the operation.

Experiment VII–B.

Cut the whole ventral cord in halves, lengthwise, *G.II.*

a. The caudal spine is thrown toward the left and remains so permanently.

b. On breathing on the abdomen and gills, the gills are retracted and the right legs alone are raised.

c. Placing the fingers on the left margin of the abdomen causes the raising of all the right legs; the legs are strongly flexed and the points thrown medianly and backward.

d. Hand on the right side produces no results, except that in some cases there is a slight start of the left legs and a faint gaping of the chelæ, but no movement at all resembling those seen on the opposite side of the body. This impulse probably reaches the forebrain through the longitudinal integumentary nerve. (Fig. 70.)

e. One hour later. Repeated several times *d*, *b*, and *c*, with same results.

Experiment VIII.

July 29. Male. The right and left halves of the cord were separated behind the opercular neuromere, by a median, longitudinal cut extending through all the abdominal neuromeres. All the free, post-oral commissures of the brain were also cut, leaving the vagus commissures intact.

I. Abdominal and Abdomino-thoracic Reflexes.—July 30. Stimulation of the left side of the abdomen caused a drawing down of the left gills and an immediate and strong upward movement of the right legs, followed by a slight raising of the legs on the left side. Stimulation of the right side of the abdomen in the same way, produced the same result, and *vice versa.* In both cases there was a movement of the tail toward the stimulated side.

The experiment shows unimpaired crossing of impulses in the vagus neuromeres.

II. Respiration.—July 29. The right and left halves of the gills were breathing in alternation, the gills on the right side being raised while those on the left were depressed. The coordination of the respiratory movements was perfect longitudinally, but the two sides were beating independently.

Experiment IX.

I. Purposeful Reflexes of the Sixth Legs.—July 15. Male. Transected the right half of the cord between the first and second gill neuromeres. (Fig. 113, *H*.9.)

July 18 and 19. *a.* Stimulation of the left side of the abdomen. Caused a drawing down of the gills on the same side, together with a spasmodic, upward, non-purposeful movement of the legs on the right side, followed by a purposeful movement of the sixth leg on the left side.

b. Stimulation of the right side of the abdomen gave same results *vice versa*, except that in this case the sixth left leg (as before) performed the purposeful movement, the sixth on the right being merely raised.

Abdominal stimulation produced no purposeful movements of the sixth leg on the cut side.

II. Yawning.—After the crab had been out of water for about an hour, it would yawn, the operculum and the first gill, both right and left, moving in the usual way, while the gills behind the cut behaved as follows: The left gills were raised in time with the operculum and first gill, although they were not raised as high as in the normal animal. The right gills did not move at all, except as they were slightly dragged upward by the left.

III. Respiration.—Eight hours after operation. In air. As the gills behind the cut began their opening phase, the left gills started first, and apparently dragged the right ones up with them. When the gills closed, the left started down first and dragged the right after. The operculum and the first gill behaved normally.

When the crab was put back in water, the respiratory movements would begin as described above, but after a while they would become more nearly normal. From this it would appear that the coordination of respiratory movements is brought about in some part of the nervous system anterior to the abdominal neuromeres. Same results were obtained on seven successive days, the abnormality of the respiration in air being greater than in water.

IV. Swimming Movements.—July 23. The right and left operculum, the right and left first gill and the four posterior left gills performed normal swimming movements in unison. All the right gills behind the cut were either quiet, or respiring, while the others were swimming. This indicates a center for the swimming movement of the gills in front of the free abdominal neuromeres.

Experiment X.

July 19, 1898. Male. Both cords were cut between the neuromeres of the first and second gills, *H.* 10.

I. Respiration.—*a.* July 29. In water. All the gills were breathing, but out of rhythm The operculum and first gill moved together, but out of time with the posterior gills. In the anterior group, the operculum was the first to start each inspiratory movement, and was followed up by the first gill. The four gills behind the cut beat fairly well together, but the rhythm within the group is imperfect and all are out of time with the anterior group. In the respiratory movement of these four posterior gills, the most posterior one was the first to start the upward movement. Results indicate that the gills behind the cut have been separated from their center of coordination.

b. July 23 to 28. The four gills behind the cut frequently performed the "cross rubbing" or "scraping" movement, the first gill not participating. This "cross rubbing" movement of the posterior gills was always followed by strong swimming movements of the operculum, first gill, and thoracic appendages. At times, the operculum and first gill would stop, while the appendages behind the cut kept on with unbroken rhythm; or the appendages in front of the cut would be performing the swimming motions, while those behind the cut were breathing as usual. This indicates a separate nerve mechanism for respiratory and locomotor activities of the gills.

Experiment XI.

In another experiment, the cord was cut behind the second gill neuromere, *H.*12. Results: 1. the three gills behind the cut made the respiratory movements more vigorously and frequently than the two gills in front of it; and 2. the operculum and the gills in front of the cut "yawned" frequently, while those behind the cut were motionless.

II. Swimming Movements.—At no time after the operation did the gills behind the cut, in experiments X and XI, perform swimming movements. The abdominal appendages in front of the cut made the swimming movements often and in a normal manner.

Miscellaneous Experiments.

The following results were obtained at various times by stimulating the cord and the peripheral nerves with an induced electric current.

a. On stimulating any one of the posterior thoracic hæmal nerves on the left side, the right legs and the right halves of the operculum and gills were raised, the legs pointing toward the region stimulated. The left legs make purposeful movements. The effect is not confined to the appendage corresponding to the nerve stimulated, since after stimulating one nerve all the legs of the opposite side are raised.

b. Stimulation of the longitudinal integumentary nerve gave no results.

c. The abdominal cord was transected between the neuromeres of the first and second gills. Stimulating the proximal end of a hæmal nerve in the isolated segment of the cord caused a raising of the abdomen, followed by a very slight rhythmical movement of the gills.

d. Stimulation of a branchial nerve causes a contraction of the legs and gills of the same side, but no rhythmical movement.

e. Stimulation of the right or left cord in front of the first abdominal ganglion causes contraction of legs and gills of the same side, but no rhythmical gill movements.

PART II.

SUMMARY OF EXPERIMENTAL AND ANATOMICAL RESULTS.

I. GUSTATORY REFLEXES.

a. Normal Action.—1. Each leg of the second to fifth pairs, when its taste organs are stimulated, performs the chewing movements alone, without starting the action in the adjacent legs of the same, or of the opposite side. 2. Stimulating the chilaria of one side may induce chewing movements in all the legs of that side. 3. The cheliceræ have no "taste spines." They are brought into action by stimulating the taste organs on one or more of the other legs of the same side. The action may then be transferred to its mate, if the stimulus is strong enough. 4. When the taste organs of several legs on the same side are stimulated, all the legs of that side work in a harmonious rhythm. 5. When both sides are stimulated, the rhythmic movements of the right legs harmonize with that of the left. 6. There are two independent movements in chewing, the lateral, or in and out movement of the jaw-like coxæ, and the thrusting of the tip of the legs in and out of the mouth.

Structure of the Gustatory Apparatus.—The principal reflexes described above can be explained by the structure of the parts involved. The conditions, so far as we have been able to analyze them by the anatomical and experimental methods, are shown in a diagrammatic form in Fig. 114. We have shown, for example, by the anatomical analysis, that : 1. The taste organ nerves of the jaws, flabellum, and chilaria form distinct fascicles, whose inner ends (after giving off local dendrites, *g.c.*^{1}) unite to form an immense, longitudinal tract, *g.tr.*, terminating in a voluminous mass of neuropile, or secondary taste center, on the neuro-lateral surface of the cheliceral neuromere (diencephalon) near the base of the cerebral peduncles, *g.c.*^{2} 2. A tract extends beyond this center along the cerebral peduncles to a tertiary center that forms a large lobe on the median face of each hemisphere, *g.c.*^{3} At the base of the hemispheres, underneath the posterior median lobes and on the anterior neural surface of the cheliceral neuromere, is a group of large nerve cells, *ch.Hc.*, which by one set of dendrites bring the secondary taste center into relation with the cerebral cortex of the same side, and by another set with the opposite side of the collar, through the forebrain commissure. 4. Finally a cluster of about fifteen large nerve cells, *H.as.*, lying a little above the taste lobe, on the median surface of the hemispheres, sends one set of extensive dendrites to the entire cerebral cortex, another to the secondary taste center, and a third along the surface of the mid- and hindbrain neuromeres, probably terminating around the motor neurites at the base of each pedal ganglion.

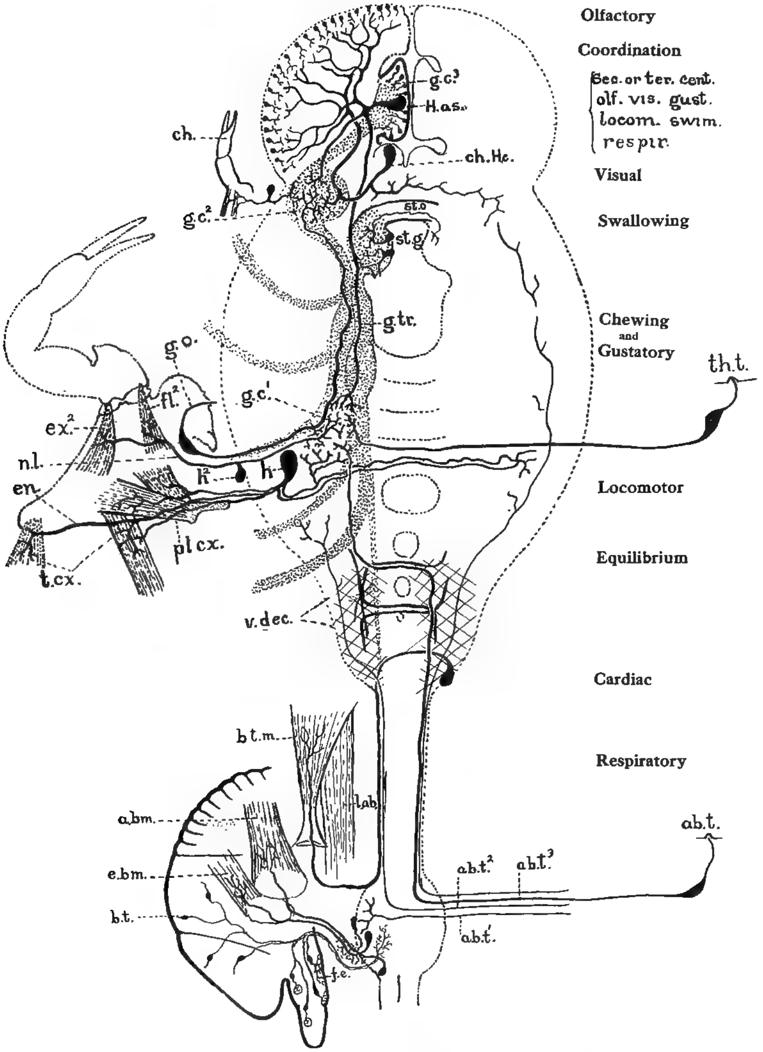


FIG. 114.—Diagram of the brain of Limulus, showing the course of the principal nerve impulses, and the location of the principal centers of control. The figure is constructed from the data obtained by experimental and anatomical methods. Only the first and fourth thoracic, and the first branchial appendage on the right side of the animal are shown. The most important points illustrated are (a) the primary, *g.c*^{1}., secondary, *g.c.*^{2}, and tertiary, *g.c.*^{3}, gustatory centers; (b) the relation of the motor, sensory, and association neurones to the muscles used in the chewing reflexes; (c) the crossed thoracic temperature impulses; and (d) the crossing of the branchio-thoracic impulses in the vagus neuromeres. The lettering of the neurones is the same as that in Figs. 56 to 66.

Closely associated with the secondary taste center is the "swallowing center," or the lateral stomodæal ganglion, *st.g.*, lying on the median margins of the cheliceral neuromere, next to the walls of the stomodæum. It is connected with its mate by a special pre-oral commissure. *st.c.*

The Nerve-muscle Chewing Apparatus.—The leg movement in chewing is produced by two muscles, a flexor and an extensor, both innervated by a branch of the pedal nerve. (Fig. 114, ex^2 and fl^2.) The motor nerve-cells of these muscles while not certainly located probably lie in, or close to, the pedal ganglion, h^2.

The jaw movement is controlled by nine muscles. The "in" movement is produced by four plastro coxals, *pl.cx.*, two in front, and two behind, going from the edge of the plastron to the sides of the coxæ; the "out" movement by the five coxo-tergals, *cx.t.*, two in front and three behind, extending from the base of the coxa to the dorsal shield. These nine muscles are innervated by the anterior and posterior ento-coxal nerves, *a.en.cx.* and *p. en.cx.* that spring from the clusters of motor cells lying on the hæmal side of the brain, one on each side of the pedal ganglion. (Fig. 66, *H.*) Each of these motor cells gives off numerous fibers to the ento-coxal muscles; to the crus of the same side, and to the opposite crus, through the corresponding commissure. (Fig. 114, *h.*)

Experimental Results.—The results obtained by cutting the collar at various places are naturally not always intelligible, but when they are they appear to be in harmony with the anatomical relations just described. These results are as follows:

1. Cutting the posterior end of one crus, or of both crura, behind, or close to the sixth thoracic neuromere does not materially affect the chewing reflexes. 2. Cutting across one crus close to the hemispheres, produces increased vigor, and a diminished coordination in the chewing movements of the legs on the cut side. The jaw movement is either unmodified or slightly diminished. If both crura are cut, the above results are obtained on both sides. These operations not only separate the hemispheres, but the main gustatory and swallowing centers from the thoracic neuromeres. The results point to the presence of separate controlling centers on each side of the forebrain. 3. An isolated segment of the collar, containing one or two neuromeres, lying between the second and sixth neuromeres, and separated from the opposite side by cutting its cross commissures, may give feeble, uncoordinated, gustatory reflexes, but such an isolated portion of the collar generally degenerated and soon failed to give further response. 4. However, in experiment III—B, the left side of the collar was completely isolated and lived without perceptible degeneration for three weeks. But this segment undoubtedly included that part of the cheliceral neuromere containing the secondary gustatory center and the swallowing center, and only a small part, if any, of the hemisphere. This segment readily produced the chewing reflexes; the reflexes were normal except for the exaggerated and uncoordinated leg movements on the isolated side, and the lack of harmony between the chewing movements on the one side with those on the other. The results show: *a.* that the coordination and inhibition of the leg movements on the one side lie in the hemisphere of the same side, probably in the large median lobe, or tertiary gustatory center; *b.* that the rhythmic control of the chewing movements of one side is located in the secondary gustatory center in the cheliceral neuromere; and *c.* that the coordination of

the movements of the right and left sides is controlled by means of fibers in the thoracic cross commissures, probably by the crossed collaterals of the motor neurones.

The Swallowing Reflexes.—There are no nerves or sense organs visible near the lips, or in the soft skin about the mouth; and no reflexes could be produced by touching these parts with food. "Swallowing" apparently depends on preliminary stimulation of the coxal taste organs. The chewing movements are often interrupted by a tetanic spasm of the legs and a prolonged "bite" of the great mandibles on the sixth pair. During this period, a muscular spasm of the stomodæum appears to take place, by means of which the materials that have been tucked into the mouth by the coxal spurs are swallowed. The reflex is probably initiated in the stomodæal ganglion by stimuli received from the anterior end of the gustatory tract.

Course of Nerve Impulses in the Gustatory, Chewing, and Swallowing Reflexes.—We may picture the probable course of the nerve impulses in the chewing reflexes as follows: Stimulation of the gustatory cell, *g.o*, may 1. discharge an impulse by the first set of collaterals directly to the motor neurones of its own segment. 2. To produce the continued rhythmic discharge, it is apparently necessary for the impulse to be conveyed to the secondary, or cheliceral center, and then back to the motor neurones of the chewing muscles. 3. Impulses may be carried from the secondary center to the tertiary center in the hemispheres; this center appears to exercise a depressing, or inhibitory, control of the motor neurones, especially of those supplying the flexors and extensors of the leg. 4. The only way to arouse the motor neurones of a given leg or jaw to normal action is via its own sensory fibers, either directly through the primary center, or indirectly through the secondary center, or both. 5. The linear coordination of gustatory movements on one side is affected by the cheliceral center of the same side. 6. Bilateral coordination is affected via the thoracic cross commissures.

The remarkable difference in the action of the same leg muscles, when stimulated via different sensory channels, *i.e.*, gustatory and general cutaneous, may be due to several causes the nature of which is very obscure. They are indicated to some extent by the known structure, and to some extent by the nature of the reaction. The general cutaneous tracts, for example, are not so sharply defined and are not composed of such distinct segmental fascicles as the gustatory tracts, which may account for the fact that stimulation of a definite group of temperature organs on one side of the shield usually produces a reaction in several legs of the opposite side, not in one. Moreover stimulation of the temperature organs produces a rather ill defined leg movement, that at once ceases when the stimulus is removed. If the taste organs are stimulated, a definite rhythmic action follows that does not cease at once when the stimulus is removed. This may be due in part to the fact that the stimulating action of the substance may in this case continue after the source of it has been removed, or in part to the presence of a "center" which continues to act after the peripheral stimulus ceases. But even these conditions do not explain the rhythmic repetition of the reactions in one case and the absence of rhythm in the other. It indicates that there is some "open and shut" mechanism that can be reached and set into action via *g.o.*, gc^1, *h*; or via *g.*, $gc.^2$, gc^1, *h.*; but not via *th.t.* $gc.^1$, *h.* or via any other way.

II. THE CROSSED THORACIC REFLEXES.

The experiments show that:

1. Gentle stimulation (temperature) on one side of the thorax first causes aimless movements of the opposite legs, followed by aimless movements of the legs on the same side. If the stimulation is increased, the legs of the same side make coordinated movements that tend to thrust the stimulating object away; and finally the opposite side may join in the coordinated movements.

2. If the nerve collar is cut on one side between, say, the second and third neuromeres, stimulation of the cut side produces the same results as before, except that the legs back of the cut, on the same side, do not make purposeful "thrusting away" movements, while those cephalad to the cut continue to do so, if the sides of the thorax cephalad to the cut are stimulated.

3. If all the free thoracic commissures are cut, the crossed reflexes cease.

These results show: *a.* that certain coordinated purposeful movements on one side of the thorax are controlled by the corresponding side of the forebrain, in all probability by the corresponding hemisphere; *b.* that the path of the direct crossed impulses is through the thoracic commissures, and *c.* that the coordination of purposeful movements on one side of the thorax with those on the other is accomplished via the commissures at the base of the forebrain.

The simpler relations of these reflex paths are shown in connection with the gustatory tracts in Fig. 114. It will be noted that while stimulation of the temperature organs at *th.t.* produce a few simple movements of several legs of the opposite side, stimulation of the taste cell at *g.o.* produces a continued rhythmic discharge into the muscles at the base of one leg on the same side, with the result that first a leg flexor, then a leg extensor muscle contracts, followed by the contraction of the four plastro coxals, *pl.cx.*, and then by the five coxo-tergals, *cx.t.*

III. THE CROSSED AND UNCROSSED ABDOMINO-THORACIC REFLEXES.

When the ventral margin of the abdomen is gently stimulated, the legs on the opposite side of the thorax are aimlessly raised, followed by a start or spasm of the legs on the same side.

Numerous experiments show that *a.* the abdominal temperature impulses may cross on entering the cord, passing cephalad to the opposite crus. (Fig. 114, $ab. t^2$); *b.* that the greater number of impulses pass up the same side of the cord they enter, and that all these impulses cross to the opposite side through the commissures of the vagus neuromeres, $ab.t^3$; *c.* that they do not cross in the free thoracic commissures.

The vagus neuromeres are therefore the centers for important decussations of impulses passing cephalad on their way from the cord to the anterior brain neuromeres, *v.dec.*

IV. Locomotion.

Locomotion is normally accomplished by coordinated walking movements of the legs, or by a rhythmic beating of the legs and gills in unison, as in swimming.

1. Cutting the collar on one side, behind the hemispheres, diminishes or inhibits the walking or swimming movements on the cut side. Such animals walk or swim in circles, turning toward the cut side because the legs on the uncut side are the most active, or they are the only ones that make any walking or swimming movements. In water, as in air, the legs on the uncut side frequently perform the normal swimming movement, while those on the cut side are quiescent, or are performing some other reflexes, as, for example, chewing. We therefore conclude that the primary reflex centers for locomotion lie in the last five thoracic neuromeres, and for the "gill swimming" in the anterior neuromeres of the cord. The secondary control centers lie in the forebrain, one on each side.

V. Equilibrium.

The nature of the apparatus by means of which the crab tends to right itself is unknown, but apparently the part of the brain in which this function is centered is near the first two vagus neuromeres. This is shown by the fact that cutting across the anterior part of the collar, on one or both sides, or destroying the hemispheres, or cutting the ventral cord behind the vagus neuromeres, does not destroy the tendency, or the power, to turn the neural side down, when free to move; while the cutting, or removal, of the vagus neuromeres does destroy this tendency.

VI. Respiration.

The Respiratory Mechanism.—There are two distinct sets of respiratory muscles, an adductor and an abductor for each abdominal appendage *a.bm.* and *e.bm.*; and a large compound muscle, the branchio-thoracic, or hypobranchial, attached by separate slips to the bases of all the branchial appendages. (Fig. 77, *B*, *b.th.m.* and Fig. 114.)

The abductors extend from the hæmal entapophyses to the anterior wall, and the adductors from the entapophyses to the posterior wall of the branchial appendages. The branchial muscles are supplied by motor branches from the branchial nerve; the sensory branches supply an elaborate system of free nerve-ends, *f.e.*, temperature, *b.t.*, and other sense organs, distributed over the surface of the appendage.

The motor neuromeres for the branchial muscles form three groups, two on the anterior hæmal, and one on the posterior hæmal side of the corresponding ganglion to the branchial nerve. (Fig. 62, H^{1-2-3}.)

Each neurone sends an enormous number of dendrites into the ganglion, mingling with the central ends of the sensory fibers, and a large number of fibers through the branchial nerve to the anterior and posterior branchial muscles. Isolation of these centers, by cutting the cord on both the anterior and posterior sides of the ganglion, does not destroy the action of the corresponding appendage.

The hypobranchial muscle extends diagonally forward from the tendinous stigmata, or hollow infoldings at the base of the appendages, to the hæmal surface of the carapace. (Fig. 77.) It serves to flex the abdomen, but primarily to draw the bases of the appendages forward and hæmally, thus expanding the chamber between the roots of the appendages, and drawing the water from the sides through the gill leaves.

It is innervated by a large, longitudinal nerve, formed by the union of seven segmental nerves, one from the hæmal nerve of the opercular segment and one from each of the six following hæmal nerves. Each segmental bundle of nerve fibers takes its origin from a cluster of neurones located on the opposite side of the next preceding ganglion, close to the reflex center for that appendage. (Figs. 59 and 60.)

Respiratory Reflexes.—No final conclusion, as to the sources of the respiratory impulses can be reached till the action of this nerve and muscle has been experimentally demonstrated. It is clear that sectioning the cord at one or more points would not be likely to greatly modify the action of the hypobranchial muscle, as it would still receive nerves from the ganglia in front of and behind the cuts. This point has been overlooked by Miss Hyde and has not been sufficiently covered by our own experiments.

It seems probable that the contraction of the muscle as a whole may be induced by impulses coming from one or more neuromeres through the roots of the anterior, or hæmal, nerves, and as such a contraction would affect all the gills at the same time it would tend to unify their action and thus materially aid the linear coordination of the respiratory rhythm.

The location of the common center controlling the whole series of branchial reflexes could not be determined, but judging from the forward displacement of the motor cells and of the central ends of the accompanying sensory fibers, it probably lies, in part, at any rate, in the vagus neuromeres. This conclusion is strengthened by the fact that the destruction of the vagus neuromeres materially modifies the respiratory activities. It apparently lowers the threshold that inhibits the "cross rubbing" or the normal respiratory movements, for if the vagus neuromeres are destroyed, or separated from the cord, gentle stimulation of the isolated gills with tactile, temperature, or chemical agents, starts the respiratory reflexes in them much more readily than in those not so isolated. Moreover, the forced "yawning" of the gills and the swimming movements, which represent a modified respiratory movement, disappear in those gills that are not directly connected with the vagus region. There is also a striking difference in the rhythm, range, rate, and spontaneity of movements between the gills cut off from the hindbrain and those that are united directly with it by one or both cords.

We may therefore conclude that each branchial neuromere contains only a part of a respiratory reflex center; and that the inhibitory control and the coordination, or unification, of the respiratory and other related gill movements is produced, in part, by the action of a special respiratory center located in the vagus neuromeres, and in part by the hypobranchial nerve and muscle.

The coordination of right and left sides is affected via the cross commissures.

Comparison with Vertebrates.—The results obtained from an experimental study of the respiratory centers of Limulus by Miss Hyde, Mr. Pearl and myself are in essential agreement, and they harmonize with Miss Hyde's work on other invertebrates and on the skate. In her admirable paper on the "Localization of the Respiratory Center in the Skate,"[1] she makes the following statements:

1. "Students working in my laboratory have proved that the relative position of the respiratory center in the central nervous system of the acrididæ is practically the same as in Limulus.

2. "The respiratory movements of the skate are segmental processes. The relationship of the respiratory organs and their segmental centers is not so obvious as it is in the lower forms (*i.e.*, Limulus). The developmental changes of shifting and consolidation have begun to mask the segmental connections of the different parts of the brain.

3. "Each ganglion, through special fibers and cells, controls the activity of the respiratory muscles with which it is segmentally related and is capable of initiating impulses that produce coordinated rhythmical respiratory movements.

4. "The medulla may be severed both from the cord and the regions of the brain anterior to it, or divided along its median suture, into two bilateral halves without impairing the functions of the respiratory center. Each half is capable of sustaining coordinated respiratory movements which part of the time may be different in rhythm on the two sides.

5. "Not only may either the spiracle and first gill arch, innervated by the seventh and ninth nerves, or the last four gill arches, innervated by the tenth, when isolated from the rest of the respiratory mechanism by a median and transverse section continue their movements, but all other than the special part of the respiratory center that controls these divisions may be destroyed, and either the four gill arches or the spiracle and first gill arch will still pursue their coordinated respiratory activity.

6. "The skate illustrates, in its type of respiratory center, an intermediate stage, between the simple segmental arrangement of the neurons presiding over the coordinated respiratory movements found among invertebrates, and the complex, modified, and specialized centers existing in higher vertebrates."

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[1] *Am. Journ. Physiol.*, 1904.

Thus the structural and physiological evidence indicates, beyond reasonabl doubt, that the vagus neuromeres (opercular and chilarial) and the five branchia neuromeres of the marine arachnids have become consolidated into a single, compac group, which in the vertebrates unites with the hindbrain to form the posterio part of the medulla.

VII. The Cerebral Hemispheres.

We have shown that in Limulus the hemispheres are primarily connecte with the sensory nerves of but one sense organ, the olfactory. They contain however, important secondary centers belonging to the visual and to the gustator organs. They are true cerebral centers, both in structure and function, an are similar to the primitive hemispheres of vertebrates, in that they regulate o control a large number of complex activities of which the several primary refle centers lie in the more remote parts of the central nervous system. They, fo example, exercise a tonic, or inhibitory, influence over the posterior part of th brain and the cord, and they are the source of impulses that check, or maintain, o coordinate, the walking and swimming movements, the leg movements in chewing and the purposeful movements of the legs in removing local irritants.

CHAPTER XII.

THE HEART.

I. Location of The Heart.

In the annelids and in some primitive arthropods, the heart is a straight tube lying on the opposite side of the body from the nerve cord, and extending practically from one end of the body to the other.

In the typical arachnids and in many of the higher arthropods (insects and crustacea), the primitive heart tube is shortened, in part by the conversion of the anterior end into a non-contractile aorta, and in part by the absence of the more posterior portion. The part that persists as a true pulsating heart is located, as a rule, in the first eight post-thoracic segments, that is in the vagal and branchial segments (Limulus and scorpion). (Fig. 3.) The heart may, in the earlier embryonic stages, extend into the sixth (scorpion) (Figs. 15 and 16, h^1), or into the fifth and sixth thoracic segments (Limulus). (Figs. 141 to 151.) But these more anterior heart segments are less highly developed, and may be reduced to a non-pulsating chamber that forms the proximal end of the aorta. The most voluminous part of the heart in the adult Limulus is its posterior part, opposite the middle branchial appendages, *i.e.*, between the third and seventh pair of ostia. (Fig. 1, *B.*)

The location of the heart is greatly influenced by, or itself controls, the location of the tracheal stigmata, the lung books, and the gills, since all these organs retreat from the anterior head region in nearly the same order, and usually occupy about the same post-thoracic segments. (Fig. 3.)

The gradual retreat of the heart and the respiratory organs from the head and thorax, and their concentration into a special group of post-thoracic segments may be readily followed to its culmination in such forms as Limulus, scorpion, and spiders. This striking process becomes especially significant when it is seen that in the vertebrates also these organs occupy, as nearly as one may determine, the same metameres. (Fig. 3, *D*, 308.)

II. Development of The Heart.

The location of the heart is determined by very remote but persistent conditions that affect the form and structure of the whole anterior part of the head and trunk. The principal event in these changes, which have been and are progressive, affecting the embryos of all segmented animals alike but in a varying degree, is the gradual disappearance from before backward of the segmented lateral plates of mesoderm belonging to the head and thoracic metameres.

In Limulus, in the scorpion, and in spiders, the surviving mesoderm of the cephalothorax consists almost exclusively of the six pairs of thoracic somites (head cavities) that give rise to the endocranium, the jaw and leg muscles, and the coxal glands (head kidney). (Fig. 138, *c.so.*)

There is a conspicuous territory, lateral to the cephalic lobes and thoracic appendages, that presents little or no indication of segmentation. (Figs. 15, 16, 19, 21, 31-33, 141-156.) It is covered by a thin layer of ectoderm with numerous underlying, oval cells, or fiber cells, that are eventually converted into muscles, or peculiar bodies resembling blood corpuscles. See vascular area (Chapter XIII, page 232.)

Back of this region the lateral walls of the embryo are divided into distinct segments. The peripheral margin of these segments, up to a comparatively late embryonic period, ends in a kind of germ wall, where the advancing sheets of ectoderm, mesoderm, and endoderm, or "yolk cells," merge into a common primitive-streak-like thickening. (Fig. 134, *g.w.*)

In the vagal and branchial metameres, the lateral plates of mesoderm consist of definite somatic and splanchnic layers, which enclose separate cœlomic chambers. In these regions, the fiber cells are absent, but numerous blood corpuscles are present, formed from liberated germ wall cells.

As the lateral ends of the mesodermic segments approach the hæmal surface, they separate from the germ wall, take on a crescentic form and, uniting with their mates of the opposite side, form the walls of a heart segment, or cardiomere. The cardiac ostia represent the spaces between the anterior and posterior walls of the adjacent segments. (Figs. 136, 137, *h.*)

Only the lateral plates of the sixth thoracic, the chelarial, opercular, and five branchial segments form definite, or permanent, cardiomeres.

The cœlomic cavities, at the hæmal ends of the segments that form cardiomeres, become partly shut off to form the pericardial chamber. The neural portion of the cœlom, belonging to the five branchial segments, forms the five great veno-pericardiac canals.

As the margins of the lateral plates advance, the cardiac nerves follow after, keeping close to the intersegmental thickenings of the ectoderm, thus reaching the heart tube opposite the intersegmental ostia, a position which they retain throughout life. (Figs. 115–151, *s.c.n.*)

As the lateral plates of the cardiac segments advance over the yolk, they expand, fan-like, into the unoccupied yolk surface in front and behind more rapidly than along the true parallels of the yolk sphere. The result is that when they unite on the hæmal surface, the anterior heart segments lie farther forward in the thoracic territory than their neural ends. This unequal displacement gradually carries the anterior end of the heart tube forward till it almost meets the anterior end of the forebrain, which is being crowded backward in the opposite direction. (Figs. 17, 26, 31, 138, 157.)

Thus in the later embryonic periods and in the adult, the original relation of the cardiomeres to the neuromeres is greatly disguised, except in so far as it is shown by the terminals of the segmental cardiac nerves.

Owing to the rapid concrescence of the more posterior lateral plates, the yolk ritory behind the tail end of the embryo is covered at an early period. Hence ther apical growth must take place in a vertical direction, or in such a manner to raise the apex of the tail off the surface of the egg. (Fig. 157, *D*.) Under se new conditions, the formation of both neural and hæmal surfaces takes ce at very nearly the same time, and under similar conditions. The heart es not extend into this region of the trunk.

It is thus seen that there are three natural divisions of the hæmal surface, ere the physical conditions are, necessarily, fundamentally different; namely, the cephalothoracic, in the abdominal, and in the caudal. The factors that duce or control these conditions are the relations that exist between the *rate* of ical and bilateral growth and the *volume* of the yolk sphere over which this wth is obliged to take place. (Figs. 17, 23, 34.)

Other Arachnids.—In the scorpion and in spiders (Epeira), the heart develops essentially the same manner as in Limulus. (Figs. 15, 16, 17, 20, 22.)

The details of the process of heart formation, as seen in sections, especially stages immediately preceding, and during the concrescence of the cardio-res, have not been worked out. They should receive more a careful study than have been able to give them.

Comparison of Vertebrate and Arachnid Heart.—A study of the early ges in the development of the heart in arachnids and primitive vertebrates ws that in both classes we are dealing with different phases of the same process. both classes, the heart is formed from the peripheral ends of lateral plates longing to a variable number of branchial metameres. (Fig. 32–33.) These ds grow in an anterior hæmal direction and concresce in the median hæmal rface, behind the anterior end of the forebrain and the cephalic navel, or ostoma.

In the arachnids, the heart is composed of a single layer of loose, striated astomosing muscle cells covered by a fibrous membrane. (Fig. 2.) The art tube is enclosed in a distinct pericardial chamber, the pericardial walls and walls of the heart being continuous at the anterior and the posterior ends, d at the points where the aortic trunks arise. (Fig. 118.) The heart is also ached to the pericardial walls throughout the entire length of the neural and mal surfaces by numerous connective tissue fibers and muscular strands.

The pericardium on the neural side forms a tough fibrous membrane of con-erable thickness, but it does not appear to contain muscular bands.

In the vertebrates, we may recognize the same kind of growth from the same gion to the same region. In its earliest condition, the vertebrate heart is an ial cord composed of a syncytial meshwork with irregular, interstitial spaces. Mollier.) This is the so-called mesenchematous stage of the amphibian and achian heart. At a later period, the primary cord is metamorphosed into a n-walled tube, the endocardial tube, and a muscular layer, or myocardium, ms around it. The two layers are separated by an extraordinarily wide space, bridged by fine fibers. This space ultimately disappears and the inner and outer tubes unite to form the definitive walls of the heart.

The volume and complexity of this primordial heart tube, its early appearance, and its wide separation from the myocardium are most remarkable. These conditions are not satisfactorily explained by the assumption that the cardiac endothelium is a secondarily acquired investment of a primitive muscular heart tube. Limulus has the largest and most complex heart of any living arthropod, and if an endothelium layer is present in any invertebrate, it should be present there, but a careful search in both adult and embryonic hearts failed to reveal any trace of such a layer. It is possible that in vertebrates, the cardiac and pericardiac walls of the arachnids have united to form a two-layered heart. But this would not account for the presence of the cardiac ganglia on the outer surface of the myocardium in vertebrates.

An alternative and preferable hypothesis would be to assume that the arachnid heart represents the ventricular portion in vertebrates, and that the posterior posterior portion of the pericardial chamber represents the thinwalled auricular or atrial portion and the venous sinus. (Fig. 44.)

III. CIRCULATION.

Arachnids.—The circulation in Limulus has reached a very high stage of development. Milne Edwards, in his classic work on the anatomy of Limulus, says, "The circulatory system of Limulus is more perfect and more complicated than in any other arthropod. The venous blood, instead of being distributed in interorganic lacunæ, as in the crustacea, is, through a great part of its course, enclosed in special vessels, having walls distinct from the adjacent organs, and often rising by branches of remarkable delicacy and passing into chambers, well circumscribed for the most part. The nourishing fluid passes from these reservoirs into the gills, and hence, by a system of branchio-cardiac canals, to the pericardial chamber and the heart, which is very large. It is then forced into the tubular, resisting arteries, which have a most complex arrangement, with frequent anastomoses and with terminal ramifications of marvellous tenuity and richness, and which can be followed even in the most delicate membranes."

The heart of Limulus is a voluminous muscular tube, ending blindly behind. It is provided with eight pairs of slit-like openings, or ostia, each opening guarded by two semilunar valves through which the blood enters the heart from the pericardial chamber. (Figs. 115-118.) The blood is pumped forward, and escapes through three pairs of aortæ, one pair of cerebral arteries, and a frontal artery. The three terminal arteries are guarded by one very large valve on the hæmal wall of the heart. The walls of the heart consist of a loosely felted mass of interwoven muscle bands, without any recognizable endothelium. (Fig. 2.)

Vertebrates.—Comparison of the circulation in Limulus with that in vertebrates is difficult. There are some striking resemblances and some equally striking differences.

The more general resemblance between the arachnid and vertebrate circu- on is shown by the direction of the blood currents and by the distribution of main arterial and venous trunks. (Fig. 118.) In Limulus, the blood flows erally and neurally through five pairs of aortic trunks. The anterior pair (internal carotids) go to the base of the brain, where they form a closed circle und the œsophagus *c.w.* (circle of Willis around the infundibulum, Figs. 43, and then backward along the brain and spinal cord. The following four rs are short trunks opening directly into two longitudinal channels in which blood flows forward *ex.c.* (external carotids) and backward (radices aortæ) o the unpaired aorta *ao.* Two large venous trunks (cardinals) collect the od from the anterior, lateral, and posterior parts of the body and conduct it to gills.

Important changes, however, have taken place that we cannot explain satis- torily. In vertebrates, the ostia have evidently closed without leaving any ce behind; and apparently one of the posterior pairs of the venous channels, . now opens directly into the posterior end of the heart, instead of into the icardial chamber (Cuvierian ducts). The relation of the gill chamber to the ta has also been radically changed.

The curvature of the vertebrate heart, its splitting at the posterior end telline veins), and its elimination from the trunk segments are more readily derstood. These conditions are undoubtedly produced by the "yolk navel," ich is in turn produced by the increasing size of the yolk sphere; that is, the diac ends of the lateral plates belonging to the branchial segments are forced the increasing size of the yolk sphere to reach the hæmal surface of the egg in gradually shortening area between the overgrowing, precocious forebrain and anterior margin of the uncovered yolk surface (yolk navel). (Fig. 17.) As s cardiac area is being continually shortened by the increasing precocity of the ebrain, and by the increasing size of the yolk sphere, and as the heart itself is antime increasing in volume, it is forced to assume the S-shaped loops so racteristic of vertebrates, in order to occupy the only space that is left open it. (Fig. 44.) These loops, once initiated, are accentuated by the unequal chanical stress of the enclosed blood current, which continues to sculpture and uld the heart walls, as a river its banks, till organic equilibrium is again ched in the four chambered heart of mammals.

The splitting of the posterior end of the heart in vertebrate embryos is the ect result of the increasing size of the yolk sphere, which favors the early crescence on the hæmal side of the head of the anterior cardiomeres, but delays concrescence of the more posterior ones, because they necessarily appear later n the anterior ones, and have to travel over the arcs of larger circles. Thus ununited posterior cardiomeres may form two divergent, pulsating vessels elline veins) along the sides of the yolk navel, long after the anterior ones have ted to form a single tube. (Figs. 17, 23.)

IV. The Cardiac Nerves and Ganglia.

Limulus gives us the most detailed available picture of the structure and relations of the cardiac nerves in invertebrates.

We recognize five longitudinal cardiac nerves extending either over the surface of the heart, or close to it; and seven or eight pairs of segmental or transverse ones, which connect the longitudinal nerves with the vagus or branchial neuromeres.

The Median Cord or Ganglion.—This is the primary nerve center for the heart. It is a median cord of ganglion cells, readily visible to the naked eye, lying on the hæmal surface of the heart and extending from one end of the heart to the other. (Fig. 115, *m.c.n.*)

It arises at an early embryonic period from a thickening of the overlying ectoderm. It probably extended, in primitive arthropods, the whole length of the body. In the forms I have studied (Acilius, Limulus, and scorpion), it extends, during the embryonic period, over a longer territory than the heart and appears to stand in the same relation to the hæmal surface of the body that the middle cord does to the neural surface. The median cord, therefore, belongs primarily to the overlying ectoderm. It lies on the outer surface of the myocardium, and is not at any point actually imbedded in it.

All the ganglion cells of the heart lie in the median cord, or at the roots of the strands that arise from it.

The cardiac plexus is an irregular meshwork of nerve fibers, arising from the median cord and spreading over the hæmal surface of the heart. The strands diminish in caliber and finally form slender bundles that penetrate the walls of the heart, where most of them appear to end in minute end plates, on the surface of the muscle strands.

The Lateral Cardiacs.—Many of the larger strands of the plexus unite on the sides of the heart to form distinct lateral nerves, easily visible to the naked eye, *l.c.n.*

The median cord, the plexus, and the lateral nerves stand out with great distinctness when treated with methylene blue, and they may be easily studied under high powers, in preparations of the whole heart of either the young or the adult animal. The lateral cardiacs never contain ganglion cells.

The pericardial nerves extend lengthwise on the side walls of the pericardial chamber, breaking up, at either end, into minute fibers, the terminations of which could not be certainly ascertained, *p.n.*

The Segmental Cardiacs.—There are seven or eight pairs of segmental cardiac nerves, *s.c.n.* $^{7-13}$. They arise from the seventh to the thirteenth hæmal nerves inclusive, in close connection with the rami communicantes of the hypobranchial nerves. (Fig. 59.) They extend to the hæmal side of the body, giving off numerous small branches to the neighboring muscles and integument. The five branchial ones turn inward, giving off rami communicantes to the peri-

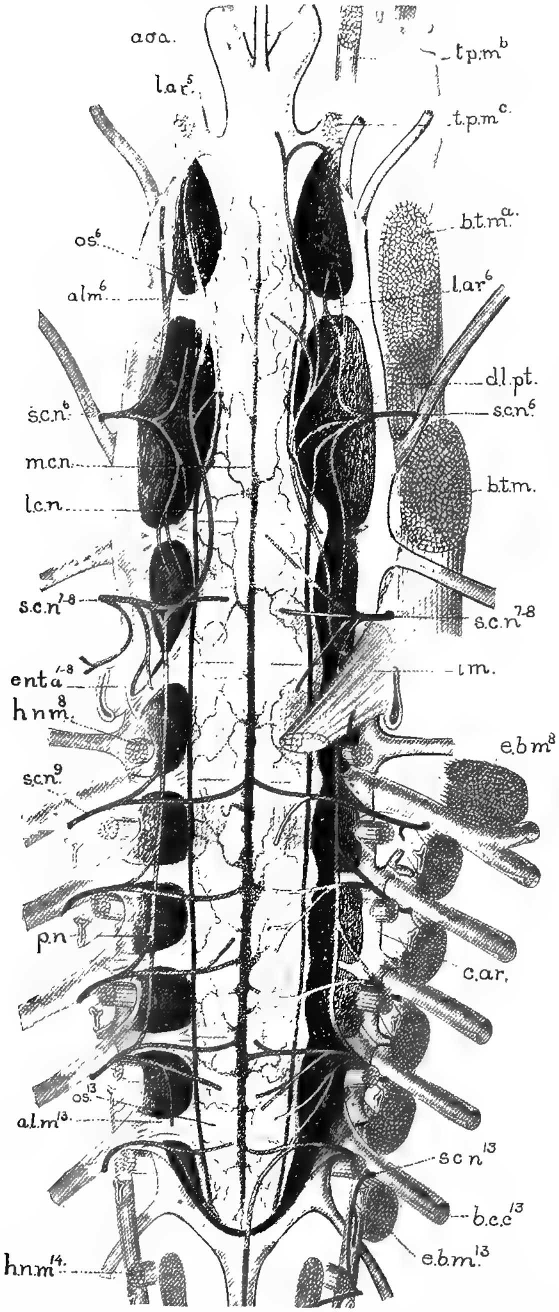

FIG. 115.—The heart and adjacent organs of an adult Limulus, showing the ostia; principal blood-vessels; ganglionated median nerve, *m.c.n.*; the cardiac plexus; the pericardial nerves, *p.n.*; the lateral, *l.c.n.*, and segmental cardiacs, *s.c.n.* 6–13. From Patten and Redenbaugh; slightly modified.

cardial nerves; some of them unite with the median cardiac, in the region of the last five pairs of ostia. (Figs. 115–117.) The segmental cardiacs of the seventh and eighth, or vagus neuromeres, unite to form one large nerve which anastomoses with the pericardial trunks, but neither it, nor the sixth, could be traced directly to the median cardiac.

* * * * * * * * *

The entire system of cardiac nerves probably represents a modification of a primitive system of longitudinal and circular integumentary nerves distributed to the skin, muscles, and other organs on the hæmal surface of the body. With the reduction of the primitive heart to a shorter, more compact organ, lying in the posterior thoracic and branchial regions, there was a corresponding reduction in the length of the several longitudinal nerves and in the number of pairs of segmental cardiac nerves uniting the heart with the nerve cords.

In some arthropods it is probable that there is some connection between the cardiac and the stomodæal nerves. (See Polici, Naples Mittheilung, 1908, and other papers by the same author.) Such a connection, if it still exists in Limulus, must be very minute, and can only be detected by a special application of the methylene blue method.

V. THE MINUTE STRUCTURE OF THE CARDIAC GANGLION.

Nerve Cells.—We may recognize in the median cardiac nerve three different kinds of ganglion cells: *a.* Small, multipolar cells that stain very quickly and deeply in methylene blue, and that form a thick, irregular covering, several layers deep, over the outer surface of the cord. (Fig. 116, *gn.c'*.) In exceptional cases, they extend for some distance on to the larger, lateral branches of the plexus, where they form irregular flakes or clusters; but I have never seen any isolated ganglion cells on the lateral, or on the pericardial trunks, or on any of the smaller strands of the cardiac plexus. I doubt very much whether any ganglion cells exist in the heart outside the median cord, or the roots of the larger strands near where they leave the cord.

In the adult, these cells are about 32μ. in diameter. They are pear-shaped, the cell body giving rise to many fine dendrites which form dense felted masses of varicose fibers. One can usually distinguish among them one long fiber, extending inward, diagonally across the inner surface of the median cord, and out of it, through one of the branches of the other side.

These cells are very numerous in the heart segments belonging to the middle branchial neuromeres, where they form a thick and continuous but irregular coating to the median cord.

Toward the anterior end of the heart, the cord becomes much smaller, and in the first three or four segments, these cells are either absent or reduced to a few, scattering clusters, usually located opposite the ostia. *b.* The second kind, *Gn.c.*, consists of giant bipolar cells, which in the adult are about 140 x 100μ.

They occupy the axial portion of the median cord, and are confined to the middle and the posterior segments, none having been observed in the first three, or in the last segment.

The body of these cells is seldom fully impregnated with methylene blue. The nucleus, central protoplasm, and spiral fibers may be faintly outlined, in sharp contrast with the small, almost black, multipolar cells. Their enormous axis cylinders, however, are usually deeply colored. They extend forward and backward, apparently the whole length of the cord, bending from side to side, and

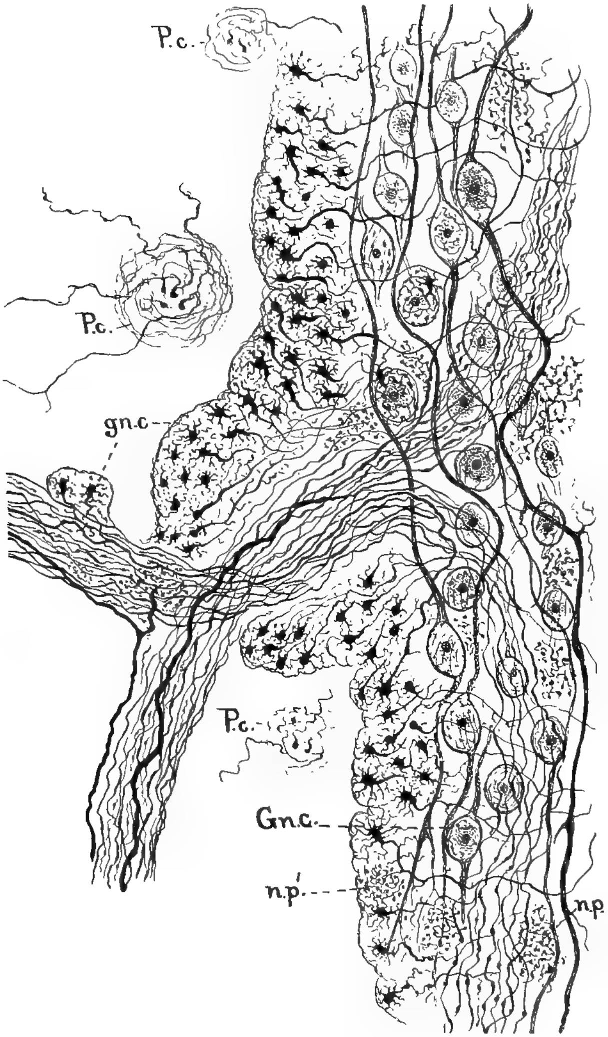

FIG. 116.—The lateral margin of the ganglionated median nerve of the heart of an adult Limulus, from the region of the sixth cardiomere; it shows the two kinds of ganglion cells, *G.n.c.* and *gn.c.*; the clusters of neuropile, *n.p.*; and the paccinian-like terminals, *P.c.*, imbedded in the muscular substances of the heart. Methylene-blue preparation.

giving off, from time to time, branching collaterals. Both collaterals and axones appear to pass out of the cord, into the lateral plexus.

The axial portion of the cord also contains irregular masses of **neuropile,** but whether they are derived from the axones of the giant cells, or from those of the multipolar ones, or from both, could not be certainly determined. When too many fibers are not colored, one may see irregular baskets of intertwining fibrils at frequent intervals all through the thicker parts of the cord, and in the larger strands of the plexus, *n.p.* Some are apparently free terminal arborescences, others form a basket work around the body of the giant cells; or several multi-

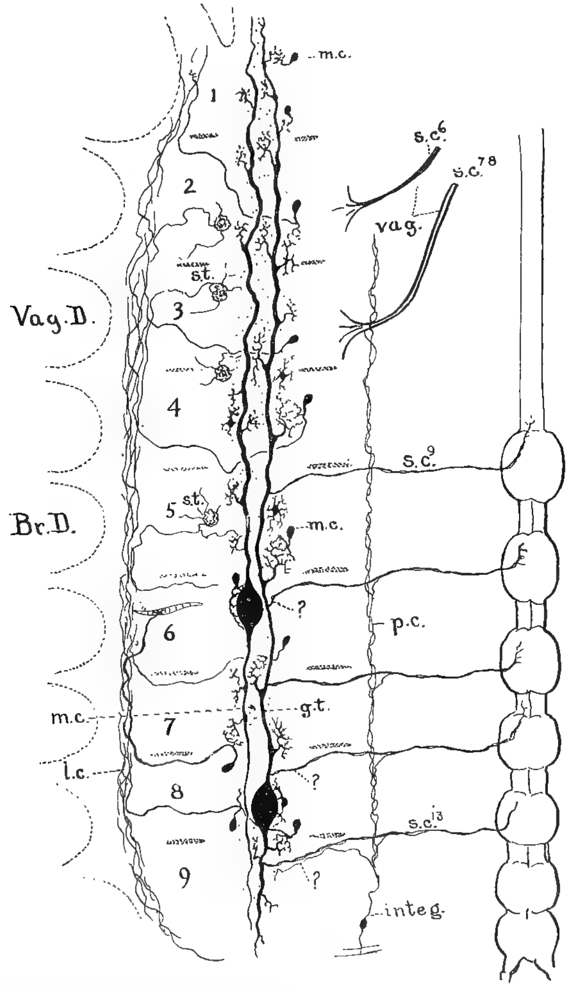

FIG. 117.—Diagram illustrating the distribution of the cardiac neurones and their probable relations to the branchial and vagus neuromeres. The heart and the nerve cord are shown projected onto the same plane *Vag. D.*, vagus division; *Br. D.*, branchial division of the heart.

olar cells, together with their dendrites, form enveloping baskets around the ody of the giant cells.

c. The third kind of cells consists of small, bipolar neurones, found in the rst three or four segments of the heart. They are not numerous, and in some ases they appear to be absent. They resemble the giant cells in shape, but are maller and are deeply stained in methylene blue.

In the young Limuli, two or three inches long, the small cells are more clearly ear-shaped and have fewer dendrites, the rounded body projecting freely from he sides of the cord, to which it is attached by one or two branching processes.

Motor Terminals.—The larger strands forming the cardiac plexus lie on he outer surface of the heart; the smaller branches gradually penetrate between he muscle bundles to the deeper layers, where one may frequently see them erminate in the characteristic motor end plates.

Sensory Terminals.—Toward the anterior end of the heart, on either side f the median nerve, there are peculiar, spherical masses dimly visible, imbedded n the muscle layers, that probably represent free sensory terminals. Two or hree nerve fibers approach these bodies and form there concentric coils of fibrillæ, ith two or three thicker vertical fibers in the center of the coils, *P.c.*

It is not possible to distinguish the fibers that enter the heart from the segmental cardiacs from those that arise in the median nerve cord. All the ganglion ells increase greatly in numbers with age.

Cardiac Ganglia in Vertebrates.—The great size of the median cardiac erve of arthropods and its conspicuous origin from the overlying ectoderm led me to look for a similar origin of the cardiac ganglia in vertebrates.

In trout embryos, in frog embryos (Rana septemtrionalis) of seven millimeters, nd in chick embryos, from thirty to forty-eight hours, there is a thin, longitudinal ord lying on the hæmal surface of the heart, which resembles the median nerve n the heart of Limulus, and which appears to be the anlage of the cardiac ganglion. n the 30–36 hour stages of the chick, it extends along the surface of the auricles nd ventricles for about 150 mm., and is connected, here and there, by swollen trands, with the overlying ectoderm.

I was not able to follow in a satisfactory manner the history of this structure, ut it seems to me probable, from its general appearance and location, that under uitable conditions it will be possible to trace its development into the cardiac anglia of the adult.

VI. Experiments on the Heart.

In my notes from the summer of 1897, I find records of observations to the ffect that the isolated heart continued to beat for many hours, either in salt soluon, or in a moist chamber; that small segments of the heart would continue to eat, provided a piece from the posterior part of the median ganglion was atached; and that separate pieces that did not contain this part of the median nerve, or from which it had been removed, ceased to beat; and finally that the anterior end of the median nerve (from the first three segments) did not control the heart beat of its territory, since, in its absence, the first three segments would continue to beat provided there was a nerve-fiber bridge to the posterior part of the median ganglion.

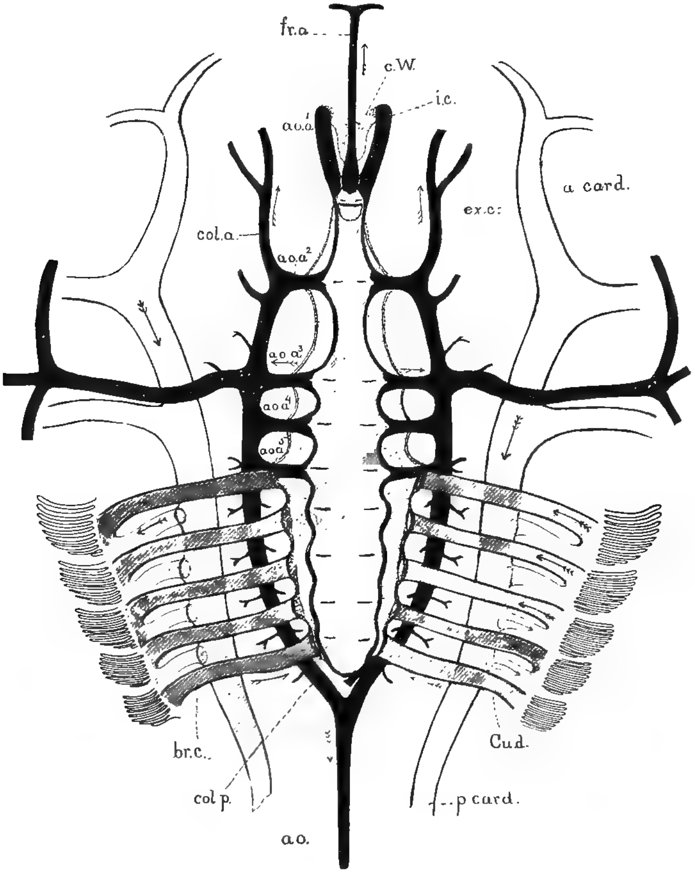

Fig. 118.—Diagram of the heart, pericardium, and principal blood-vessels of Limulus. Arterial trunks in black; veins in half tone. Seen from the hæmal surface.

The following is a record of some experiments made three years later, by R. Pearl, a student in Dartmouth College working under my direction:

A. July 27, 1900. The heart was exposed and cleaned of connective tissue.

a. Stimulation of the median longitudinal nerve with a weak current caused one long continuous systole. *b*. Stimulation of the lateral cardiac nerves caused an increase in the strength of the systole and in the rapidity of the beat. The rhythmical beat continued during the stimulation. On removing the electrodes a complete diastole followed. During the stimulation there was no complete relaxation of the heart muscles between systoles. *c*. Stimulation of the gmental and the pericardial nerves gave no results. *d.* The median cardiac erve was now cut (transected) about one-third the distance from the anterior id of the heart about in the middle of the third cardiomere. Rhythmic pulsation that part of the heart in front of the cut stopped for half an hour. At the end this time the anterior part began to beat again. *e.* Dissected out, and removed, piece of the median cardiac nerve, about three-fourths of an inch long, from the iterior end of the posterior part left after the first operation. All pulsations of ie section of the heart without any median nerve (*i.e.*, the fourth cardiomere, pproximately) immediately ceased, while the parts in front and behind connued to beat rhythmically. After an hour, the fourth cardiomere recovered nd began beating with a rhythm of its own, distinct from that of the posterior art of the heart. *f.* Stimulation of the lateral nerve of the fourth cardiomere, bout one hour after operation *e*, caused one strong contraction of that part of the eart instead of the increased beat, as before. Stimulation of the lateral nerve f the posterior cardiomeres gave the same results as before, *i.e.*, acceleration and ugmentation of the beat. *g.* Stimulation of the hæmal nerves of the branchial euromeres, or of the branchial nerves, or of the ventral cord itself, produced no fect on the heart beat. Stimulation of a lateral cardiac nerve, after removal of ie median nerve, caused a contraction on the stimulated side only.

B. **Rhythm of Heart Beat after Stimulation.**—Counts were made of the umber of beats per minute of the normal unstimulated heart, and also during imulation of the various nerves. The results will be presented in tabular form.

a. Unstimulated, 32 beats per minute.

Electrodes on the median nerve, 24 beats per minute.

Electrodes on a lateral branch of the median nerve, 12 beats per minute.

Electrodes on a lateral branch of the median nerve, 14 beats per minute.

Stimulation of the lateral cardiac nerve caused a contraction of the side of the eart stimulated, but did not affect the rhythm of the opposite side.

b. Unstimulated, 24 beats per minute.

Electrodes on median nerve (near middle of heart) 8 beats per minute.

Electrodes on median nerve (posterior end), 20 beats per minute.

Electrodes on lateral branch of median nerve, 6 beats per minute.

c. Placing the electrodes underneath the median nerve near the middle of ie heart, inhibits the beat of the whole heart.

d. Placing the electrodes so far as possible on the muscles only of the heart, oes not perceptibly affect the beat. Stimulation of the anterior abdominal erves, or the abdominal neuromeres does not cause any perceptible change in the hythm.

Carlson (*Am. Journ. Physiol.*, 1894 and 1905) has made more elaborate exeriments on the heart of Limulus than we have, but so far as our experiments and is overlap, they are in agreement on the most important points. Carlson, howver, was not aware of certain details in the histological structure of the median erve, as indeed we were not at that time, which are essential to the interpretation of the experiments. Although he appears to have been influenced only by his experiments on the living heart of Limulus, he has come to conclusions similar to our own. He says (*Am. Journ. Phys.*, 1905, p. 472):

"We find in the heart of Limulus a condition similar to that in the vertebrate heart, the venous end of the heart exhibiting the greatest automatism, the aortic end, the least, or no, automatism." There is another similarity between them, in that "the regions of the heart exhibiting the greatest automatism have the greatest number of ganglion cells." "And still another similarity in the distribution of the ganglion cells with reference to the myocard." "In the vertebrate heart, they are situated, in the main, on the surface of the myocard, and this is also their position in the Limulus heart."

VII. THE HEART. SUMMARY AND CONCLUSION.

Interpreting the preceding data on the morphology, minute structure, and the activities of the heart, we may draw the following conclusions:

1. The heart of Limulus may be divided into two parts: a. An anterior, or vagus division, consisting of three cardiomeres derived from the mesodermic segments of the sixth, the seventh, and the eighth metameres, *i.e.*, from the sixth leg, chelarial, and opercular metameres. The segmental cardiacs of this division are united with the pericardial nerves but not directly with the cardiac ganglion. The vagus division of the heart has a greatly diminished ganglionic center and is devoid of the giant ganglion cells. It exhibits little or no automatism. b. The posterior, or branchial division of the heart is derived from the mesoderm of the five gill-bearing metameres. Each of these cardiomeres is connected with its corresponding neuromere by a segmental cardiac nerve, from which branches go to the cardiac ganglion and to the pericardial nerves. It contains the greater part of the small ganglion cells and all of the largest bipolar cells. It exhibits marked automatism. In the dead heart there is a perceptible constriction between the vagal and the branchial divisions.

2. The vagal and the branchial divisions of the heart in Limulus are comparable with the bulbar and ventricular divisions of the heart in vertebrates. That the heart, as a whole, is comparable with that of the vertebrates is shown by the fact that both organs arise on the hæmal side of the head by the concrescence of mesoblastic segments derived approximately from the same metameres. In both cases, the absence of the cardiomeres in the forebrain region, and in the greater part of the hindbrain region, may be traced to the absence there of the segmental lateral plates of mesoderm.

3. The giant bipolar cells of the branchial division of the heart of Limulus are the primary agents in producing the rhythmic beat of the entire heart. Any part of the heart separated from these cells ceases to beat. When the heart is stimulated by laying the electrodes on the under side of the median nerve, the only place where the giant nerve cells are fully exposed, the heart at once ceases to beat.

4. We may picture to ourselves, for the sake of an initial working hypothesis, that the elements have some such arrangement as shown in Fig 117. It is assumed; *a.* that the giant bipolar cells are the inhibitory agents and the centers from which the rhythmic impulses radiate to all parts of the heart; *b.* they are probably connected with the adjacent dorsal and lateral integument through branches of the segmental nerves, and with the ventral cord, via the five or more segmental cardiacs. The latter probably consist, in the main, of axones from the giant cells, and possibly of axones from cells located in the branchial neuromeres; *c.* the dendrites of the giant cells are probably confined to the median cord; they do not appear to extend into the plexus on the hæmal surface of the heart, or into the lateral nerves; *d.* the small multipolar cells are probably motor cells, distributing their fibers through the main branches of the plexus to the lateral nerves, and then forward (and backward?) to their terminals in the muscle cells of the heart; *e.* afferent sensory fibers probably run from their paccinian corpuscle-like terminals either directly to the median cord, or to it via the lateral nerves.

On these assumptions, we may explain the experimental results as follows:

Placing the electrodes on the lateral nerves, or on the median surface of the median one, or on the main transverse branches of the plexus, inhibits the heart-beat to a varying extent because of the variable number of accelerator or inhibitory fibers that are contained in a given nerve branch, or of the number of small ganglion cells overlying the larger ones in the median cord. The automatism of the branchial section of the heart is due to the presence of the giant bipolar cells, from which the rhythmic impulses pass in an axial direction along the giant nerve tubes the whole length of the heart. From these tubes numerous collaterals are given off right and left, apparently connecting with the motor cells which are found along the entire length of the heart, but less abundantly at the anterior than at the posterior end. The giant cells are covered on the hæmal and lateral sides by thick layers of motor neurones, hence they can be reached only from the under side of the median cord. When the cord is stimulated from that side complete inhibition of the heart-beat follows.

It is difficult to understand why stimulation of the vagus and branchial neuromeres and of the segmental cardiacs has so far produced no noticeable effects. It is probable that a more careful investigation of this point will furnish important results.

THE NERVOUS SYSTEM AND SENSE ORGANS OF VERTEBRATES AND ARACHNIDS.

General Summary of Chapters I-XII.

1. The foundations of the nervous system of vertebrates are laid in the trochosphere or cœlenterate stages, and the most important steps in its early evolution were made in the rotifers, phyllopods, marine arachnids, and ostracoderms.

2. In all segmented animals the central nervous system is morphologically identical.

3. In all segmented animals the three primary axes of bodily growth have the same relation to the neural axis, *i.e.*, apical growth extends in a cephalo-caudal direction parallel with the neural axis; transverse growth extends right and left at right angles with the neural axis; and radial growth extends in an ovocentric direction approximately at right angles to the other two.

4. The three axes of morphological and functional differentiation are coincident with, and follow the same direction as the axes of growth.

5. The axes of growth and differentiation lead in directions of diminishing returns.

6. In embryonic growth the ratio between the relative rate of apical and bilateral growth, and the radius of the yolk sphere determines the relative time, place, and conditions for the formation of the organs on the hæmal or aboral surface of the body.

7. The volume of the yolk sphere has been the most important variable factor in modifying the mode of growth and the form of the body in the segmented animals. Its increasing volume in the rotiferphyllopod-arachnid phylum has in the higher arachnids and in the vertebrates greatly exaggerated the differences between the neural and hæmal surfaces, and has been the chief cause of the linear distortion and profound modification of the hæmal portions of the cephalic metameres.

8. In the phyllopod-arachnid-vertebrate phylum the body grows by the spasmodic generation of new groups of metameres at the caudal end of the body. The new metameres of each generation are at the outset unlike those of the preceding generation. Each generation of metameres gives rise to one of the primary functional and morphological subdivisions of the body.

9. Cephalic organs and cerebral centers are laid down at the same time and in the same order, each reflecting the condition of the other. The linear arrangement of the principal functional centers in the arachnid brain was determined by the historic order in which the principal subdivisions of the body were generated during the phylogeny of the phyllopod-arachnid stock. The cephalo-caudal order in which the principal functional centers are arranged in the vertebrate brain indicates the historic order in which the corresponding peripheral organs were evolved in the arachnids.

10. The distribution of functions and organs is determined primarily by the nature of apical growth and by the conditions under which it takes place. It is subject to a progressive readjustment due to a give-and-take exchange between the new and the old organs in response to the physical demands incident to increased size, and to other conditions created by growth. The actual arrangement has been worked out subject to the following factors: 1. The necessary precedence in functional activity; 2. priority in origin and the consequent preemption of territory; 3. the demand for a location essential to effective action.

11. The transfer of functional centers always takes place in a cephalo-caudal direction. The process consists in the progressive elimination of muscular, excretory, nutritive, and structural tissues from the anterior end of the head, and the corresponding increase of the same structures at some point farther back, the degree of elimination varying, in the main, with the linear and lateral location of the parts concerned. On the other hand, the primary sense organs, visual, gustatory, and olfactory, and their cerebral centers, never shift their relative positions, and steadily increase in volume and structural detail.

Hence there are three factors that determine the character of the anterior end of the body; 1. the progressive elimination of the more lateral, non-sensory parts; 2. the increasing development of the more axial sensory and nervous ones; and 3. the establishment of nervous continuity between the old nerve centers at the anterior end of the body and the new ones at the posterior end as fast as the latter are formed. Hence the anterior end of the body throughout the arachnid-vertebrate stock tends to become more and more sensory, coordinating, and administrative in character, while the posterior portion serves as the site for the more modern and the more highly specialized functions.

12. From the very earliest stages in the evolution of metamerism, the forebrain region has been devoted to vision and coordination. The first group of metameres to appear behind or around the mouth (diencephalic and mesencephalic) were devoted to locomotion and to tasting, seizing, chewing, and other ingestive functions. With the increased size due to the addition of a new group of metameres, respiratory and circulatory organs became essential and they made their appearance behind the ingestive region. Thus the three main functional divisions of the head, the visual and coordinating, the gustatory and ingestive (including the primordial endocranium for the attachment of chewing muscles) and the cardiac and respiratory regions were established according to the historic and inherently necessary order of their evolution. They were elaborated and still further emphasized by the elimination of all other tissues and organs foreign to these functions.

13. All the segmental sense organs had primarily some of the characteristics of visual organs. They were located along the lateral margins of the medullary plate in the fore- and midbrain regions. Throughout the entire phyllopod-crustacean-arachnid-vertebrate stock two pairs of ocellar placodes are united to form a true parietal eye. The retinal placodes of the parietal eye are located at the dilated distal end of the vesicle; the proximal end is usually tubular and opens either on the outer surface of the head, or into the forebrain vesicle.

Two other pairs of placodes form the stemmata, or frontal ocelli of insects, or the frontal organs of phyllopods and various crustacea. In Limulus (probably also in trilobites and merostommata) they become metamorphosed into true olfactory organs and represent the preliminary stage of the olfactory organs of vertebrates.

The lateral or compound eyes of arthropods belong to the most posterior procephalic, or first post-oral segment. They become involved during the embryonic stages in the palial fold that grows over the forebrain, giving rise, in the vertebrates, to the lateral eye retinas.

The auditory organs arose from a large midbrain placode near the base of the fourth pair of thoracic appendages. (Limulus.)

14. The parietal eye is the most ancient of all cerebral sense organs and attains its characteristic structure and location at a very early period in the history of the arachnid phylum. It is usually functional before the lateral eyes have made their appearance.

The site of the locomotor organs follows the center of gravity backward, those in the oral region giving place to those of the mesocephalon; the latter to those in the postcephalic and caudal regions. The excretory, digestive, and reproductive organs follow in the same direction. (Fig. 308.) Their nerve centers are of small size and their change of location does not visibly modify the character of the nerve cords.

The lateral eyes are the next oldest. They are highly developed and important functionally in the adult stages of nearly all the higher arthropods. During the ostracoderm stage they were involved in the cerebral vesicle, and for a time became practically useless, the parietal eye being the only one that was in a position to serve as a visual organ. In the true vertebrates the lateral eyes regained their function, and that of the parietal eye gradually disappeared.

The olfactory organ, while derived from organs probably as old as the parietal eye, did not take on the morphological characters or the function of an olfactory organ till the highest stages in the evolution of the marine arachnids were reached.

The auditory organ is the most recently acquired. It is dormant in the arachnids, and apparently begins its period of growth and functional activity in the lower vertebrates. It is the only one of the primary sense organs that shows a notable increase in morphological complexity and in the range of its functional activities during the evolution of the vertebrates.

15. The special cutaneous organs of arthropods include two distinct kinds, the taste organs and the slime buds. Both sets of organs perform various functions and initiate various reactions, but all of them may be properly called taste organs, since they react to a variety of chemical substances, either in the food or in the surrounding media. Both kinds may be widely distributed in various parts of the body, but those belonging to this category are sharply localized, and are included, either separately or combined, in segmentally arranged fields that are provided with special nerves and special tracts and centers in the brain.

In Limulus, taste organs are found in the mandibles of the thoracic appendages, except the first and last pair, in the chilaria, and the largest field of all in the flabellum. In the scorpion they are found in the maxillaria, the genital papillæ, and the pectines. In the mandibles of Limulus, the taste organs and slime buds are located in separate fields, and both sets on stimulation produce chewing reactions. In the scorpion the genital papillæ and the pectines illustrate the conversion of entire appendages into complex sense organs. The taste organs and slime buds increase by division; the former may thus give rise to numerous sensory cells arranged in long, straight lines.

The segmental taste organs and slime buds of arachnids are the forerunners of the special cutaneous organs of vertebrates; the taste organs of the arachnids corresponding with the taste buds of the vertebrates, and the slime buds probably in part with the neuromasts or lateral line organs. The fields of taste organs and slime buds of the arachnids are represented in vertebrates by the placodes which initiate a line of taste organs, or of neuromasts. The structure of the organs, the number and location of the principal lines of organs in the embryo, their relation to peripheral nerves, and to the tracts in the brain, are in the main very similar in both vertebrates and arachnids. (Figs. 58 and 65, *g.n.r.*)

In Limulus the enormous integumentary nerve of the cheliceral segment, Fig. 70, deserves special attention. It resembles the ramus lateralis accessorius, which in ganoids and bony fishes is distributed to the back, tail, and fins, wherever taste buds are found (Johnston). Unfortunately the character of the terminals to this remarkable nerve in Limulus was not determined; but it is unquestionably a purely sensory nerve, supplying the neural surface of the entire posterior part of the body. Its ramification is specially rich around the entrance to the gill chamber.

16. The general cutaneous sense organs in Limulus are scattered over all parts of the body. They represent various minor modifications of the slime buds, taste buds, and of free nerve endings, and serve either as tactile, temperature, or chemotactic organs. They are connected with a loose subdermal nerve plexus which, in the thoracic and abdominal shields, is derived from the ramifications of the hæmal nerves; that on the surface of the gills, operculum, and terminal joints of the leg is derived from the ramifications of the neural nerves.

The central terminals of the general cutaneous components of the hæmal nerves end in a large tract on the median side of each crus, hæmal to the gustatory tract. (Fig. 56, *G.c.tr.*)

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17. The peripheral nervous system of arachnids attains a condition similar to that in vertebrates. There are two main systems of mixed nerves, the neural and hæmal. The neural nerves have enormous ganglia which develop independently of the neural axis; the hæmal nerves are without ganglia. Both sets remain separate in the anterior head region, but in the posterior head region, and in the trunk, they may unite to form nerves of the spinal cord type, that is, single nerves with separate roots, ganglionated neural ones and non-ganglionated hæmal ones.

18. Further specialization takes place through the separation from the primitive segmental nerves of those components that have similar peripheral and central terminals, and their union to form a new system of nerves with a common central

tract and a common centre, *e.g.*, the segmental gustatory nerves. Or the nerves from a special group of neuromeres may break up into several sets of components which then reunite to form new groups. For example, in the vagal and branchial complex of arachnids, which represents seven neuromeres, we may recognize the following groups of more or less independent components: *a.* the combined, almost exclusively sensory nerves of the first two or three vagal appendages (scorpion); *b.* and *c.* the cardiac and intestinal components; *d.* the mixed nerves supplying the appendages, gills, lung books, or operculum; and *e.* the combined motor components that constitute the hypobranchial nerve which supplies the compound hypobranchial muscle derived from all the branchial and vagal segments.

19. The extent to which segmental nerves have been reduced to a single set of highly specialized components, or broken up into several independent sets of components, decreases in a cephalo-caudal direction. For example, each of the three forebrain neuromeres in arachnids contains only the purely sensory nerves of the olfactory organ and of the parietal eye and lateral eyes. In the six following thoracic segments the nerves are largely sensory, the motor components being reduced to the relatively small nerves supplying the muscles of the legs and those passing from one side of the carapace to the other, or to those holding the endocranium in place. All the procephalic and mesocephalic hæmal muscles have disappeared.

20. A still further reduction of motor components took place in the vertebrate brain with the fusion of the anterior thoracic appendages to form the immovable anterior arch of the mouth (pre-maxillæ and maxillæ); with the reduction of the free thoracic appendages to external gills; with the fixation of the endocranium by its fusion with the exoskeleton; and finally with the atrophy of nearly all the branchial musculature in the air-breathing vertebrates.

21. The most important events in the conversion of the arachnid type of brain into the vertebrate type were the transfer of the lateral eye placodes to the interior of the cerebral vesicle; the closing of the neurostoma by the closure of the medullary plate; the transfer of the optic ganglia to the roof of the midbrain; and the union of the branchial neuromeres with those of the vagus region.

CHAPTER XIII.

EARLY STAGES OF ARTHROPOD AND VERTEBRATE EMBRYOS.

I. Primary Causes of Differential Growth.

Before we attempt to explain the meaning of the various embryonic stages in arthropods and vertebrates, it is desirable to reach some conclusion, if possible, as to the general nature of the causes, or conditions that are likely to control the initial stages of growth. Even if it is quite impossible to detect the real causes, it is well to make perfectly clear, merely as an aid to exposition, the mental attitude in which the writer approaches his problem.

It is apparently assumed by some authors that differential growth takes place in developing eggs because in some predetermined manner certain agents distribute to their proper places preformed materials, which then develop into definite organs because they are made of the same material from which those organs arose.

Such artificial explanations are now found only in the biological sciences and are to be regarded as the decadent offspring of the doctrine of special creation. They are pernicious, because the clever juggling of words and images fixes the attention solely on the imaginary structure of imaginary things, thus leading one to overlook the sequence of form and of physical and chemical conditions that constitute the only measurable or accessible properties of living things.

An erratic boulder does not grow into a mountain like the one from which it came, even if it is made of precisely the same kind of materials. And even if some metaphysical geologist should succeed in picturing a planatasmal geophore that was a mountain in miniature, or that stood for one, or represented one, or was capable of becoming one, it makes little difference what expression one uses, the real problem, and the only one of interest to a matter of fact geologist, would be: What was the sequence of events in the evolution of that mountain? What were the conditions immediately preceding each step in the process?

The biologist should approach the problems of growth and morphology in the same spirit. Let him study the changes of form and action as they occur, with the hope of discovering a sufficient cause for each one. He should not use omnipotence, either of a creator, or of heredity, or of chromosomes, to short circuit the process of evolution.

I shall therefore throw aside, for the time being, all preconceived ideas as to the ultimate composition of the ovum, or of the growing embryo, and shall consider, as they appear at successive periods, some of the simpler physical and chemical conditions likely to be determining factors in differential growth. It is assumed that under certain fixed uniform conditions protoplasm, or some of its constituents, has the property of growing, that is of producing more material like itself; the growth taking place in the three planes of space at a uniform rate and to an unlimited extent. If any deviations from these results occur, it must be due to new conditions that arise either outside the growing mass, or which are locally created within the mass by growth itself.

It is evident that a single cell, or a group of like cells, endowed with this initial power of self increase, in the very act of growing necessarily creates internal, locally diverse physical and chemical conditions; and that these unlike conditions will be arranged in regular graded zones. As it appears that these zones of unlike conditions, in the main, coincide with the zones of histological and morphological differentiation, they may be fairly assumed to be the principal causes of that differentiation. That is, it appears that progressive differential growth is self-creating, and that homogeneous, or undifferentiating growth is an impossibility.

The details in the end results may be colored or modified by the presence at the outset of foreign materials, or by changes in the external environment, but they appear to play such a subordinate part, compared to the internal conditions created by growth itself, that for the present they may be neglected. The medium in which growth takes place can never be homogeneous as regards the intensity, or the location of the sources of light, heat, gravity, and chemical agents, so that each part of a growing mass will have its own particular relations to its surrounding medium. The rate of growth, and its character will be variously modified by these local conditions, so that neither a homogeneous body, nor a spherical body could be produced, and, so far as we know, never is produced. The inevitable result is some modification of a sphere consisting of concentric shells or strata, each stratum having various local modifications of its surface.

If our initial mass of protoplasm begins its growth laden with dead or inert materials, or on the surface of a yolk sphere, diversified local conditions are created at each stage of growth that have a very definite directive influence on each subsequent stage of growth.

It has long been recognized that the presence of yolk modifies the rate of cell division and the character of the cells produced. But it has not, I believe, been heretofore recognized that: 1. Radial symmetry is an inevitable result of the physical conditions created by growth; 2. that the morphological structure of a large class of animals is profoundly modified by the prevailing volume of the yolk sphere over which the initial growth takes place; 3. that the gradual increase in volume of the nutrient surface, accompanied by apical growth, necessarily results in an unlike bipolar concrescence, bilateral symmetry, and a linear sequence of unlike physical conditions, that in turn produce a linear series of unlike organs; 4. that the overlying strata formed in a spherical mass of cells, or in a disc growing on a nutrient surface, such as ectoderm, somatic and splanchnic mesoderm and endoderm, are the expression of the various physical conditions successively created by growth. In other words, the whole triaxial framework of any animal may be regarded as the inevitable expression of conditions successively created by growth, or by the conditions under which growth takes place. External environment and natural selection have nothing to do with these conditions, neither does "heredity" initiate, or control, or create them; it merely imitates or repeats them. Hence, as a creator of the foundations of organic structure, we may eliminate natural selection, and external environment, together with heredity and all its ministering tribe of "corpuscles," as we have eliminated the Gods of Love, of War, and of Peace.

Let us illustrate our meaning more specifically. If cell division takes place in two superficial planes at right angles to each other, a regularly expanding polygon is formed. With its increasing area, the two division planes will tend to fall into radial and tangential planes, and the polygon will become a flat, circular disc, provided the rate of division in these planes coincides with the ratio between the radii and the circumference of expanding circles. But as soon as such a disc is formed, the central cells are placed under different conditions from the marginal ones, as to nutrition, respiration, and tension; and in addition, the latter are advancing into new territory by their own growth, and at the same time they are crowded over it at a constantly increasing rate, by the division of those cells that lie nearer the center than they do.

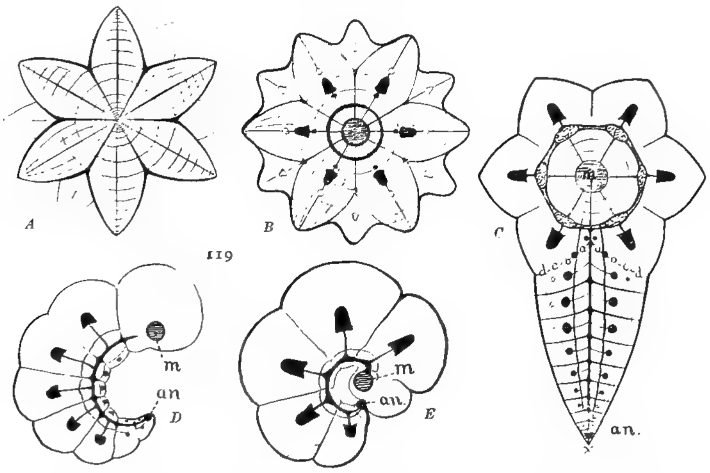
Thus a difference between the local rate of cell division, the local rate of cell displacement, and the local rate of histological differentiation is established. As the local augmentation or diminution of growth produced by these conditions has no constant relation to the increasing radii and circumference, it follows that the actual form of the disc will be a resultant of the various sets of forces. The surface layers will not fit the deeper ones, or the central portions fit the periphery. The disc must, therefore, either change its marginal contour, or its surface contours, or both. That is, the areas of unequal growth stresses must express themselves either in a disc with a broken contour (a symmetrical polygon, hexagon?), or in a circular disc with symmetrically placed infoldings, or eruptions of its surface, or both. (Fig. 119, *A.B.*)

If we now consider the vertical increment of our hypothetical group of cells, it is clear that the conditions change more rapidly in a vertical direction, with increasing thickness, than in a superficial horizontal one, with increasing width. There is consequently a greater modification of the rate of growth and of specialization in a vertical direction than in a horizontal one. The inevitable result is, therefore, not a homogeneous sphere, but a lens-shaped disc composed of unlike concentric strata, *i.e.*, ectoderm, mesoderm and endoderm, each stratum composed of zones of unlike organs, concentric with the point of initial growth.

Thus a plan of an adult radiate, for example, seen from its oral surface in mercator projection, presents a succession of ring-like zones, intersected by radii, marking the distribution of like parts. The central area represents the point of origin of the endoderm, or the blastopore, or the opening to the primitive gut. Around this opening the various organs are arranged in concentric circles that are formed at successive periods, the oldest and most highly specialized around the central infolding, the newest and least specialized on the periphery.

The bilateral type appears to have arisen from the radiate by a local outgrowth from it, not by a transformation of its entire body. The outgrowth gave rise to the new body, and the old body became the head of the new animal.

A premonitory stage of this transformation may be seen in the one tentacled cœlenterate larvæ, as I pointed out in 1889, and the same type may be again seen in the trochosphere, and in the early embryonic stages of all segmented animals We may represent such forms, laid down in mercator projection, by a racquet-shaped plate, the large anterior end representing the body of the cœlenterate that is to become the head, the handle representing the outgrowth from it that is to form the new body. (Fig. 120.)



FIGS. 119–120–121.—Diagrams. in mercator projection, illustrating the three principal types of growth, and the coincident morphological and physiological differentiation. FIG. 119.—Radial type, showing the lines of unequal physical and chemical stress created by radial growth, and their coincidence with the lines of morphological differentiation. FIG. 120.—Apical bilateral type, showing the origin of bilateral symmetry, apical growth, and metamerism, as a result of unequal radial growth. FIG. 121.—Apical asymmetrical type, or false radial type, derived from the apical bilateral type, by the suppression of growth on one side.

Whatever may be the cause of the unequal radial growth, once established, it automatically creates bilateral symmetry and metamerism. To illustrate: If in a growing circular disc, there is, for any reason, a local increase of radial growth, the resulting form will be oval, or triangular, or banjo-shaped. (Fig. 120.) The isogeminal lines will then form two similar, converging series on either side of the enlarged radius. At any time in the history of this organism, there will be a graded linear series of cells, from the oldest at *a*, to the youngest at *an*, and a double graded series from any point in *a–an* to the right, or left.

There can be but two points in the entire mass at any time that are alike as to age, an environment, each one lying in a corresponding position to the other on opposite sides of the principal axis of growth. As a result of apical growth, a graded, tri-axial series of unlike environments, and three similar graded series of cells, unlike as to age is established. This dual series of unlike conditions, and cells of unlike lineage, coincides, as nearly as may be determined, with a third and fourth series, namely the lines of morphological and physiological differentiation; hence, the conclusion is justified that the two latter are the formal, or kinetic expression of the two former. That is, metamerism, or the succession of unlike parts in a cephalo-caudal direction, bilateral symmetry, or the succession of unlike parts in a bilateral direction, and the formation of superimposed germ layers, are the inevitable results of the locally diverse physical and chemical conditions, and the locally diverse cell lineages created by apical growth. They cannot therefore be the result of the unfolding, or distribution, of diverse specific formative materials.

It would therefore appear that there is a definite order in which various tissues are automatically created by their individual environments, the degree of histological specialization having a constant time and space relation to the germinal axis. That is, if we assume that the nervous tissue is the most highly specialized, then it is clear that at any period of development, the most highly specialized tissues predominate in the germinal axis, and that: *a*. the grade of specialization diminishes from any point in that axis right and left to the germinal margin, or to the periphery of each half metamere; and *b*. the grade of development of each member of the half metamere reaches its maximum at some point behind the cephalic end of its series, and gradually diminishes toward the germinal apex at the caudal end of the body. (Fig. 157.)

It will also be observed that in passing from the outside of the sphere inward, the degree of morphological and physiological complexity in the four superimposed layers varies inversely as the distance from the germinal axis.

Conclusion.—Continuous aggregation of like materials is an impossibility, because all growth, or aggregation of materials, automatically creates for each of the constituent parts unlike time and space conditions, which in turn control further growth and differentiation. The unlike conditions thus created, tend to form parallel, or concentric, isogeminal and isomorphic shells and zones, the resulting form, mode of growth, and action of the constituent parts being the visible expression of the local conditions created by growth.

Natural selection, external environment, and heredity play no part in the creation of the physical and chemical framework of living things.

II. MORPHOLOGICAL INTERPRETATION OF THE EARLY STAGES OF EMBRYONIC GROWTH.

All metazoa may be reduced to one of two types of structure, the radiate and the bilaterally symmetrical. These two types have not arisen independently of each other; they are genetically related, the latter being derived from the former. The bilateral type may become secondarily asymmetrical (certain molluscs and arthropods), or, by the complete suppression of one side, it may develop into a new type of radial structure (echinoderms), without thereby destroying or completely disguising the basic elements of bilateral structure and of metamerism.

In all these varying forms, the part of the embryo that represents the cœlenterate ancestor is the head, and the primitive infolding, or ingrowth in the center of the head region, represents the remnants of the cœlenterate enteron. This is the only part of the embryo that may be properly called a gastrula. The opening of the gastrula becomes the opening to a subsequent ingrowth, the stomodæum; or the stomodæum is formed, as nearly as may be determined, at the point where the gastrula infolding, or the so-called blastopore, closed.

That is, in bilaterally symmetrical, or in segmented animals, or in their derivatives, the true gastrula is formed at the head end only, and the permanent mouth is formed from it, or in its place. When a germinal ingrowth forms in the post-cephalic region, it is not to be regarded as a blastopore, but as a telopore, or as one of the various stages of the axial infoldings that arise as a secondary result of apical growth.

A cœlenterate type of animal represented in mercator projection, or as laid down in enbryo on a large yolk sphere, would take the form of a thin circular disc, with the nerves, sense organs, and appendages arranged in concentric and radiating lines around a central, enteric infolding, or ingrowth. (Fig. 119, *A.B.*)

In the arachnid embryo, the cœlenterate stage is represented by the circular germinal disc, with its central infolding. (Figs. 123–124.) This disc becomes a part of the head, or procephalic lobes of the future embryo, while the trunk is an outgrowth from its posterior margin.

In the later stages, we may recognize the remnants of the primitive, radiate nervous system, in the system of radiating and concentric nerves formed from the walls of the stomodæum. If we evert the stomodæum, and project it with its nerves on the central area of the germ disc, where it originally belonged, the radiate arrangement of the stomodæal nerves is apparent. (Fig. 35.)

In vertebrates, a part of the stomodæal ring is still recognizable in the cerebellar commissure and the side walls of the diencephalon, while the location of the blastopore, and of the invertebrate stomodæum is indicated by the infundibular perforation of the brain floor, and by the pit-like infolding in the center of the procephalic lobes during the open medullary plate stage. (Figs. 25, *st*, 46, *st.co.*) During the gastrula stage of the metacœlenterates, therefore, the primitive mouth, or blastopore, is surrounded by a closed nerve ring like that of their cœlenterate prototype. On this interpretation, the union of the margins of the germinal disc represents the closing of a yolk navel on the hæmal surface, not the concrescence of the blastopore on the neural surface. Such a concrescence of the blastopore is only conceivable on the untenable assumption that the yolk sphere completely fills the gastrula mouth, and that the neural surface of segmented animals represents the aboral or hæmal surface of a cœlenterate.

Wherever yolk is present in small amounts in the egg, it may be held within the endoderm cells. But if it is very voluminous it forms an inert, extra-cellular mass, over which the cells spread in all directions from an initial center that always represents the beginning of the oral or neural surface. Around this center, the various organs are arranged in a definite order, from the center outward.

Embryonic growth on a yolk sphere, therefore, always begins near, or centers in, the primitive oral region and spreads from it toward the aboral surface.

If there is but little yolk present, the aboral surface may be formed during cleavage, and at practically the same time as the oral surface. But in proportion as the yolk increases in volume the formation of the aboral surface is delayed, because it can only be completed by the growth of the margins of the germinal disc around the yolk.

Thus growth on the oral and growth on the aboral surface of the embryo are totally distinct processes, and always take place under different conditions and in opposite directions. On one side it is centrifugal, on the other centripetal. The uncovered yolk mass, or yolk navel, always lies on the opposite side of the egg from the blastopore and the germinal axis.

The subject of apical and bilateral growth, or of radial and bilateral symmetry has more than a purely academic interest for us, because the interpretation of bilateral animals in terms of radiate ones, is the key to the problems of germ layers, gastrulation, and concrescence, throughout the entire series of segmented animals. The conditions creating bilateral symmetry and metamerism are so fundamental, that it is hardly conceivable they could be otherwise than they are. There is no reason whatever to doubt that the fundamental relations of the nervous axis, blastopore, primitive mouth, and yolk sphere, and the main axes of differential growth are the same in cœlenterates and in all bilateral acrogenous animals.

The axes of growth and of differentiation are the most important means of orientation, and should be carefully considered in all attempts to compare one great group of animals with another.

Gaskell, Herrick, and others fail to recognize these fundamental relations. Gaskell maintains that the "ventral" or neural side of an arthropod is the same as the hæmal or "ventral" side of a vertebrate, and that the vertebrate nerve cords represent those of an arthropod, transferred from the "ventral" side of the one to the "dorsal" side of the other. There are only two possible ways in which such a transfer could take place. One way would be for them to migrate over the surface of the yolk, right and left, uniting on the opposite side. In this case, among other equally obvious difficulties, the original lateral margins of the cords would be united in the median line, all the ectodermic territory, originally covered by, and giving rise to the peripheral nerves and sense organs, would be extinguished; and the outgrowing peripheral nerves would be directed into the canalis centralis, with no visible means of escape. The second possible way would be for the cords to migrate bodily through the yolk, in which case they would reach the opposite side inside out, or upside down; that is, with the proliferating nuclear surface on the deeper face of the cords, instead of the outermost surface as it actually is. In order to meet the demands of his theory, Gaskell turns the arthropod embryo inside out and upside down, and reverses its axes of growth and of specialization.

Gaskell entered the field of embryology as a novice, and at once became hopelessly confused by the conflicting usage of the terms "dorsal" and "ventral," and he still remains so, because he did not establish a fixed basis for orientation. The result is familiar enough. In spite of the testimony of his own senses, all his rivers persist in flowing up hill, and the north pole of his compass points due south.

Gaskell at least makes a valiant fight to save the pieces of the invertebrate nervous system, even if he does annihilate the rest of the animal in the attempt. Prof. C. J. Herrick's effort is not as praiseworthy, since he discards altogether a "perfectly good" nervous system, and substitutes for it a new one created out of empty space.

III. Early Stages of Limulus.

The development of Limulus will serve as a convenient basis for a comparative study of the embryology of vertebrates and arachnids. I have given little attention to the maturation, fertilization, and cleavage, devoting most of my time to the general form of the body at successive stages, and to the method of growth of the various organs.

Observations were made on the living eggs during the cleavage and gastrula stages. But most of the drawings, up to the appearance of the appendages, were made from eggs hardened in picro-nitric, or Perenys fluid, and viewed as opaque objects, after removing the membranes. The older stages were drawn from embryos that had been stained in various ways, and cleared in cedar oil or balsam.

The earlier stages were most conveniently obtained by artificial fertilization; the later stages were obtained from the nests in the sandy beaches of Woods Hole, where, in 1893–94, most of the embryological work on Limulus was done.

In artificial fertilization, the female is opened and the eggs poured into a shallow glass dish. By carefully tilting from side to side, the ripe eggs may be made to adhere to the bottom and sides in a compact single layer. After a few minutes they may be rinsed off in fresh sea water, removing the clotted blood and immature eggs, and then fertilized.

The eggs in some crabs are a dull slate color, in others pink or buff, or of various intermediate shades. When first taken from the body, they are shriveled and distorted, but after a short time in sea water, they become plump and round.

During the first thirty-six hours after fertilization, their form and appearance change rapidly. At eighteen hours, most of them appeared to segment into two unequal blastomeres. (Fig. 122, *a*.) About two hours later, they again assumed a regular outline, some of them meantime showing on the upper surface a radiate appearance which soon disappeared. (Fig. 122, *b*.)

1. Cleaveage.

About forty-eight hours after fertilization, broad furrows, filled with small spherical bodies, appear on the upper surface of the egg. There is no regularity in the direction of these cleavage planes, or in the form of the blastomeres, although a four cell stage resembling that of many amphibia, is frequently seen. (Fig. 126, *c.*)

Cleavage is most marked on the surface that happens to be uppermost. Eggs with ten or twelve prominent blastomeres on the upper surface may be perfectly smooth and apparently unsegmented on the under side. However, when stripped off the glass and inverted, segmentation appears on the smooth under surface in about fifteen minutes, and in half an hour it may be almost as complete as it was on the original upper surface.

There, is however, a distinct polarity to the egg that is not influenced by its position, for cleavage ultimately makes greater progress on that side of the egg that is to become the neural surface, irrespective of whether it faces up or down. On the fourth or fifth day, most of the eggs are covered with a single layered blastoderm on one side, while the opposite side was still occupied by large yolk spheres.

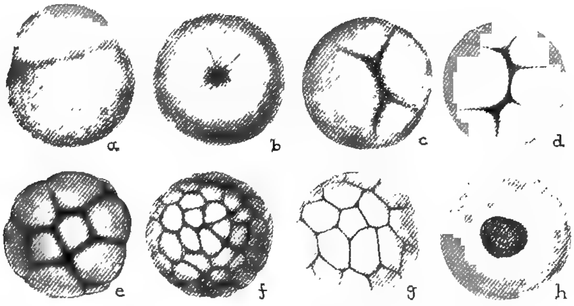


FIG. 122.—Cleavage stages, and yolk navel, *h*, of Limulus eggs.

In many cases, the blastoderm, spreads over the opposite side of the egg in an advancing fold, the uncovered yolk either protruding from the opening, or lying a little below the general surface. The uncovered area is usually circular, but it may be quite irregular, and varies in size from an opening one-third the diameter of the egg to that of a pin hole. (Fig. 126, *h.*) The yolk plug thus produced has nothing to do with the formation of germ layers. It resembles the condition seen in the early stages of certain ganoids, cyclostomes, and other fishes, but it has no parallel, to my knowledge, in the invertebrates.

On the eighth day, a single layered blastoderm covers the entire egg, enclosing numerous nucleated yolk spheres.

Comparison of Arachnids and Vertebrates.—The cleavage in the arachnids presents an interesting intermediate series of stages between the typical centrolicithal type of insects and that of the lower vertebrates.

In Limulus, there is a distinct approach toward the partial cleavage of the amphibia and cyclostomes. In Telyphonus (Schimkewitsch), the form of the blastomeres, and the size and location of the resulting segmentation cavity are very similar to the corresponding structures in the frog's eggs.

In the scorpion, which possesses one of the largest eggs among the arthropods, all the early divisions take place on the surface of the yolk (Brauer), producing a typical meroblastic cleavage, and a small sharply defined blastodisc very similar to that in the teleosts.

In many insects and spiders, the early divisions take place in the interior of the egg, and all the nuclei thus produced may move to the surface to form the blastoderm, from which yolk cells and mesentoderm cells arise by a subsequent process of division and ingrowth. But in some insects and arachnids, cleavage nuclei remain in the interior of the egg as the so-called yolk nuclei, which, as a rule do not give rise to the definitive endoderm. In Limulus, the condition appears to be exceptional, in that most of the yolk cells derived from the early cleavage nuclei, persist as the permanent lining of the midgut and its diverticula. Although accessions are subsequently made to the yolk nuclei by the ingrowth of cells from the germinal disc and germ wall, no definite bands of columnar endoderm cells, such as those seen in insects and crustacea, are formed.

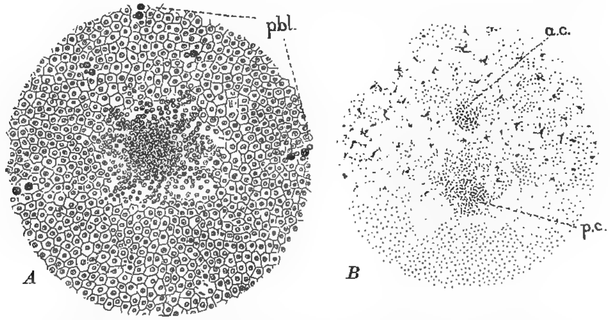


FIG. 123.—*A*, Surface view of the blastoderm and primitive cumulus of Limulus, showing the beginning of gastrulation, *a.c.*, and the formation of the primitive germinal area, *p.b.l*; *B*, later stage showing the increasing number of inner layer cells that mark the boundaries of the germinal area, and the formation of the posterior cumulus, *p.c.*, that marks the beginning of the trunk, and of teloblastic, or apical, growth.

On the whole, the cleavage seen in the arachnids (Limulus and the scorpion) is very similar to that of primitive vertebrates, and affords us a satisfactory basis for the interpretation of the later stages of development in the arthropod and vertebrate stock.

2. The Germ Disc or Primitive Cumulus.

The embryo first appears about four and a half days after fertilization, as a very faint, white, germinal spot. Later, it may be a minute, roughened papilla, partly surrounded by a shallow groove, and situated in the center of a flat germ disc.

Early in the fifth day, the germ disc forms a prominent, mound-like elevation, or cumulus, with the germinal spot now forming a crater-like depression at its summit. (Fig. 124, *A′.A″.*) In sections, the cumulus appears as a thickening of the blastoderm, with scattering cells arising from the whole of its inner surface, and with a cloud of cells migrating from the central depression, or gastrula, into the yolk.

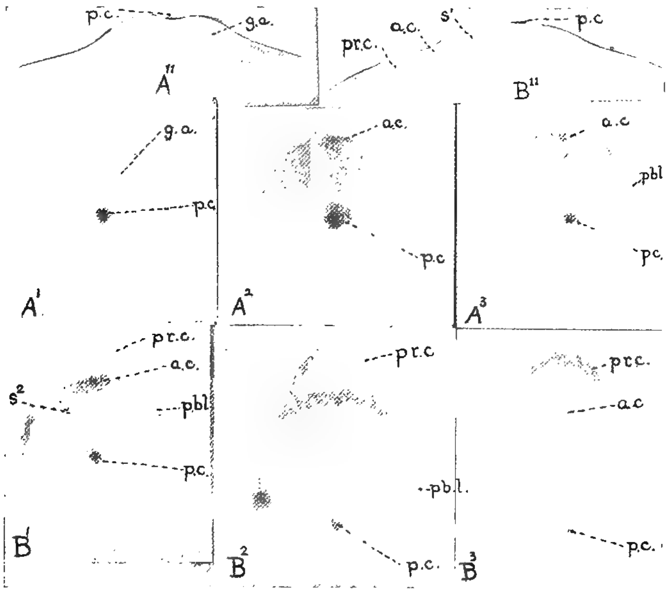


FIG. 124.—Limulus embryos, seen as opaque objects, in surface views and in profile. The figures show the primitive cumulus, the expanding germinal area, and the beginning of the separation into head and trunk.

3. Formation of Metameres.

On the sixth and seventh days, the first traces of metamerism appear. Some of the events that take place at this time are difficult to observe. They are best seen by selecting the most conspicuously marked eggs and examining them by reflected light.

In stained, surface views of the germinal area, large nuclei may be seen on its margin, sometimes arranged in pairs, two nuclei on the right, two on the left, and one or more on the anterior margin. (Fig. 123, *A.pb.l.*) These nuclei appear to initiate the formation of the germwall and the periblast, or marginal yolk cells. In later stages, the inner and outer cell layers become a little thicker or darker, over the anterior half of the germinal area, and two germinal spots are now visible, an anterior and a posterior one. (Fig. 123, *B.*, *a.c.* and *p.c.*)

When studied as opaque objects, an earlier stage of the germinal area than the one just described has the appearance shown in Fig. 124, A^1. A shallow groove subsequently divides the cumulus into a darker anterior, and a lighter posterior part (Fig. 124, A^2.); and finally a faint depression appears on the right and left, and on the anterior and posterior margins of the cumulus. A^3.

In still older specimens, the anterior half of the previous cumulus now appears as a faint, wave-like ridge, in front of the reformed cumulus; the ridge representing the forehead, or procephalic lobes. B^1., *pr.c.* On the anterior half of the cumulus, is the beginning of the second thoracic metamere, s^2; the posterior germinal spot marks the beginning of the telopore, *p.c.* The anterior germinal spot lies between the procephalon and the second metamere, *a.c.*

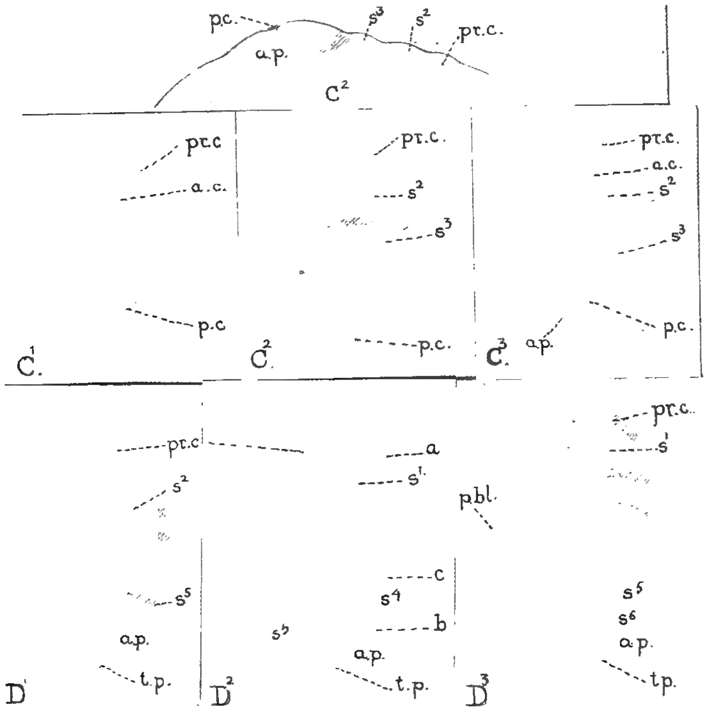


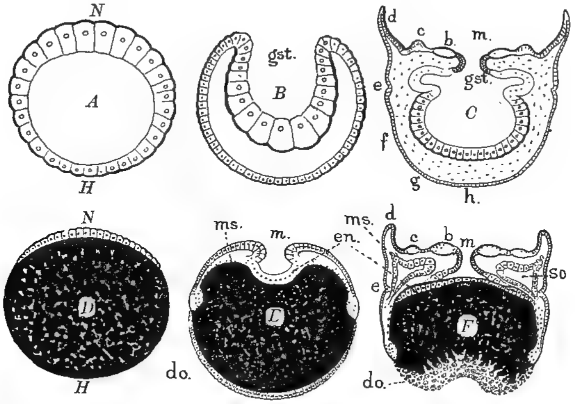
FIG. 125.—Limulus embryos, seen as opaque objects, showing the formation of the first six thoracic metameres, and the gradual infolding of the proliferating cells in the posterior cumulus to form a primitive streak, or telopore.

In a short time, the posterior half of the primitive cumulus rounds out into a new cumulus with a germinal depression on its posterior side B^2 and B^3. The remaining thoracic metameres are formed in a similar manner, by successive, wave-like elevations, on the anterior slope of the terminal cumulus, or anal plate. (Fig. 125.)

The second, third, and fourth thoracic metameres form in regular order, and are of about equal proportions. There is then a distinct pause, followed by the appearance of the fifth and sixth metameres. (Fig. 125, D^3.)

The more posterior thoracic metameres are cut off from the anterior margin of the anal plate, as rather narrow bands or ridges, s^5 and s^6. Later their peripheral ends join the germ wall and spread rapidly in a lateral direction. The cheliceral metamere, s^1, appears at a relatively late period between the cephalic lobes and the second thoracic metamere. (Fig. 125, D^2.)

The sequence in the development of the abdominal metameres is similar to that of the thoracic. First, the operculum and first gill appear, then a pause, followed by the remaining gills in order. Finally the chilaria appear at a late period in front of the operculum. (Figs. 141, 142.)



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FIGS. 126 AND 127.—Diagrams to illustrate the methods of cleavage, gastrulation, and the growth of the germ layers and the cephalic navel in a yolkless egg, and one with yolk. The yolk is shown in black.

The further growth of the metameres and appendages is shown by the figures and need not be described in detail. We would, however, call attention to the fact that there is a period when the second, third, and fourth thoracic metameres are especially conspicuous, and the appendages first to appear are formed on these metameres. (Fig. 140.) During this period, the fifth and sixth metameres and the whole abdominal region may be deeply depressed, sometimes forming a deep infolding, on the floor of which the abdominal appendages are developed. All the thoracic appendages have appeared by the tenth or eleventh day.

4. **The Gastrula.**

Returning to stage *A*. We have seen that two distinct median germinal spots appear near the summit of the primitive cumulus.

The anterior one (Figs. 123 and 124, *a.c.*) comes to lie near the center of the future procephalic lobes. It soon disappears from surface views, but remains visible in sections as a mass of "yolk cells,"128 D^a. *a.c.* It augments by division, and by the migration of new cells from the surface, up to stage *G* and *H*, when under favorable conditions it may be seen even in surface views, as a deep lying cloud of cells, now showing the peculiar histological characters of degeneration. (Fig. 140, *G.a.c.*)

The stomodæum appears shortly after stage *E*, on the anterior margin of the procephalic lobes, its inner end coming to lie in the midst of this cloud of degenerating nuclei. (Fig. 140, *G*.) After stage *J*, no trace of these yolk nuclei is visible.

I have pointed out that a similar condition exists in Acilius and other insects, and that it is probably characteristic of arthropods in general. This infolding is the only one in arthropods that, in respect to the time of its appearance, its location, and its products, can be regarded as a gastrula, and we shall designate it as such.

5. The Germ Wall.

The germ wall is a narrow, unsegmented zone of proliferating cells, first seen along the margins of the germinal disc, and later along the sides of the embryo up to the last stage in the closing of the hæmal surface, *g.w.*

The pairs of large nuclei in stage *A* (Fig. 123, *p.bl.*), located on the margins of the germinal area, mark the beginnings of the germ wall and of the periblast.

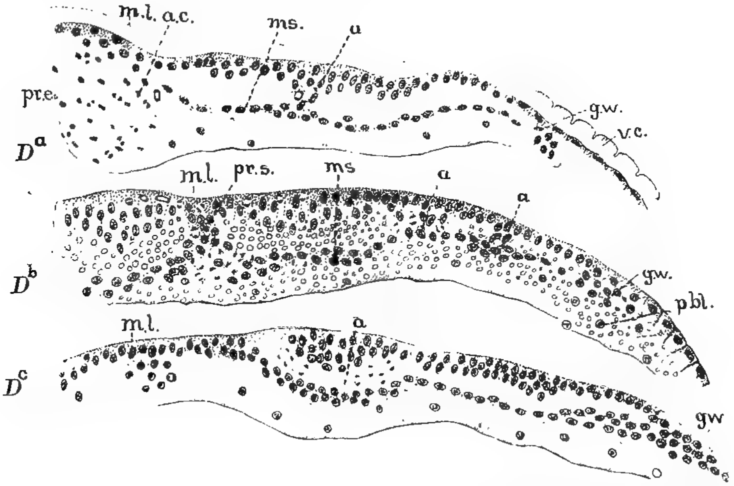

FIG. 128.—Sections of the germinal area of Limulus in stage *D*, showing the formation of the inner layers, and the extension of the germinal area by the growth of the germ wall, *g.w.*, over the surface of the yolk. The local inward proliferation of the blastoderm to form, in part, the mesoblastic somites, is shown at *a.*; *m.*, median line. Sections Da and Dc from the procephalic, and anterior thoracic, regions. Section D^b. from the region of the primitive streak, *pr.s.*

At these points an inward proliferation develops, in surface views appearing as faint spots or depressions; later they form a conspicuous marginal band or thickening. (Figs. 125, 128, 140, *g.w.*)

The inward proliferation along this margin is similar to that at the apex of the body. As the germinal margin spreads over the surface of the yolk, it leaves behind a trail of differentiated ectoderm, mesoderm, and yolk cells, or periblast. It ceases to produce new periblast after stage *J*, but it continues to proliferate the definitive ectoderm and new ectoderm, probably up to the time the cephalic navel closes.

On either side of the germ wall there is a sharp distinction between the definitive ectoderm and mesoderm on the one hand, and the single layer of columnar blastoderm cells on the other. (Fig. 129.)

* * * * * * * * *

It thus appears that in Limulus the formation of germ layers is not a particular event in the development. It takes place at different times and in widely different parts of the germinal area. In fact, the production of germ layers may occur wherever early growth takes place, as for example, on the sides of the anal plate, where the mesoblastic somites are formed; in the germ wall, where the germ layers in the lateral ends of each half metamere are formed; in the telopore, where the axial tissues arise; or in the comparatively late stages of development, where mesodermic tissues appear to arise from various local modifications of the ectoderm. The formation of germ layers is not, therefore, synonymous with gastrulation, nor is it to be regarded as a modification of gastrulation, which, as we understand it, is that particular process by which an organ representing the enteron of a cœlenterate was formed; as for example, the central ingrowth of the primitive cumulus, and of the procephalic lobes. The formation of the germ layers from the telopore and germ walls, is ontogenetically and phylogenetically a later and a different process. It is the embryonic method of growing a new body on an old head, the head representing the ancestral cœlenterate body. Neither the embryonic method of postcephalic growth in segmented animals, nor the great variety of tissues and organs produced by it, are comparable with anything that takes place in the cœlenterate.

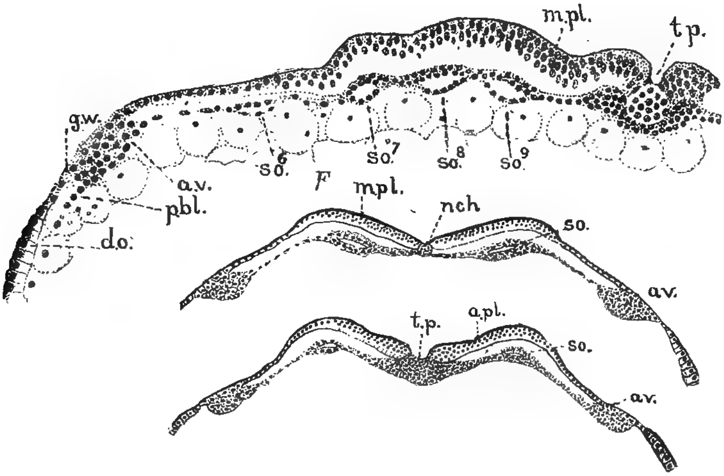

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FIG. 129.—Section through the primitive streak of Limulus, stage *G*, showing mesoblastic somites, germ wall, periblast, etc.

FIG. 130.—Sections of same stage through posterior parts of the anal plate.

6. The Mesoderm.

The Sources and Kinds of Mesoderm.

We may distinguish four sources from which the mesoderm takes its origin, viz: *a.* the procephalic mesoderm, arising by delamination from the anterior portion of the primitive cumulus; *b.* the axial mesoderm (primitive streak) from the axial teloblasts; *c.* the mesoblastic somites, from the sides of the anal plate; and *d.* the lateral plates, from the germ wall.

a. Procephalic mesoderm. In the procephalon the mesoderm forms a single unpaired, thin-walled chamber, approximately coextensive with the cephalic lobes. It arises by delamination from the anterior half of the primitive cumulus; it is not divided into an axial cord, somites, and lateral plates, and does not appear to be comparable with that in the trunk. (Fig. 123, *B.*) It disappears without giving rise to any permanent organ or tissue, except the investment of the stomodæum and forebrain.

b. The postoral mesoderm consists of the axial cord, somites and lateral plates. These three subdivisions are present in the whole postoral region or trunk, but they may be very unequally developed. A striking feature in the arachnids and vertebrates is the large size of the somites of the midbrain region, and the atrophy of the corresponding lateral plates.

1. *The axial cord* arises from successive proliferations, located in the median line at the posterior end of the body. After the first one or two segments are formed, an unsegmented, axial cord appears, extending forward from the center of the anal plate to the stomodæum. Its presence is indicated, either by a faint, median shadow (Fig. 125, *C.p.c.*), or by a groove, or "primitive streak" (Fig. 128, D^b. *pr.s.*), or by a sharp depression, or telopore. (Fig. 140, *t.p.*)

The axial cord gradually breaks up, from before backward, into *a.* the ectodermic middle cord, from which arises the median nerve and the epithelium of the canalis centralis; *b.* into the mesodermic lemmatochord, or notochord; and *c.* into the primary germ cells. (See notochord.)

The axial mesoderm shows little or no trace of segmentation and never contains a cœlomic cavity.

2. *The Somites.*—The thoracic and abdominal metameres are formed as paired, wave-like ridges on the anterior lateral margin of the posterior cumulus, or of the anal plate. At the same time, a band of mesoderm cells separates from the inner surface of each ridge, giving rise to a pair of mesodermic segments, which, as fast as they separate from the outer cell layer, form hollow, thick-walled somites. In the later stages, the posterior abdominal somites arise as segments of the wing-like expansions of mesoderm formed beneath the ectoderm, on either side of the telopore. (Fig. 130.)

From the somites arise the longitudinal muscles and cartilages of the appendages, the endocranium, the genital and nephric ducts, and the nephric tissue.

3. *The Lateral Plates.*—The lateral end of each primitive somite retains its connection with the proliferating surface cells that constitute the germ wall. As the germ wall spreads over the yolk, it gives rise to the lateral plates, or that part of the mesodermic segments lying lateral to the zone of appendages. The lateral plates are merely lateral extensions of the somites, and like them each one consists of somatic and splanchnic layers, and may enclose a cœlomic cavity. The somite is the product of the apical growth of the anal plate; the lateral plates are produced by the lateral extension of the germ wall. The peripheral margins of the lateral plates finally lose their connection with the germ wall, and the cell layers separating adjoining cœlomic cavities break down.

From the lateral plates arise the extra embryonic blood corpuscles, the cardiomeres, pericardial chamber, and the longitudinal, hæmal muscles.

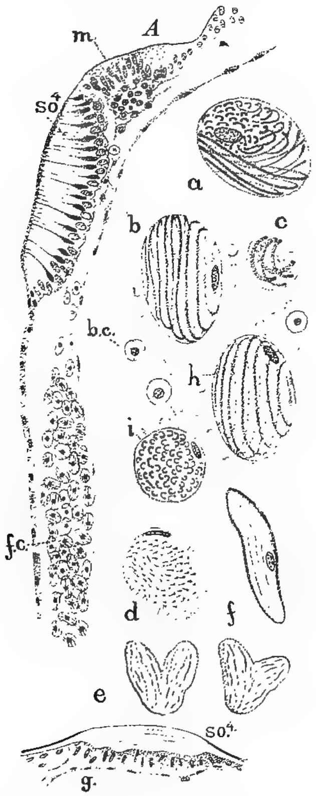

FIG. 131.

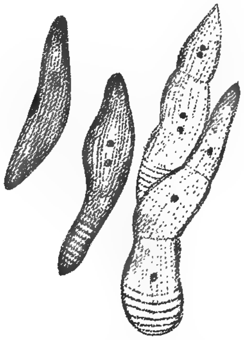

FIG. 132.

FIG. 131.—Section through the fourth segmental sense organ, $s.o.^4$, of the thorax of an embryo Limulus, about stage I, together with the adjacent margin of the germ wall with its mass of fiber cells, *f.c.*; *a.* to *i.*, fiber cells of the same stage more highly magnified; *d.e.f.*, similar cells from the adult, in a free amœboid condition, and in fission; *g.*, same sense organ with its lens-like chitenous thickening during the trilobite stage.

FIG. 132.—Clusters of fiber cells from the posterior, hæmal region of the thorax, about stage N, showing mode of division and their transformation into muscles. Limulus

Lateral Plates in the Frog.—The mesoderm forming the segmented lateral plates of the post-thoracic metameres plays such an important part in the development of the arthropod embryos, that one might reasonably expect to find some trace of them in vertebrates. With this object in view, specially prepared frogs' eggs were studied in a strong oblique light. In this work I was aided by Mr. A. O. Kelley, a graduate student at Dartmouth, and the figures and descriptions on this point were worked out by us together, in 1906–07.

A considerable number show two or three pairs of lateral plates; a very few show a larger number, as in Fig. 159. In this specimen, the anterior plates, which apparently belong to the post-branchial metameres, are directed downward and forward as if they were growing around the egg below the gill plates, just as the post-vagal segments of the arachnids encircle the egg on the hæmal side of the appendicular arches. (Figs. 17, 19.) The segments decrease in length caudad, and the most posterior ones are directed downward and backward toward the closing telopore, forming a distinct welt on either side.

The lateral plates quickly disappear, so that it was not possible to follow them into later stages.

Although these results are very meager, it nevertheless seems probable that the figures in question are to be regarded as a faint recurrence of the concrescing segmented lateral plates of mesoderm so conspicuous in the arachnids.

The Fiber Cells.—One of the chief products of the germ wall is a thick band of rounded or oval cells, that we shall call fiber cells. They lie in the first five thoracic segments in an intermediate zone median to the germ wall. They have a remarkable structure and history; some give rise to definite muscles; some persist in the adult as a peculiar type of spindle shaped semi amœboid cells resembling blood corpuscless; others, after forming muscles, degenerate during the later embryonic and larval stages.

In the earlier stages, the fiber cells cannot be distinguished from the other cells in the germ wall. (Figs. 128 and 129.) In stages *J* and *K*, they form a broad, thick band of large oval cells, rather loosely arranged, and presenting a very striking appearance. (Fig. 131, *A.f.c.*) Each cell contains a small eccentric nucleus and a highly refractive, colorless fiber. The latter may run in a regular spiral direction, filling the entire cell, or it may form regular loops arranged in compact bundles that stand at various angles with each other; *a*, *b*, *h* and *c*. Aside from the fiber, the cells appear empty and colorless, although in some cases they may have a dense, slightly colored envelop, *f* and *d*.

In stage *G*, the fiber cells are clearly visible in surface views as a dark inner border to the germ wall, and extending from the cheliceral segment, where it is especially enlarged, to the anterior border of the sixth segment. (Figs. 141–144, *a.v.*)

The band increases in width and continues to advance toward the hæmal surface. In stage *H*, it forms an equatorial girdle, the two extremes having meantime united behind, and almost united in front. (Figs. 141 and 144, *a.v.*) After it passes the equator the posterior limb moves rapidly forward, swinging into a hæmo-neural direction, thus shifting the center of the closing ring toward the anterior hæmal portion of the thorax. (Figs. 147 to 149.)

Meantime the yolk mass of the thorax, and a little later that of the abdomen, divides into distinct lobes, the future enteric pouches. Important agents in bringing this about are the hæmo-neural muscles of the thorax. There are eleven pairs of these muscles attached to the middle of the dorsal shield in the adult, making five pairs of complicated markings on its inner surface. (Fig. 155.) Six pairs of tergo-plastrals arise from the endocranium, and five pairs of tergo-coxals from the coxal joints of each thoracic appendage, two in front and three behind. These muscles and the spaces between the developing gut lobes are important conduction paths for the distribution of the fiber cells.

The muscles arise at a very early period from the anterior and from the posterior wall of each mesodermic segment, close to the somites. They form the only suggestion of segmentation that is to be seen in the lateral plate area of the thorax. (Figs. 142–151, $hm.m^{1-5}$.)

At first the tergo-coxal muscles lie in a nearly horizontal plane, their median or neural ends attached to the ectoderm between the bases of the thoracic appendages. (Fig. 142.) Their lateral ends gradually advance with the germ wall toward the hæmal surface, and as they swing into a nearly vertical position, they cut the thoracic yolk mass into five great lobes, which ultimately become the five main liver lobes, or enteric pouches, of the thorax. (Figs. 142–151, $hn.m^{1-5}$.)

In stages *K* and *L*, the fiber cells begin to scatter in different directions. Many leave the surface and penetrate the interior of the thorax, following, in the main, the channels between the yolk lobes formed by the hæmo-neural muscles.

During stage *L*, embryos seen from the hæmal surface show the fiber cells as two large mottled patches on the anterior lateral surface of the thorax. (Fig. 149, *a.v.*) The clear oval area between them represents the cephalic navel, or the depression where the remnant of the blastoderm is passing into the interior of the yolk.

The fiber cells congregate in great numbers along the sides of the cephalic navel, and around the hæmal ends of the first five pairs of hæmo-neural muscles, where they form dark colored, conical or wedge-shaped masses of cells. (Figs. 146–149, $hn.m^{1-5}$.)

It will be observed that up to the present time the fiber cells have a very definite distribution, and except for a few scattering clusters they are absent from the sixth thoracic, the vagus, and the abdominal segments. (Figs. 148 and 149.)

The metamorphosis of some of these loose oval fiber cells into muscles is very rapid and takes place a little after stage *M*, when the embryo is taking on the trilobite form, and pigment has appeared in the eyes. At this period, the cells stain more readily; the fiber is less distinct, forming finer parallel fibrils; the nucleus takes up a central position; and the cells elongate somewhat and unite end to end in irregular rows. (Fig. 132.) In the more advanced stages, a central canal has formed, in which the dividing nuclei are arranged in a single row and the beginning of cross striations is seen on the free, more or less pointed ends of the cells.

Two great masses of these muscle cells are formed on either side of the cephalic navel and of the anterior end of the heart. From them are developed two pairs of muscles. One pair, the inter-tergals, lies on either side of the heart,

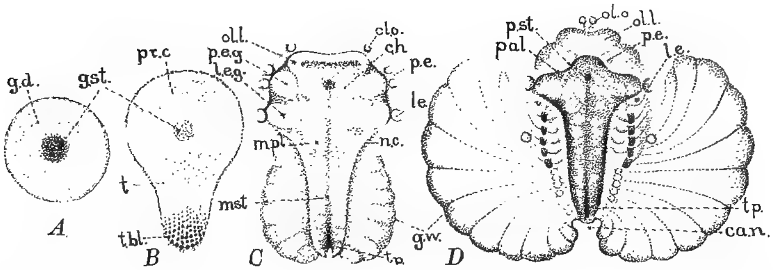

FIG. 133.—Diagrams, in mercator projection, illustrating the mode of growth of arachnid embryos during the early stages; *A*, primitive cumulus, in the radiate or gastrula stages; *B*, appearance of the posterior cumulus and the teloblasts, or the beginning of apical growth and the differentiation of the primitive head and trunk; *C*, appearance of the medullary plate; the procephalic lobes; the marginal sense organs and ganglia; the telopore; and the segmentation, and lateral expansion, of the posterior portion of the germinal area; *D*, appearance of the thoracic appendages; the growth of the palium over the procephalic lobes; the post-anal concrescence of the lateral plates of the germinal area; and the forward extension of the vagal and anterior abdominal plates.

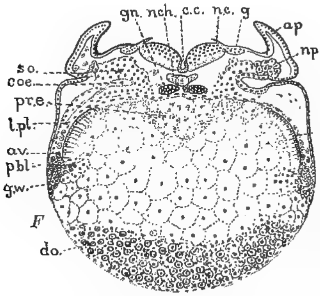

FIG. 134.

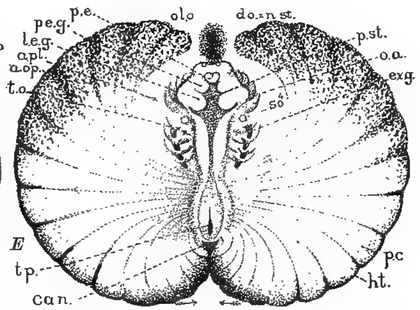

FIG. 135.

FIG. 134.—Schematic cross-section of an arachnid embryo in the anterior thoracic region, showing the relative positions and the mode of growth of the principal organs.

FIG. 135.—Schematic figure, in mercator projection, showing further concrescence of the germ wall, in a hypothetical, large yolked embryo. The cephalic navel appears just in front of the procephalon, as the anlage of the hæmastoma, and the anterior appendicular arches are beginning to close in the hæmal surface of the procephalon.

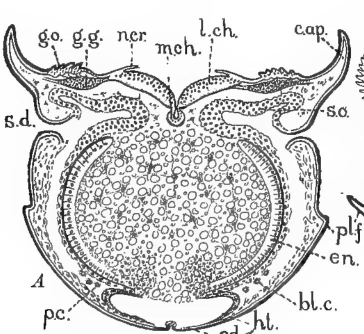

FIG. 136.—Section of a later stage in the same region.

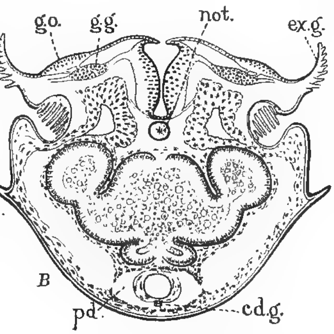

FIG. 137.—Section of a still later stage in the branchial region.

At the time of hatching, it is very voluminous, and is apparently confined to the thorax. (Fig. 151, *in.t.*) In the later stages, it undergoes considerable reduction, and its posterior end becomes attached to the anterior margin of the abdominal shield. (Fig. 77, *in.t.*)

The other large muscle developed from the fiber cells is the anterior end of the hypobranchial. (Fig. 77, *B.b.th.m.*) This muscle also becomes greatly reduced in volume in the older stages, and its anterior end retreats to a more posterior position.

Many other fiber cells become scattered irregularly along the margins of the thoracic shield, in the spaces left free by the contracting liver lobes. Here they elongate and form the small, scattered bundles of muscle fibers that permanently unite the neural and hæmal walls of the cephalic buckler.

The metamorphosis of fiber cells into these particular muscles on the hæmal surface of the thorax, takes place at a very late period, long after the endocranium, the hæmo-neural, and other muscles have become clearly differentiated; and no other muscles than those mentioned are formed in this manner. At the time the fiber cells undergo their metamorphosis, the yolk lobes are invested with a thin cellular layer, so that it is hardly probable that any of them are absorbed in the yolk with the hæmal blastoderm.

A large number of fiber cells, however, never form definite muscles. They persist through life, loosely distributed throughout the lacuna spaces in all parts of the body, although they appear to be more numerous at the base of the appendages and in the anterior portions of the cephalic shield.

In the half grown Limuli, and even in the adult, they may be readily recognized by their large size, peculiar structure, and coloring. They generally preserve the spindle-shaped form, but appear to be somewhat amœboid, or rather euglenoid, and some have been observed in division. (Fig. 131, *e.*) The fiber is now much less refractive and has lost its distinctly spiral arrangement, apprearing as longitudinal striæ that converge toward either end.

The remarkable history of the fiber cells indicates that they are the degenerating remnants of the longitudinal hæmal muscles of the first five thoracic segments. Only a part of the large number of cells actually form muscles; the others become free cells that may be regarded as a special type of blood corpuscle, although they do not appear to circulate freely in the main blood channels.

In the spiders and in the scorpion, the same kind of fiber cells are present. Juts what their history is in these forms has not been definitely determined. Various authors, who have apparently seen them in the spiders, state that they give rise to blood corpuscles.

Whether these cells ultimately give rise to true blood corpuscles or not was not determined.

Blood corpuscles of the usual type arise from the peripheral ends of the lateral plates of the thoracic and abdominal segments, and at these early stages can be readily distinguished from the fiber cells. (Fig. 131, *b.c.*)

Assheton[1] has described some peculiar wandering cells, of unknown fate and significance, that appear in many parts of the body on the sixth and seventh days of incubation in Gymnarchus nitolicus, p. 369–370. In their distribution, size, "peculiar refrangent qualities" and in the "ribs which run from pole to pole," they greatly resemble the fiber cells of the arachnids and I have no doubt they are in reality the same kind of cells.

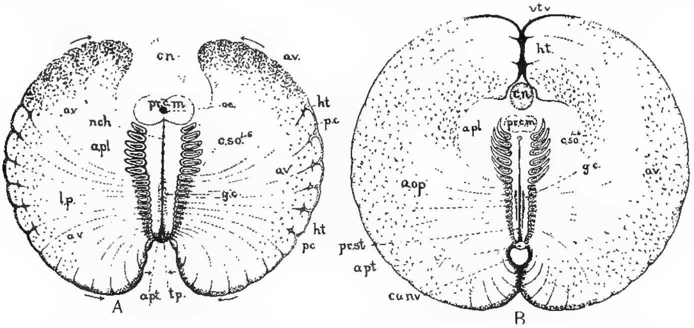

Fig. 138.—Schematic diagrams in mercator projection, at two different stages illustrating the arrangement and mode of growth of the mesoderm and its derivatives in an arachnid embryo.

Similar cells have also been described by Plehn, 1906, in teleosts. They are oval, thick-walled cells with a small excentric nucleus and with numerous fine, highly refractive, unstainable rods or threads, all converging toward the non-nucleated pole of the cell. They are widely distributed in the walls of blood vessels and in lymphoid tissue, and are said to form a secretion that is probably emptied into the blood. See also Phoronis and Lernæa, p. 447.

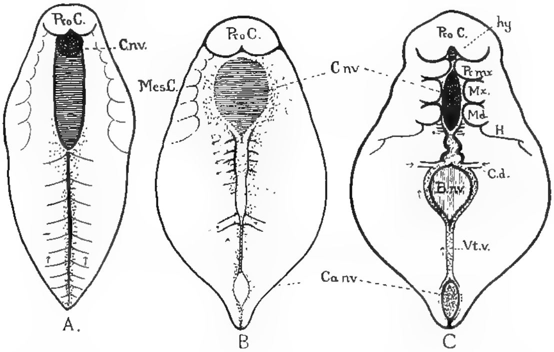

Fig. 139.—Schematic figures of the hæmal surface of arthropod and vertebrate embryos, to illustrate the method of closing the hæmal surface in large yolked embryos. *A*, Insect type, with elongated cephalic navel; *B*, arachnid type with larger yolk sphere and overhanging or projecting cephalic and caudal lobes; *C*, vertebrate type, with a relatively larger, more posteriorly located, yolk sphere; with cephalic appendages concrescing around the cephalic navel; and with delayed concrescence of the centrally located cardiomeres, thus giving rise to the bifurcated heart tube, and to the middle, or belly, navel.

Vascular Area.—From the preceding descriptions it will be seen that an extra-embryonic area is established in the arachnids in which we may recognize the

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[1] The Development of Gymnarchus Niloticus. The work of John Samuel Budget, Cambridge, 1907.

beginnings of a vascular area, a pelucid area, and a germ wall, having a structure, arrangement, and mode of growth similar to the corresponding ones in the vertebrates.

A comparison of the numerous sections given by S. Mollier to illustrate the development of the blood will show that the structure and mode of growth of the vascular cords in amphibians and cyclostomes are essentially the same as in Limulus.

The principal difference in our descriptions relates to the origin of the cells in or near the germ wall. Many students of vertebrate embryology state that yolk cells migrate into the germ wall and give rise to blood cells. In Limulus, according to my description, while it is true that many cells originating in the germ wall pass out of it into the yolk, there is no indication that the yolk cells migrate in the opposite direction into the vascular cell cord. As the pictures presented by the vascular cell cords in vertebrates and arachnids are identical, the difference undoubtedly lies in the interpretations, not in the processes.

It will be seen from an inspection of the diagrams illustrating these conditions in mercator projection, that along the periphery of the germinal area in typical arachnids such as the scorpion, the spiders, and Limulus, there is a zone of dividing cells that constitutes one of the earliest and most important sources of blood corpuscles. (Fig. 138, *av.*) It may therefore be called the vascular area. Owing to the forward growth of the abdominal lateral plates and the absence of such plates in the thoracic region, a barren extra embryonic area is formed around the head, which may be regarded as the beginning of a pellucid area. (Fig. 138, *B. a.pl.*)

It will be seen that when the same conditions are shown from the hæmal surface of the egg (Fig. 139, *A*,*B*.), the concrescing germ walls form a median band or cord of yolk cells, heart cells, and blood cells, extending from the posterior margin of the dorsal organ, or cephalic navel, to the caudal navel.

In the vertebrates, we may recognize a modification of this condition, due largely to the increase in the size of the yolk sphere. (Fig. 139, *C*.) When the latter is of considerable size, the hæmal concrescence of the germ wall, in the middle sections of the body, is delayed, or does not take place at all. Thus a potential, or real, belly navel is formed, dividing the primitive vascular cord into three sections. The definitive heart arises from the anterior section that lies between the cephalic navel, or mouth, and the belly navel. In the middle section, the vessel remains in a paired condition, forming around the navel a vascular ring, the anterior part of which represents the Cuvierian ducts, or the proximal ends of the vitelline veins. The posterior ends unite behind the belly navel to form the posterior section of the primitive vascular cord, which is continuous, at its posterior end, with the hæmal lip of the blastopore, or caudal navel. From the posterior section is formed the unpaired vitelline vein, which represents the non-contractile caudal end of the arachnid hæmal vessel. (Compare also Figs. 17, 23, 31, 34, 43.)

IV. The Cephalic Navel, Dorsal Organ, or Neostoma.

Limulus.—During the primitive cumulus stage, the blastoderm outside the germinal area consists of a single layer of sharply defined cells. At this period, the "vicarious chorion," a thick membrane secreted by the superficial cells of the eggs, is smooth and structureless over the germinal area, but over the blastoderm it is divided into polygonal plates, one for each blastoderm cell. (Fig. 128, *v.c.*)

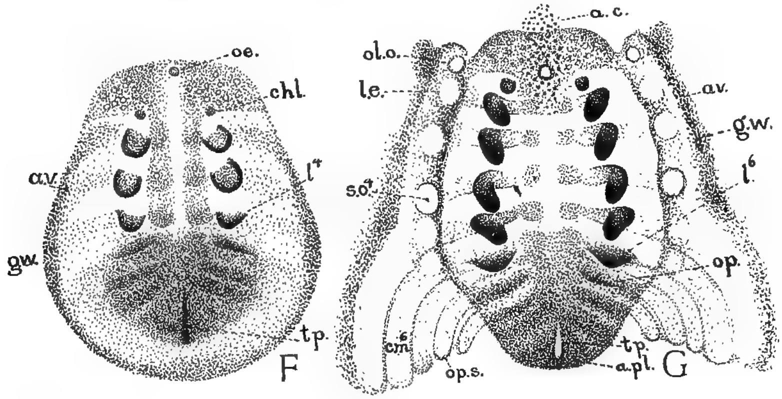


Fig. 140.—Limulus embryos in stage F and stage G, the latter in mercator projection. The lateral plates of the sixth thoracic and anterior abdominal metameres, and the segmental sense organs, are clearly shown.

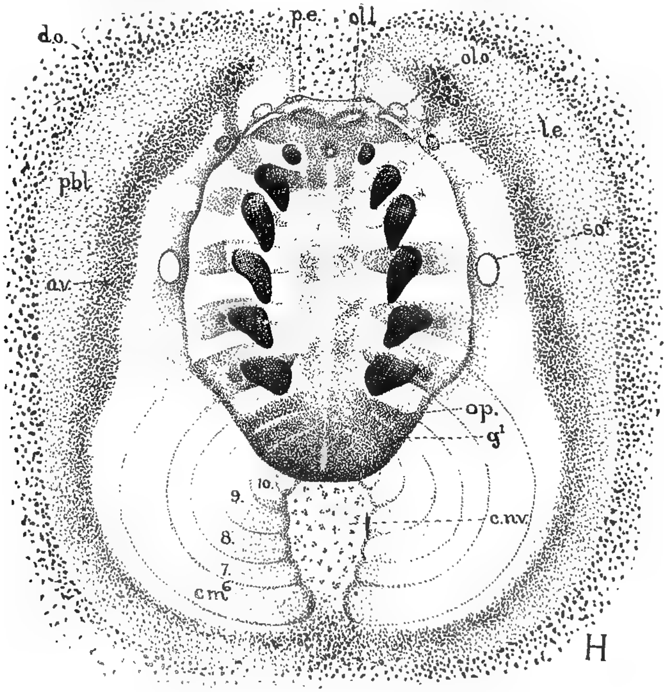


Fig. 141.—Same, stage H, mercator projection. The first five thoracic metameres and the procephalic lobes have no segmented lateral plates.

The membrane soon separates from the embryo, and later from the blastoderm. The blastoderm cells meantime become very deep and columnar, the nuclei and dense cytoplasm collecting at their outer, and numerous yolk particles, at their inner ends. (Fig. 129, *d.'o.*) At this period, the blastoderm cells beyond the embryonic area are everywhere sharply cut off from the yolk, and there is no migration of cells from one to the other.

In stage *G* (Fig. 143), the blastodermic nuclei, along a narrow zone just beyond the germ wall, take on a sharper and darker color, *do.* During stages *H* and *I*, the zone widens, gradually spreading over the entire blastoderm. This change in the appearance of the nuclei marks the beginning of a rapid proliferation, and subsequent degeneration of the blastoderm cells. During this process, the chromatin collects into larger, intensely stained particles; the columnar cells divide, take on a spherical, or oval form, and pass in great numbers into the yolk, where they form a very conspicuous mass of loosely arranged cells. (Fig. 134, *d.o.*)

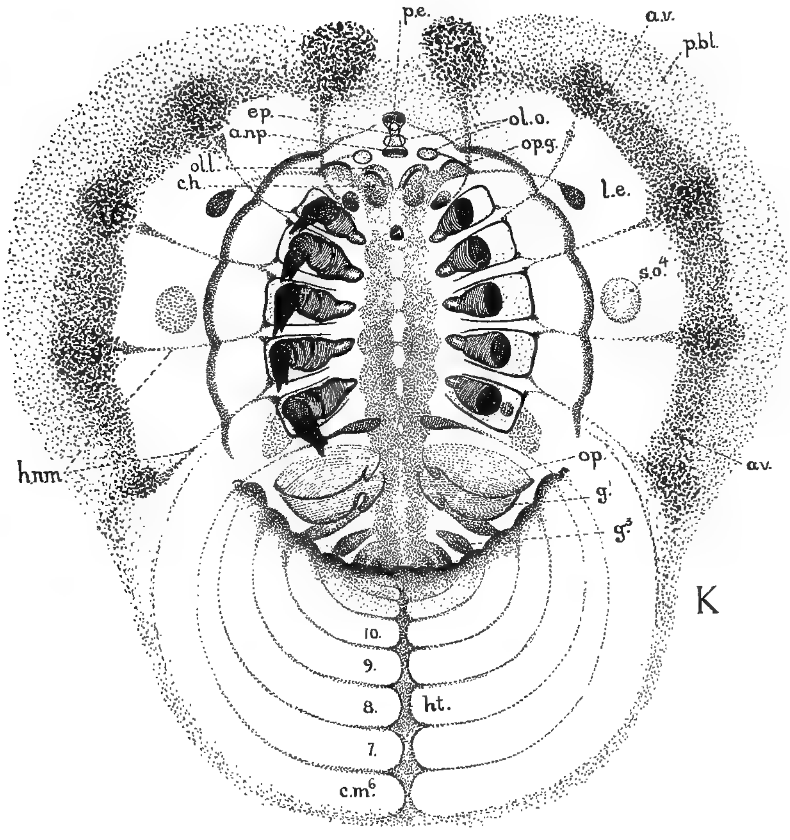


FIG. 142.—Same, stage K, mercator projection. On the right, the ends of the thoracic appendages are removed.

The cytoplasm of these cells soon becomes fainter and more transparent, and finally disappears. The coarse irregular nuclear masses break up into very fine granules, which become scattered through the yolk and absorbed.

Meantime, as the germ wall passes the equator of the egg and advances toward the anterior hæmal surface, it surrounds a gradually narrowing area, where the degenerating blastoderm cells are being crowded into the yolk and overgrown by the germ wall and its products. The ingrowing blastoderm, and the narrowing ring formed by the germ wall and vascular area, constitute the cephalic navel. (Figs. 139–149, *c.nv.*)

When the vascular area and germ walls finally close in the hæmal surface, the entire extra-embryonic blastoderm and its products have disappeared in the interior of the egg. Owing to the shape of the yolk sphere, and to the unequal expansion of the thoracic and abdominal lateral plates, the greater part of the blastoderm is crowded into the anterior portion of the mesocephalon, and is last seen disappearing into the yolk just behind the procephalon. (Figs. 149, 150, *c.nv.*)

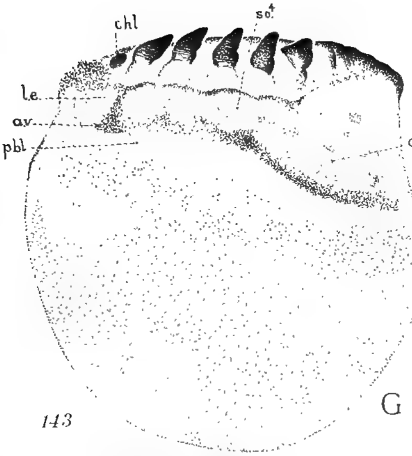
In stage *O*, the last remnants of these cells may be seen scattered about in the yolk contained in the first four pairs of enteric pouches. (Fig. 151.)

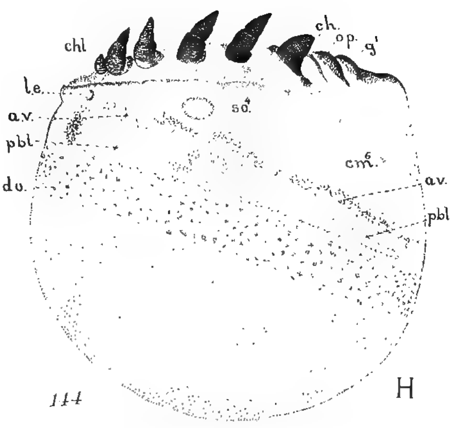
Other Arthropods.—The cephalic navel of Limulus without doubt represents one phase of the structure familiar in insects, crustacea, and myriapods, and which is usually spoken of as the "dorsal organ." It has only recently been recognized in the arachnids. I have found a similar structure to that of Limulus in the scorpion, and, according to Schimkewitsch, one is found in Pholcus and probably in Telephonus. One has also been described in the copepods. (Fig. 272, *B.*)

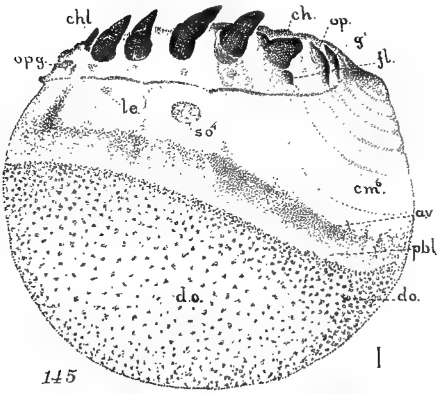
In the crustacea, the conditions centered in or around the cephalic navel give rise to a variety of structures. It may be a transitory, embryonic gland-like organ, as in isopods; a larval organ serving for temporary attachment, as in cladocera (Figs. 8, 9); or a voluminous outgrowth that serves throughout life for the attachment of the animal to some inanimate object, or to its host, as in cirripeds and parasitic copepods. (Figs. 275, 282, 283.)

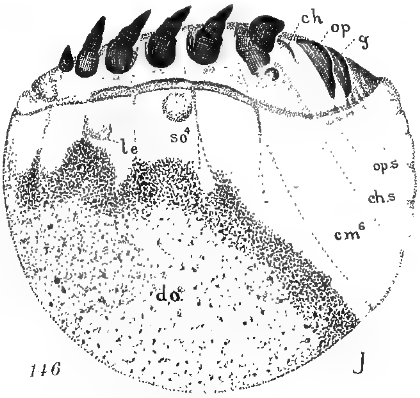
The cephalic navel, in one form or another, is therefore found in all classes of arthropods. What its original significance may be is not apparent. But its function, when it has one, and its location and general mode of growth are constant.

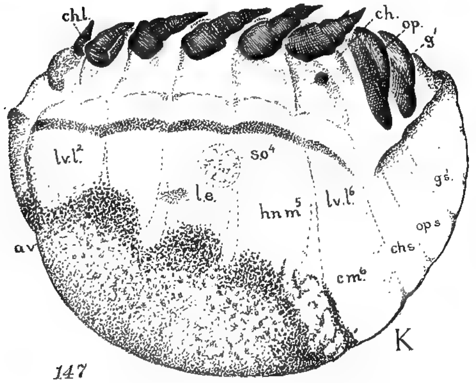
There are clearly two factors involved in its formation: 1. the low pressure area formed by the degenerating hæmal blastoderm; and 2. the convergence of the margins of the germinal area toward the center of degeneration. The invagination of the degenerating blastoderm into the yolk, and the closure of the germinal area around it, gave rise to a fistula-like communication between the enteron and the exterior. This opening may close up completely during the embryonic stages, leaving no scar behind (insects and arachnids); or around the point of closure scar-like glandular structures or outgrowths may develop that serve as temporary or permanent means of attachment (crustacea, cirripeds), or in parasitic forms











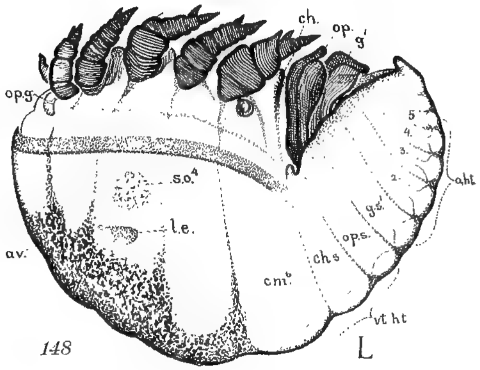


FIG. 143.—Limulus embryo, stage G. Note the segmental sense organs, and the absense of segmented thoracic plates.

FIG. 144.—Same, stage H. The hæmal portion of the blastoderm, just beyond the germ wall, is beginning to proliferate, marking the beginning of the dorsal organ, or cephalic navel, *d.o.*

FIG. 145.—Same, stage I. The entire hæmal blastoderm is in active proliferation.

FIG. 146.—Same, stage J. The germ wall and vascular area are very conspicuous; the posterior limb of the germ wall has moved forward to the hæmal portion of the thorax, narrowing the area of the cephalic navel.

FIG. 147.—Same, stage K. The abdominal lobe is distinctly marked off; the lateral eye, *l.e.*, has moved backward into the fourth thoracic segment, and the cephalic navel is confined to the hæmal surface of the anterior thoracic region.

FIG. 148.—Same, stage L. The full complement of branchial segments have appeared, and the margins of their lateral plates have united on the hæmal surface to form the heart; the lateral eye lies hæmal to the thoracic sense organ.

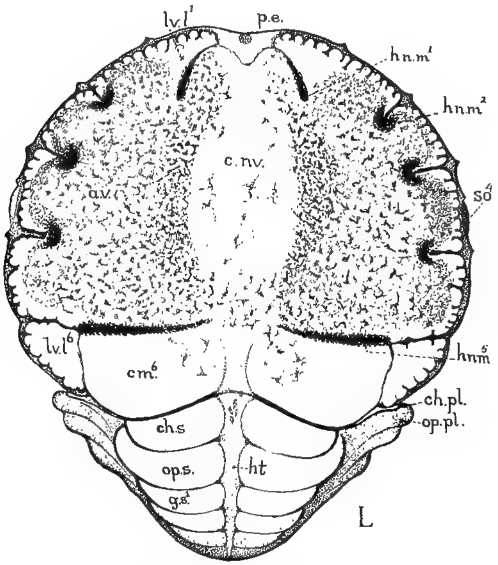


FIG. 149.—Same, stage L, seen from the hæmal surface, showing the completion of the sixth thoracic and all the abdominal segments. Five great masses of fiber cells, surround the hæmo-neural muscles *h.n. m.* $^{1-5}$, that divide the thoracic yolk mass into five lateral lobes.

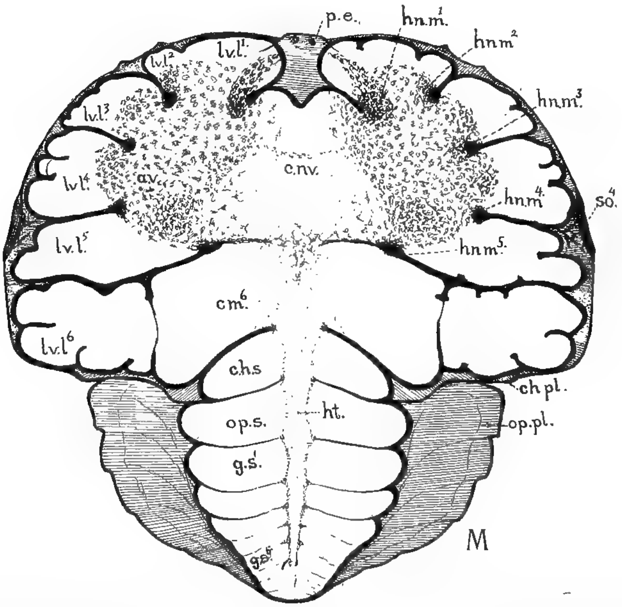


FIG. 150.—Same, stage M. Two great masses of fiber cells *av.*, and the remnants of the hæmal blastoderm, are seen on either side of the cephalic navel, *c.nv.*

as a means of absorbing nutrition. In the vertebrates, tunicates, enteropneusta, amphioxus, and pterobranchia the cephalic fistula became a permanent opening into the enteron, thus giving rise to a new oral opening, or hæmostoma, at the time when the old mouth was about to close up.

V. Concrescence and the Caudal Navel or "Blastopore."

We have seen that the body of segmented animals consists of an axial cord and a right and left series of segments, or half metameres, and that the body grows in length by the formation of new segments at the anal plate, and in breadth by the increase in length of the half metameres. But as each half metamere grows older and longer its peripheral end increases in width faster than its central end. Hence, as new segments are successively formed, the lateral margins of the germinal area increase in length faster than the axial, and the germinal area, instead of forming an elongated band of nearly uniform width, or a triangle, forms first a heart-shaped figure, and finally one in which the peripheral margins concresce in front of and behind the main axis. (Fig. 157, *A.C.*) When this has

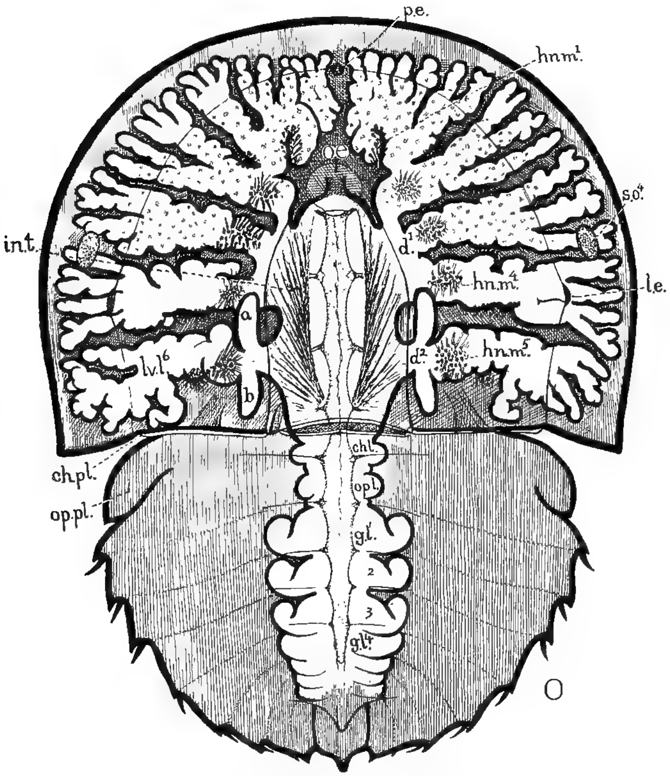


FIG. 151.—Same. Embryo just before it escapes from the inner egg membrane, stage O. The cephalic navel has closed and the degenerating remnants of the hæmal blastoderm are seen enclosed in the first four pairs of liver lobes, giving them a mottled appearance. The lobes are still partly filled with yolk.

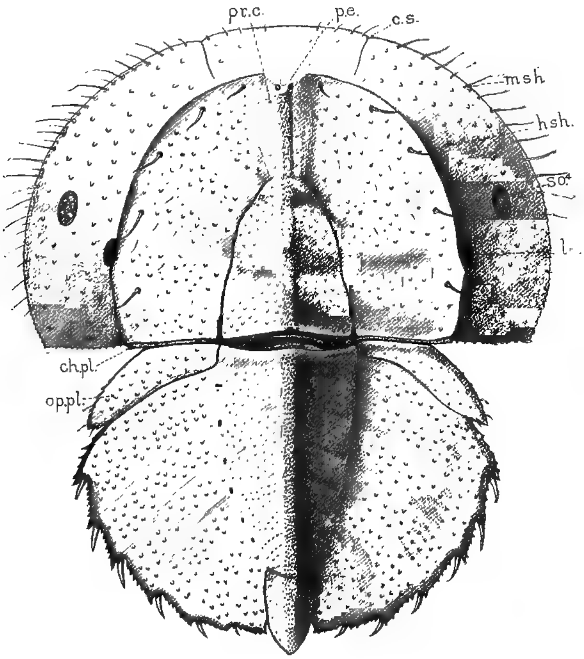


FIG. 152.—Limulus larva in the trilobite stage. Hæmal surface.

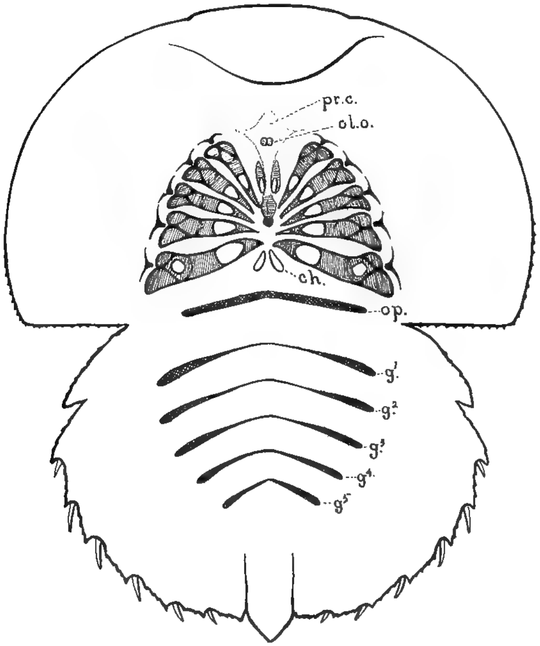


FIG. 153.—Same from the neural surface, the free portions of the appendages removed.

taken place, apical growth can no longer proceed over the surface of the yolk, it must take place by the piling up of one segment on top of another, in the shape of small closed rings.

Concrescence, therefore, is the inevitable result of apical and bilateral growth over a spherical yolk surface.

The amount of concrescence in a given animal depends on the ratio of marginal to apical growth, and upon the radius of the yolk sphere. Another factor that materially affects the form of the embryo, is the gradual suppression of the lateral margins of the more anterior segments.

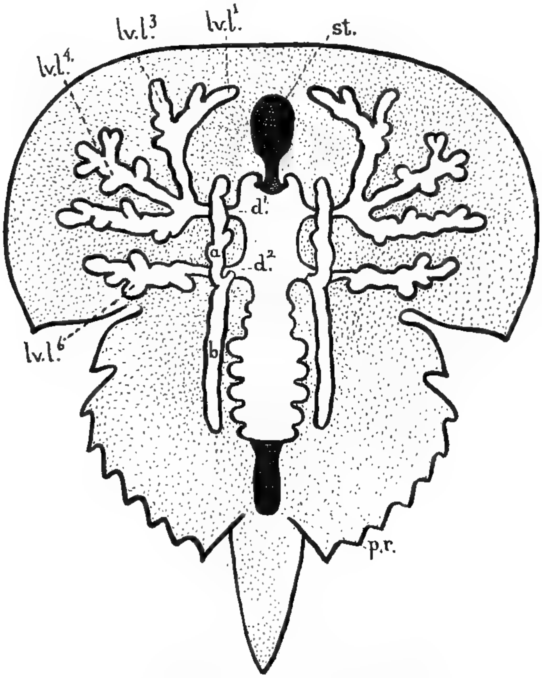


FIG. 154.—Young Limulus, after the shedding of the trilobite shell. The segmental sense organs of the fourth thoracic segment, and the procephalic sutures of the trilobite stage, have disappeared.

Embryonic apical growth represents the phylogenetic method of adding new body segments to the old, but it is accomplished in a very different manner in one case from the other. The embryo, for example, produces a succession of flat bands on a curved, or flat surface, each one arising under different conditions from the preceding one, and forming closed rings as best they may. In the adult ancestral forms, all the new segments were produced under essentially like conditions, that is, as small closed rings at the apex of a cylinder.

In Limulus, an oblong area is enclosed between the posterior part of the concrescing germ wall and the broad anal plate. This area and its surrounding germ wall, I shall call the caudal navel. (Fig. 141, *c.nv.*)

The inward proliferation in this region is very conspicuous and might be mistaken for an extension of, or as a product of, apical growth. This is not the case. The yolk cells, or endoderm cells, formed around the posterior end of the primitive streak and from the walls of the telopore, belong to the primitive germinal area, and are the products of true apical growth. The post-anal proliferation in the caudal navel is of a different nature. It represents an isolated part of the degenerating hæmal blastoderm, enclosed by a narrowing area formed by the germ wall. The area is finally closed over by the definitive ectoderm, leaving behind a special cloud of mesoderm and yolk cells formed by the united germ walls.

* * * * * * * * *

The conditions just described for Limulus and other arachnids give us the clue to the correct interpretation of the phenomena of concrescence in the vertebrates. Here there is no doubt a true axial, or apical growth, and a false axial growth formed by the post-apical concrescence of two bands representing the proliferating margins of the germinal area. But in vertebrates it is difficult to distinguish between that part of the embryo formed by apical growth and that formed by concrescence, and it has been assumed that there is no real distinction between them. The primitive streak of vertebrates for example is often regarded as an ancient line of concrescence, and the real concrescence that takes place behind it, as a continuation of the same process, more formally expressed. Both the primitive streak and the actual line of concrescence are supposed to represent different phases of "a modified method of uniting the lips of a greatly elongated gastrula mouth." Minot. Embryology, p. 126. But according to our interpretation, there is no remnant whatever of a gastrula mouth at the caudal end of any segmented animal. The real apex of the body is an actively growing point composed of proliferating teloblasts that give rise to the axial parts of the body. True axial growth cannot take place by concrescence, because the parts thus united represent the extreme lateral or hæmal ends of the metameres forced into the neural, or axial, position by the peculiar exigencies of apical growth on a spherical surface.

We may recognize in vertebrates, as in arachnids, an axial telopore, or primitive streak, and post-apical concrescence of the margins of the germinal area. But these modes of growth are so blended with one another in vertebrates that it is extremely difficult to tell where one begins and the other ends.

The actual separation of the products of teloblastic growth varies widely in different segmented animals. But the differences are in degree, or in method, not in kind, or in end results. For example, in forms like Cymothoa, there is a transverse row of large superficial teloblasts, which like the cells at the apex of a growing plant stem, give rise in the most precise and regular manner, to the various parts of the trunk.

In Limulus, in birds, reptiles, and mammals, there is a true axial infolding or primitive streak, and the various products of apical growth that extend forward from it may be recognized almost as fast as they are laid down. In amphioxus and the tunicates, there is a much more extensive apical infolding, and the products of apical growth, which form the walls of the infolding, are not formally separated into endoderm, mesoderm, and notochord till a relatively late period. To call this infolding an "archenteron," or "primitive gut," and to then conclude that the notochord was once a part of an alimentary canal, because it is for a brief period united with the definitive endoderm, is no more justifiable than it would be to assume that the endoderm is historically derived from an internal skeleton, because for a time it is continuous with the notochord.

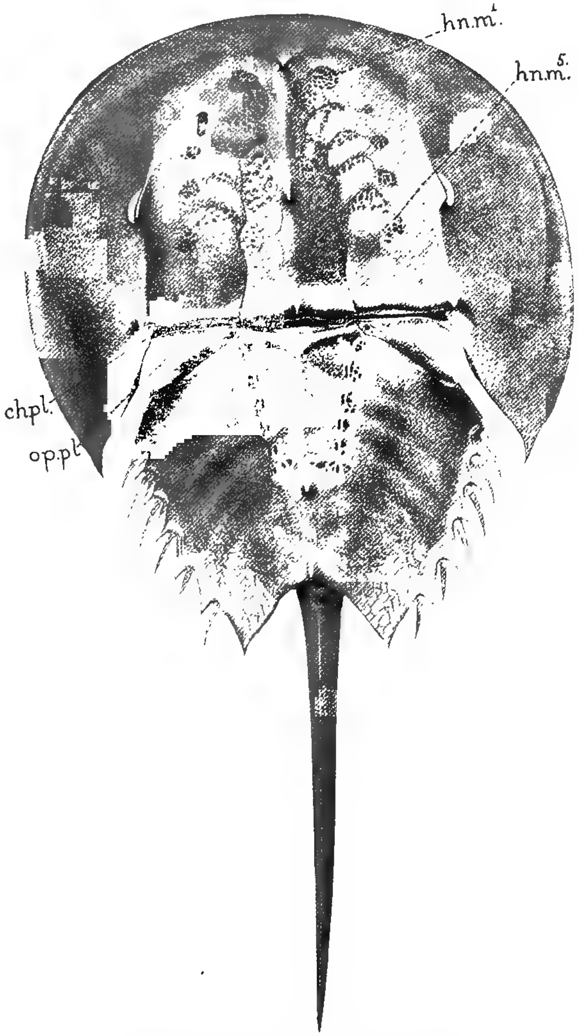


FIG. 155.—Photograph of a half grown Limulus

As I pointed out in my first contribution on this subject, in 1889, the only available criterion as to what constitutes endoderm is evidence that it forms the lining of a functional alimentary canal. From this point of view, it is clear that the only parts of the so-called "archenteron" that can be justly regarded as endodermic are the two lateral bands that in both vertebrates and arthropods actually form the lining of a functional alimentary canal. (Fig. 270.)

True gastrulation, comparable with the formation of an enteric chamber in cœlenterates, is a much less important process in arthropods and vertebrates than has been supposed, and is confined to the central region of the procephalon.

CHAPTER XIV.

THE OLD MOUTH AND THE NEW; LOCOMOTOR AND RESPIRATORY APPENDAGES.

The closing of the invertebrate mouth, the formation of a new one, and the evolution of segmental appendages into leg-jaws, gill-sacs, and locomotor appendages are complex independent processes, but they are so interwoven with one another in the early history of the vertebrates that they may be appropriately treated together.

The salient features of the mouth and appendages in arthropods and vertebrates may be contrasted as follows:

a. In arthropods, the mouth lies on the neural surface, and the foregut passes through the brain floor between the two nerve cords, just behind the forebrain. (Fig. 43.) In vertebrates the mouth lies on the hæmal surface of the head, and the foregut, without passing through the brain floor, leads directly into the midgut. (Fig. 44.)

b. In arthropods there are many pairs of appendages, the most conspicuous ones being arranged in rigid metameric order either on the sides or on the neural surface of the first thirteen to eighteen metameres. They may be absent in some metameres, while in others they assume a great variety of forms suitable for locomotion, sense organs, jaws, gills, etc. (Fig. 3, *A.C.*) In primitive vertebrates, metamerically arranged appendages like those of arthropods, appear to be absent. The paired locomotor appendages, when present (pectoral and pelvic fins) are not segmentally arranged; they are merely local expansions of longitudinal folds, and they always lie posterior to the (16 ±) metameres that constitute the head.

c. In arthropods the jaws are formed from several pairs of modified legs that belong to the metameres lying just behind the forebrain. The basal joints of the leg-jaws act as crushing mandibles, or as supplementary jaws. In chewing, tasting, or preparing food, they work crosswise, to and from the median neural line. In true vertebrates the jaws, in the adult stages, consist of two unpaired arches, or an upper and a lower jaw. They lie on the hæmal surface instead of the neural, and in chewing move forward and backward instead of crosswise.

d. In the arthropods, respiration is usually accomplished by means of specially modified appendages that either project outward above the surface of the body, or inward, forming ectodermic pouches, with vascular, lamellate walls. In fishlike vertebrates the gills may, for a brief early period, consist of external appendages of ectodermic origin, but in their later stages they consist of pouches that lead from the gut to the exterior; and the whole or a part of the respiratory tissue of the gill pouch is said to arise from the endoderm.

These striking differences are apparently irreconcilable, and have led many zoologists to the conclusion that there can be no direct genetic relation between these two groups of animals. We shall show in this chapter that there is no real foundation for this belief, for when the facts are known and their meaning is made clear, it will be seen that the vertebrate organs in question are of the same nature as those in arthropods. It is true they have undergone a remarkable metamorphosis, but it is one brought about in a perfectly natural and consecutive manner by the action of definite internal forces that can be recognized and their probable effects, in a measure, estimated.

* * * * * * * * *

Argument.—Briefly stated, the argument and the evidence to be presented is as follows: We shall show 1, that during the evolution of the arthropods the primitive entrance to the midgut was being gradually closed, and in some cases actually was closed, because the mouth was shifting into a more and more inaccessible position, and because the stomodæum was becoming more and more constricted by the growth of the surrounding organs. The remnants of this now useless passageway may still be seen in its proper position on the floor of the closing neural canal of vertebrates; this passageway is the infundibulum, and the remnants of the foregut is the saccus vasculosus and the posterior part of the hypophysis.

2. That the foundations of a new mouth are already established in arthropods in the cephalic navel, or so called "dorsal organ," which lies on the hæmal side of the head in a position corresponding to that of the mouth in vertebrates. It affords a transitory opening from the exterior into the midgut, and it, or the adjacent tissues, may serve as a means of attaching the animal to foreign objects, or to its host. Thus in the arthropods, an organ of very great antiquity and habits long established are prepared to perform the work of a new mouth after the vertebrate fashion, as soon as the old mouth becomes permanently closed.

3. That in the arthropods several pairs of leg-jaws surround the mouth on the neural surface of the body, and that the prevailing conditions in the arthropod head tend to crowd the basal portions of these appendages toward the hæmal surface so that they converge around the infolding cephalic navel in the same manner that the oral arches of vertebrates converge around the mouth. It will be shown that in vertebrate embryos the oral arches first appear on the neural surface as three or four pairs of appendicular arches, and that they then gradually shift toward the hæmal side, converging toward the "anlage" of the new mouth, and forming the paired rudiments of the premaxillary, maxillary mandibular, and hyoid arches. These paired arches finally unite, the first two pairs forming the upper, and the third pair, the lower jaw.

4. That in the ostracoderms, the oldest fossil vertebrate-like arthropods, the mouth lies between paired jaws, which in chewing move to and from the middle

line. Here, therefore, the adult condition of the jaws is intermediate between the typical arthropod and the typical vertebrate condition, and is similar to the condition of the jaws in the higher vertebrate embryos.

5. That the gill pouches of vertebrates may be interpreted as invaginated respiratory appendages, which have become secondarily united with enteric pouches.

6. That the free portions of the cephalo-thoracic appendages of arthropods are represented in vertebrates by embryonic oral tentacles, such as the "balancers" and the external gills of amphibian larvæ, and the oar-like appendages of the ostracoderms.

7. That the paired appendages of typical vertebrates, *i.e.*, pectoral and pelvic fins, arise from a new generation of post-branchial metameres that are not represented in arthropods. The lateral fold from which they arise may be regarded either as a marginal fringe of rudimentary appendages or as a series of keel-like pleurites.

I. The Closing of the Old Mouth.

It will be recalled that the alimentary canal of arthropods is formed in three separate sections, the midgut arising from the endoderm, while the foregut and hindgut arise from separate infoldings of the ectoderm. (Fig. 43.)

The infolding for the foregut, or stomodæum, is always formed in the median portion of the procephalic lobes (Fig. 25); the lateral cords lying on either side of it, and cross commissures in front and behind. (Fig. 46, *A*.) As these important parts of the nervous system are formed at a very early period and are never known to be absent, the stomodæum is securely trapped in a nerve ring from which there is no escape.

There are several factors in the evolution of arthropods that steadily work toward the closing up of this old passageway, or which make the access to it more and more difficult.

In the more primitive arthropods there is ample room for the stomodæum and for the passage through it of a liberal supply of food. But during the phylogeny of the phyllopod-arachnid stock there is a great increase in the volume and compactness of the anterior cranial neuromeres, which narrows in a very marked degree the opening between the nerve cords for the passage of the stomodæum. Moreover, in all arthropods there is a tendency for the rostrum, which represents a fused pair of appendages lying in front of the mouth, to gradually work its way backward, thus covering up the original site of the mouth, or carrying the entrance to it a long way back of its original position. (Figs. 3, 46.) It may then be surrounded by projecting appendages, or it may lie at the bottom of a long atrial chamber, access to which can be obtained only in an indirect or roundabout manner, as in cirripeds (Figs. 274, 275), cladocera and phyllopods (Figs. 7, 9 and 273.)

In many cases, the animal can never bring its mouth in direct contact with its prey. Liquid foods must be pumped through long capillary tubes, formed by the projecting parts of leg-jaws, as in many insects and arachnids; or microscopic organisms must be kicked toward, or into the mouth, by the movements of the legs, or of the posterior part of the body, as in cirripeds and cladocera.

In some cases, a combination of such conditions has actually led, in the later stages of development, to the complete closure of the foregut, as in the adults of certain lepidoptera and ephemeridæ, which cease to feed after metamorphosis; or in certain cirripeds, where the stomodæal opening into the midgut is closed soon after the larval stages. (Figs. 280, 281.)

Thus we may recognize in the arthropods a steady, underlying trend toward a more compact, voluminous nervous system, and toward a less efficient stomodæum. These internal conditions rigidly prescribe the possible modes of life that are open to the animals in which they prevail. The pending extinction of the foregut is the dominant factor in the life history of the arachnids, for it has made a liquid diet, sucked through capillary tubes, imperative. For that reason a blood sucking, or a parasitic mode of life, is practically universal among them, just as sucking the blood of animals, or the juices of plants, is universal in certain groups of insects. In all these cases, the animals appear to be making the best of a desperate situation, adjusting their lives with great precision to meet the inevitable march of events within.

Another important factor in the closing of the old mouth was the conversion of the medullary plate into a medullary tube. This process is well advanced in the arthropods, reaching its highest development in the arachnids. There a true cerebral vesicle is formed that includes the whole forebrain, although the advancing palial fold of the embryo just fails to reach and enclose the oral region. (Fig. 46, *B*.)

In the arachnids we may recognize all the important preliminary steps, such as the formation of neural crests, axial infolding, and a forebrain palium, leading up to the conversion of the medullary plate into a medullary tube. But in no arthropod does the process reach a condition that definitely shuts up the oral opening inside the neural tube, thereby cutting off access to the foregut from the outside world.

But this event does take place in the vertebrates. In the frog embryos, during the open medullary plate stage, we may see a minute pit with a faint prominence in front of it that appears to represent the rostrum and stomodæal infolding of the arachnids. (Fig. 25.) As the medullary plate closes, the pit deepens, giving rise to the infundibulum, or the ancient passageway for the stomodæum, while the epithelial sac that lines it and projects out of it, is the saccus vasculosus and the posterior part of the hypophysis, or the remnants of the stomodæum itself.

We have shown in the chapters on the nervous system that the location and relations of the principal nerve centers and tracts, and especially the location of the primary gustatory and swallowing centers is entirely in harmony with this view.

At just what stage in the closing of the medullary plate, the mouth ceased to communicate with the exterior cannot, at present, be determined. The final closure was no doubt hastened by the crowding of the optic ganglia upward and backward over the oral region. This would leave the broadest part of the primitive brain, *i.e.*, the region of the fourth ventricle and the rhomboidal sinus, wide open; and in this region, which is now covered only by the choroid plexus, there remained, probably for some time, an opening through which the old stomodæum could communicate with the exterior. (Figs. 3, 46, *D.*)

Thus, with the knowledge acquired after the event, we may look back a few million years, and trace with our mind's eye, the slow, inevitable approach and consummation of the most momentous event in organic evolution.

II. The New Mouth.

A group of animals in which the natural growth of one essential part inevitably eliminates some other part equally essential, is doomed to extinction, unless among the organs already at hand a radical redistribution of functions is possible at the moment the critical period arrives. No organ was ever created, we may be sure, to meet an organic crisis in the future, or was ever produced, de novo, at the demand of a present necessity. We are bound to assume that unless a suitable organ stands ready to do the work of the one that has been eliminated, no way out of the difficulty is possible.

Such was the situation when the great crisis in the evolution of vertebrates was at hand; either the evolution of the brain must cease, or a new entrance to the midgut must be established elsewhere. The alimentary organs proved most pliable. But how significant it is that the momentum of nerve growth should so dominate the growth of other organs, and the form of the nervous system so modify that of the whole body!

No doubt one important factor in the competitive development of brain and stomodæum is the increasing volume of the yolk sphere; for the presence of more yolk postpones to a later and later embryonic stage the time when the stomodæum becomes functional, and thus allows the precociously developing nervous system to undergo its early stages of development, unmodified by the action of the stomodæum in feeding.

In the arthropods, a very old organ, the "dorsal organ," or cephalic navel, having originally a very different function from that of alimentation, stood ready to take the place of the old mouth that was being slowly eliminated. Its presence alone made the existence of the vertebrates, as we know them, a possibility.

We have shown in a previous chapter, that the "dorsal organ," in part at least, is the product of the mechanical conditions created by apical growth on a spherical surface. It is, as it were, a vortex center, toward which all the adjacent organs converge. It exists, either actually or potentially, on the anterior hæmal surface of all arthropod embryos, its definitive position being controlled, in any given case, by the shape and volume of the yolk sphere, and by the amount of "cephalization" that has taken place.

"Cephalization" takes place according to a definite law of growth which applies to all segmented animals. According to this law, the lateral members of the anterior metameres tend to atrophy in proportion to their relative distance from the median line and their nearness to the anterior end. In other words, there is a steadily progressive tendency to eliminate by degeneration, the lateral members of the more anterior metameres, and to enlarge and specialize the median ones.[1]

Thus in the higher arthropods there are no fully developed appendages or other somatic organs lateral to the procephalic lobes; and no organs in the lateral plate region of the first nine or ten metameres. The scanty, or degenerating, tissues that form where the lateral organs should be, are gradually crowded by the growth of the more vigorous posterior ones into an oval area on the hæmal surface of the embryo, just behind the forebrain, where the degenerating hæmal blastoderm sinks into the yolk and is absorbed. (Fig. 135.)

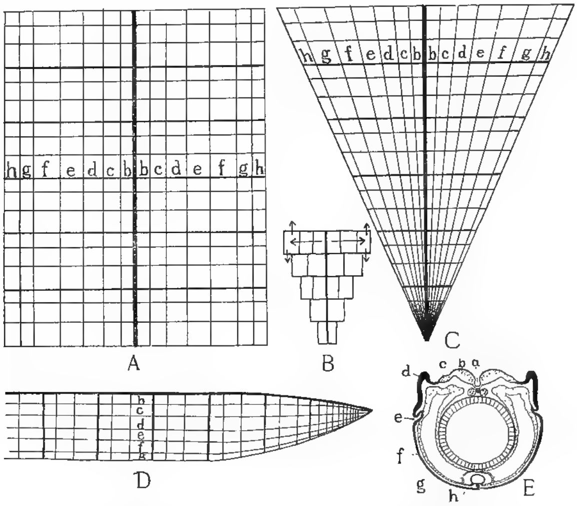


Fig. 156.—Diagrams to illustrate the method of bilateral apical growth. *A*, Hypothetical symmetrical checker board arrangement of unlike parts in mercator projection, seen from the neural surface; The serial equality (homology), of the elements is supposed to be perfect. *B* and *C*, Approximate method of producing such a field by a combination of apical and bilateral division of units. *D*, The same, seen as a cylindrical object from the side. *E*, The same, in cross-section, composed of four, unlike concentric superimposed layers.

In insects, the ruptured embryonic membranes play an important part in this process; they complicate it, but do not alter its essential nature. In many arthropod embryos, the dorsal organ becomes a formal invagination into the yolk, with well-defined epithelial walls, or it may consist merely of a great cloud of ingrowing cells. In both cases, the deeper cells are the first to dissolve in the yolk mass that will later be enclosed within the midgut.

A "dorsal organ" of some such nature as this occurs in all classes of arthropods.

[1] Not to be confused with median fusion and degeneration. See p. 277.

I have called it a cephalic navel, or cephalic fistula, because it is a center of convergent growth; a region of ingrowth, or outgrowth, around the point where the hæmal surface of the head and the gut is finally closed.

The cephalic navel usually closes during the embryonic stages, leaving, in a morphological sense, a barren area behind. But in many cases, either the dorsal organ, or some other organ in the same place, persists as an adhesive disc, or a voluminous outgrowth, by means of which the animal attaches itself to some foreign object. In some parasitic cirripeds, the cephalic outgrowth is buried in the tissues of the host, the old mouth closes, and the animals are then said to absorb nutrition through the walls of the cephalic outgrowth.

We have merely to assume for certain stages a somewhat longer duration than now occurs in any arthropod, to make the dorsal organ a new gateway to the gut; for surely a cephalic fistula leading into the midgut, permanently open at both ends, and used to hold fast to animate, or to inanimate objects, is competent to take the place of the old mouth.

The closing of the old mouth and the evolution of the new one, therefore, was going on in the same animals at the same time. The critical period of substituting one for the other was during the embryonic stages, when both of the organs may have opened into the gut at the same time. During the embryonic stages, a considerable time would be available for readjustment, for owing to the large amount of food yolk in the eggs of primitive vertebrates, a relatively long time might elapse before the absorption of food from without became imperative. Whether the actual closing of the old mouth, or the opening of the new one, took place first or last, is of little consequence, for the consummation of one event would probably accelerate the advent of the other.

III. The Jaws or Oral Arches.

In reconstructing the history of the vertebrate mouth, it is not enough merely to account for the closing of the old mouth and the origin of the new opening into the alimentary canal. To make the account complete, it is necessary to explain the origin of the important organs which surround it, such as the jaws, or oral arches, the hypophysis, tear duct, and the principal outgrowths from the adjacent pharyngeal cavity.

The circumoral organs of primitive vertebrates are best interpreted as the remnants of several pairs of arthropod leg-jaws, or other appendages, that have been crowded onto the hæmal surface by the peculiar mechanical conditions which prevail in the developing head.

An arthropod appendage may be defined as an ectodermic outgrowth consisting of several branches, or stems, located on the hæmal or lateral side of the body, adjacent to the main nerve axis. In the higher forms, *e.g.*, the arachnids, one stem forms the typical appendage. On its median basal margin is a prominent sensory spur, or gustatory organ, from which in the early embryonic stages arises a large ganglion, that lies between the appendage and the medullary plate. (Fig. 136.) On the outer margin there may be a second row of sense organs, and various infoldings of an excretory or respiratory nature. On its posterior basal surface a gill, or respiratory plates or filaments, may be developed.

Each appendage is associated with a hollow block of mesoderm, or somite, that lies beneath the basal lobe, and gives rise to the associated muscular and excretory tissues. (Fig. 134, 138, *so.*) The mesoderm extends beyond the appendages as a thin double layer of cells, the lateral plates, from which the somatic and splanchnic tissues of that metamere, if any are present, arise, *l.pl.* The cavities enclosed in the mesoblastic somites, so long as the somites retain their identity, do not communicate with one another. On the other hand, the space between the somatic and splanchnic layers of the successive lateral plates, is not divided into separate compartments (thorax), or if it is (abdomen), they speedily break down, forming a continuous cœlomic chamber on each side of the body. The third elements associated with the appendages are the outgrowths from the mid-gut that form the so-called "liver lobes," or the enteric diverticula, or the gut pouches. (Figs. 150, 154, 179, 180.)

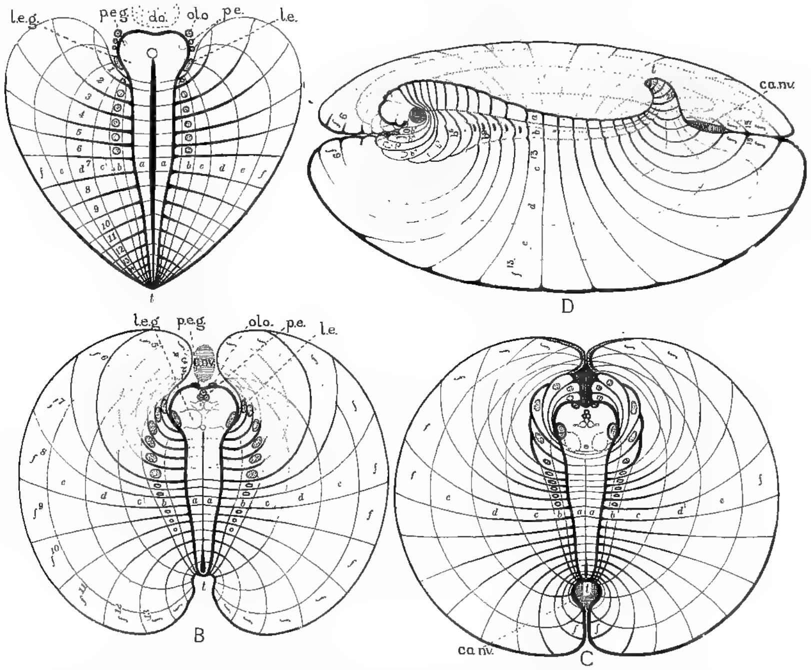


FIG. 157.—Diagrams illustrating the growth of organic films on a nutrient surface. The figures are intended to show how association, and the time element involved in combined apical and bilateral growth of an organic film on a plain, or spherical nutrient surface, automatically creates lines of unlike conditions that are coincident with the lines of morphological and physiological specialization. *A B* and *C*, Successive stages in the growth of such a film, showing the necessarily unlike character of the initial and terminal element (cephalic and caudal), and of the median and lateral ones, and that this unlikeness increases with the progress of growth. *D*, A still older stage, in side view perspective.

In dealing with the morphology of a true segmental appendage, we must recognize and account for these various parts.

As a rule, the free part of the oral appendages in arthropods is very small, or even absent, while the basal portion, the somite, sense organ, and ganglion, may be of considerable size. If this condition is associated, as it usually is in the higher arthropods, with a voluminous and precocious forebrain, a large yolk sphere, and with the absence of lateral plate structures, the tendency during the early embryonic periods will be to raise the forebrain off the yolk surface and thrust it forward, leaving the way open for the basal lobes of the more anterior appendages to unite on the hæmal surface, around the center formed by the cephalic navel. (Figs. 17, 31, 33, 135.)

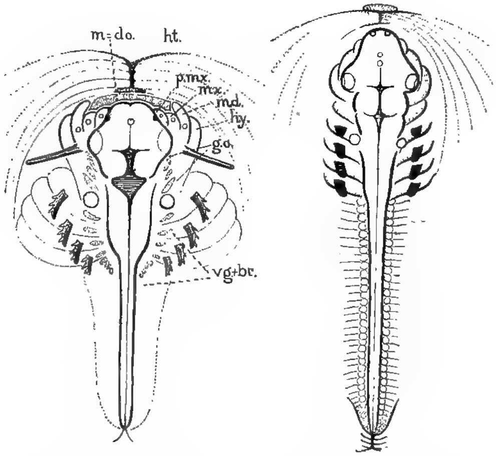


Fig. 158.—Mercator projections of vertebrate embryos.

Under the influence of these conditions, the more anterior appendages in certain adult arthropods have been transferred, either to the anterior surface of the head, to a position halfway between the neural and hæmal surfaces, *i.e.*, the cheliceræ of arachnids (Figs. 17, 43), or almost to the hæmal surface, *i.e.*, the antennæ of cladocera (Fig. 9), and many parasitic copepods (Figs. 282, 283); or they are transferred definitely to the hæmal surface, close to the region of the cephalic navel, *i.e.*, the antennæ in all cirripeds. (Figs. 274, 280.)

It is seen, therefore, that in the arthropods the increasing size and precocity of the forebrain, the degeneration of the lateral members of the anterior metameres, the increasing size of the yolk sphere, and the time factors involved in apical growth on a spherical surface, all conspire to crowd the appendages and their associated parts toward the hæmal surface of the head. (Compare the mercator projections in Fig. 157 with Figs. 17, 31, 32, 158, 160.)

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Development of the Oral Arches in the Frog.—In the embryos of primitive vertebrates, the transfer of oral arches to the hæmal surface of the head is accomplished in the manner indicated for arthropods, and the successive steps in the process may be followed with comparative ease in the frog.[1] In the study of this process in the frog, large numbers of eggs were hardened, usually in chromic or picric acid solutions, the membranes removed by eau de Javelle, and the most sharply sculptured specimens examined as opaque objects, under a strong oblique illumination.

Soon after the closure of the medullary plate one may see the outlines of two or three pairs of faintly marked ridges that represent the earliest stages of the oral arches. (Fig. 159.) Behind them are two pairs of more prominent ones, representing either the first two gill arches, or the hyoid arch and the first gill arch. The primitive oral arches curve downward and forward, eventually uniting between the anterior end of the brain and the anlage of the sucking disc, at the point where the mouth appears later. (Fig. 160.)

The general appearance of the primitive oral arches, and the rate at which they concresce, varies considerably in different embryos, and it has not been possible to identify them with those that are seen in this region at a later period, but the two shown in Figs. 159, 160, appear to represent the anlage of the premaxillary and maxillary arches. After concrescence takes place, the arches, for a short period, become indistinguishable.

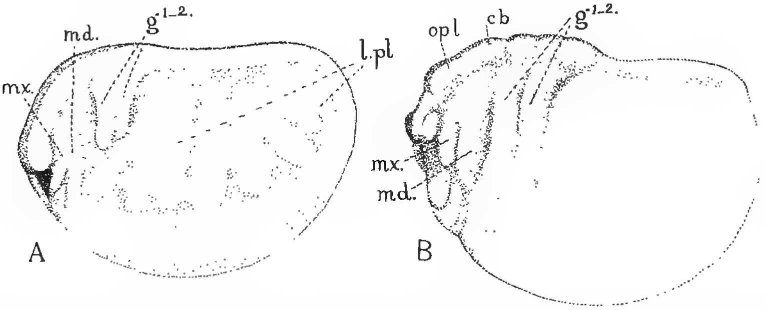

Fig. 159.—Frog embryos, seen from side, showing the extension of the primitive oral arches, gill arches, and lateral plates, toward the hæmal surface. Rana septemtrionalis.

In the following stages (Fig. 161, *A*), the oral region is bounded in front by a conspicuous transverse groove that terminates at either end in the nasal pit, *ol.o.*; on the posterior side it is bounded by the sucking disc. A longitudinal groove now extends along the middle of the intervening space, intersected by three transverse ones, a small pit being formed at each intersection. The oral field is thus divided into at least three pairs of lobes that are clearly serially homologous with one another. The first pair represents the premaxillæ, *p.mx.*, the second, the maxillæ, *mx.*, and the third, the mandibles, *md.*

In the following stages, the lobes become more prominent, and the longitudinal groove becomes deeper and wider, *B* and *C*. The premaxillary lobes then

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[1] Mr E E. Just, 1906, and Mr. A. O. Kelly, 1908, students in biology at Dartmouth, have assisted in working out the history of the embryonic and larval jaws of the frog.

unite, obliterating a part of the median groove. Between the anterior margins of the premaxillary lobes a small pit is left that gradually deepens, forming the anlage of the hypophysis, *D*, *E*, *F*, *hyp.*

The prominent maxillary lobes move laterally and forward and unite with the premaxillæ, although they are still distinctly marked off from them by the second transverse groove, *E* and *F*, *mx.* This groove finally extends past the olfactory pits toward the eyes, probably initiating the formation of the tear duct. The mandibular lobes, meantime, have become very prominent. Later they unite in the median line to form the lower jaw, *E* and *F*, *md.*

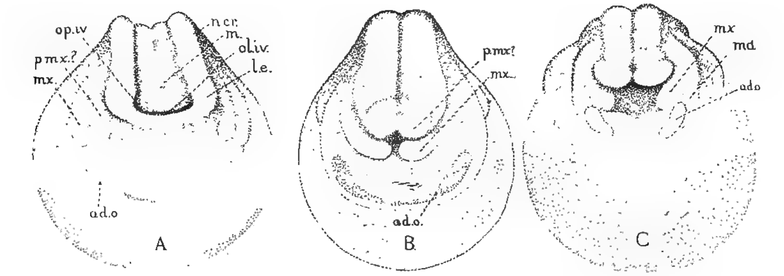


FIG. 160.—Frog embryos seen from the anterior end, showing the concrescence of the oral metamers in front, and on the hæmal side of the fore brain. Rana septemtrionalis.

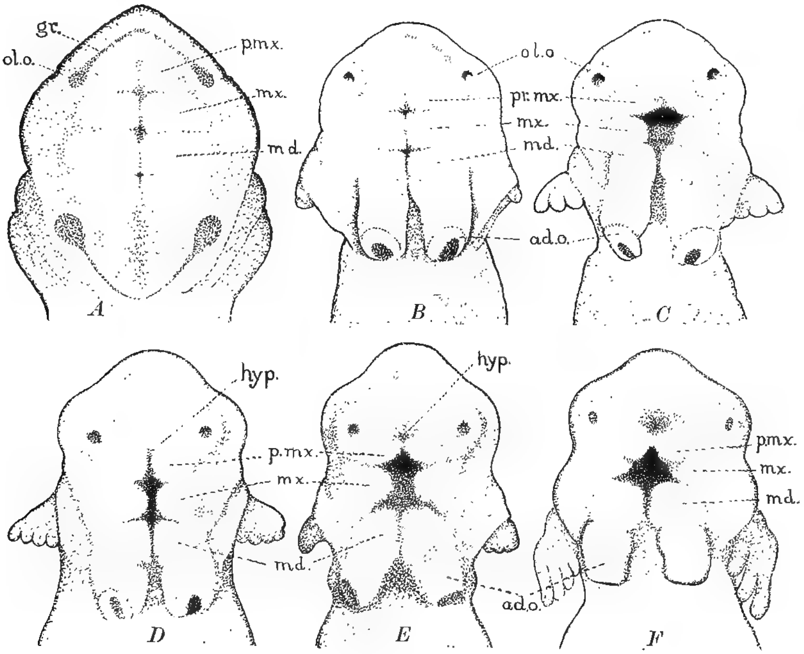


FIG. 161.—Frog embryos, seen from the anterior hæmal sufrace of the head, showing successive stages in the concrescence of the three pairs of oral arches, the pre-maxillæ, maxillæ, and mandibles, and their relation to the apex of the forebrain, to the mouth, hypophysis and sucking discs. R. septemtrionalis.

In the early larval stages, all traces of the paired oral arches have disappeared and we have instead the characteristic larval mouth of the amphibia, with the V-shaped mandibles and the maxillæ sheathed in horn, surrounded by prominent lips. The latter form a shallow antechamber fringed with sensory papillæ, that resembles the pre-oral in chamber Amphioxus, Bothriolepis and the cyclostomes. (Figs. 164, 165, 166, 177–178.)

The mouth itself, owing to the gradual union of the paired arches on the hæmal surface, undergoes a remarkable transformation. It first appears as a very long median furrow. As the anterior end is obliterated by the union of the premaxillæ and the posterior end by the union of the mandibles, the remaining median portion widens, taking on first an hexagonal contour, and then the form of a transverse slit, with a continuous maxillary arch in front and a mandibular arch behind. (Fig. 161.)

The median groove that initiates the opening into the enteron, may be regarded as the remnant of the primitive cephalic navel of arthropods, and its subsequent changes in form, as the result of the way in which the oral arches unite around it.

The anterior end of this groove, or the part lying, during the earliest stages, between the premaxillary lobes, becomes deeper than the rest, and marks the beginning of the mouth, *C*. A little later, this depression is most pronounced between the maxillary lobes, *E* and *F*.

The hypophysis may be regarded as the remnant of a pair of excretory glands similar to those on the outer margin of the anterior cephalic appendages in arachnids. In ancestral vertebrates they were probably situated on the margins of the premaxillary lobes, their unpaired condition being due to the median fusion of the appendages to which they belonged.

The "tear duct" may be regarded as a specialization of the groove that originally separated the maxillary and premaxillary arches.

The development of the mouth and oral arches of the frog may be regarded as the typical mode of development in vertebrates. A condition like that just described is clearly present in other amphibia, as in Amblystoma (Fig. 168), and in the sturgeon (Fig. 174). Even in the mammals we may see indications of the same structure, the fronto-nasal process probably representing in part the fused premaxillary lobes of the frog.

In Bdellostoma, three pairs of oral lobes, comparable with those in the frog are preserved even in adult stages. (Fig. 175.) In petromyzon there has been a greater median fusion, for the remnants of the premaxillary lobes, the olfactory pits, and the hypophysis have apparently been absorbed in a single median infolding lying in front of the maxillary arch.

In the most primitive vertebrate-like animals of all, the ostracoderms, the mouth parts of the adult were in a condition similar to those of Bdellostoma, or to those in the embryonic stages of the frog and sturgeon. (See Chapter XX, p. 373.)

Conclusion.—We may therefore conclude that the mouth of vertebrates is surrounded by at least three distinct pairs of segmentally arranged arches, comparable on the one hand with the gill arches of the postoral region, and on the other with the cephalic appendages of arthropods.

The prevalent view, first advanced I believe, by Gegenbaur, that there is in vertebrates but a single pair of oral arches consisting of the mandibles—the maxillæ being regarded merely as a forward extension of their proximal ends—was based largely on the relations of the skeletal structures of adult fishes, and is clearly untenable.

IV. The Gill Arches and the External Gills.

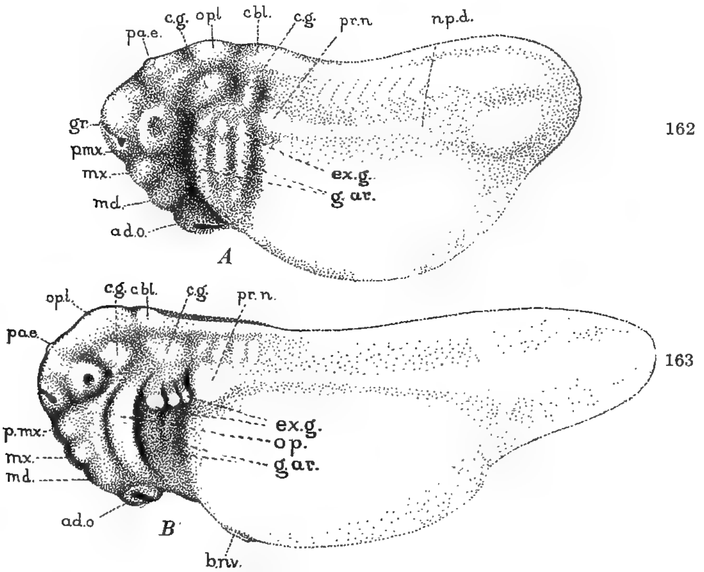
The oral arches are clearly comparable with the gill arches that lie behind them. In the embryos of primitive vertebrates, however, the gill arches, owing to their more posterior position and to the presence of cardiac elements on their lateral margins, do not unite on the hæmal surface of the head, although the more anterior ones move almost as far in that direction as the oral arches do. (Figs. 162, 163, 168.)

A conspicuous feature of the gill arch in primitive vertebrates is the external gill. Budgett has well described them as follows. He states (p. 274), that in Lepidosiren, Protopterus, and in the more primitive amphibia, each gill "arises as an outgrowth from the outer side of the visceral arch, and is composed of a mesenchymatous core with ectodermal covering. . They develop well before the perforation of the gill clefts. . . . and the aortic arch itself is in early stages simply the vessel of the external gill." He concludes that the external gills are organs of great antiquity, which were probably characteristic of primitive vertebrates, not merely larval adaptations of no special significance.

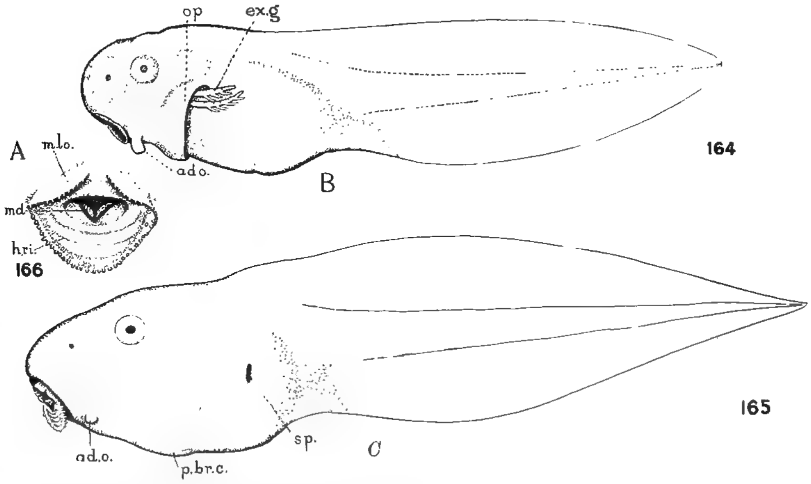
For my own part, I see no reason to doubt that the external gills of vertebrates represent the remnants of the thoracic appendages of their arthropod ancestors, for they strongly resemble them in form, position, and direction of growth. Compare, for example, the external gills of an embryo Protoperus (Fig. 173), with those of an arachnid (Figs. 26–32), and observe also the identity in their arrangement on the mercator projections (Figs. 157, 158), and the details of their structure and mode of branching.

In many primitive vertebrates, similar organs are found on the oral arches. In the larvæ of Amblystoma (Figs. 168, 169), there are long rod-like appendages attached either to the mandibular or to the hyoid arch. These so-called "balancers" are clearly serially homologous with the external gills of the more posterior arches. Similar organs are found in other amphibia, as in Zenopus (Fig. 170); the great oar-like appendages of the ostracoderms are in all probablility of a similar nature.

In the frog, the adhesive discs appear to represent the remnants of vestigial appendages or external gills, belonging to either the mandibular, or the hyoid arch. Note for instance their positions in Figs. 161, *E* and *F* and in Figs. 164, 165, 167, *a.d.o.* In adult cyclostomes in place of these organs, there are three pairs of tentacle-like appendages, belonging apparently to the premaxillary, maxillary, and mandibular arches (Fig. 175); and in embryo sturgeons, there appears to be a pair of similar structures on the premaxillary and one on the maxillary arch. (Fig. 174.) In Polypterus, Budgett has described a "cement organ," similar to the mandibular glands of the frog, located at first in front of



FIGS. 162 AND 163.—Frog embryos, seen from the side, showing the beginning of the external gills, or cephalic appendages, operculum, cranial ganglia, and oral arches. R. septemtrionalis.



FIGS. 164, 165 AND 166.—Young tadpole of R. septemtrionalis. Fig. 164.—Tadpole from the side, showing early stage in the formation of the peribranchial chamber. Fig. 165.—Same; older stage; gills completely enclosed in peribranchial chamber. Fig. 166.—Oral region, from in front.

the mouth, but finally coming to lie inside of it, apparently on the premaxillary lobes (Figs. 171, 172.) Premaxillary discs also occur in Lepidopterus and Amia.

* * * * * * * * *

There can be but one inference from the facts that have been enumerated, namely, that the so-called "visceral arches" of vertebrates represent the basal lobes of the cephalo-thoracic appendages of their arthropod ancestors and; that the external gills, the balancing organs of amphibia, the cephalic oars of ostracoderms, the tentacles, and adhesive discs of the oral arches in embryonic fishes and amphibia are serially homologous structures, representing the remnants of the cephalothoracic appendages themselves.

Similar modifications of the appendages frequently occur in various classes of arthropods. For example, in insect embryos (Blatta and Acilius) the first pair of abdominal appendages are reduced to gland-like discs or cups, very similar in appearance to the cement glands on the oral arches of embryo fishes and amphibia. Beyond this, their function and significance is unknown. In many crustacea, entomostraca, and cirripeds, one or two pairs of degenerate cephalic appendages terminate in adhesive discs by means of which they fasten themselves to foreign objects, or to their hosts, just as larval vertebrates use their cement glands for a similar purpose.[1]

It remains to be seen how far a more detailed study of the structure and growth of the oral arches in primitive vertebrates will confirm the above interpretation. So far as we know, there is nothing in the embryonic history of the mesodermic head cavities, or of the oral arch nerves and ganglia, that conflicts with it, while all the data available concerning the superficial form and the mode of growth of these organs lend it their unqualified support.

V. The Gill Sacs. The Thyroid and the Thymus.

In many fishes and amphibia the external gills disappear and their place is taken by internal gills developed at a later period from the walls of gill sacs or pouches. The latter are formed between the gill arches by an infolding of the ectoderm that unites with a tubular outgrowth from the mesenteron. It is not clear whether the new gill lamellæ arise solely from the entodermic, or from the ectodermic part of the gill chamber, or from both, although the prevalent opinion strongly favors the first alternative.

However that may be, it is a fact, the significance of which is readily apparent, that in the arachnids there is the same kind of gill sacs, having the same relation to external appendages, located in the same region of the head, and having the same relation to enteric outgrowths, as in the embryos of primitive vertebrates.

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[1] The origin of the secreting surface of the cement glands from the endoderm is not in conflict with this view. It merely confirms the interpretation of the several oral arches as serially homologous with the gill arches.

In the crustacea the gill usually consists of a special plate, or plume-like process arising from the basal lobe of a biramus appendage. In Limulus and in the eurypterids, it consists of many lamellæ arising from the covered posterior basal surface of the abdominal appendages. (Fig. 5.) In abnormal limulus embryos, the thoracic appendages are often completely infolded, forming a leg pocket instead of a leg process, suggesting the infolded respiratory appendages that have become the normal condition in the air breathing arachnids. In the case of the scorpion, the respiratory lamellæ arise from an infolding just behind a small, rudimentary appendage; the latter then disappears without forming a part of the gill chamber.

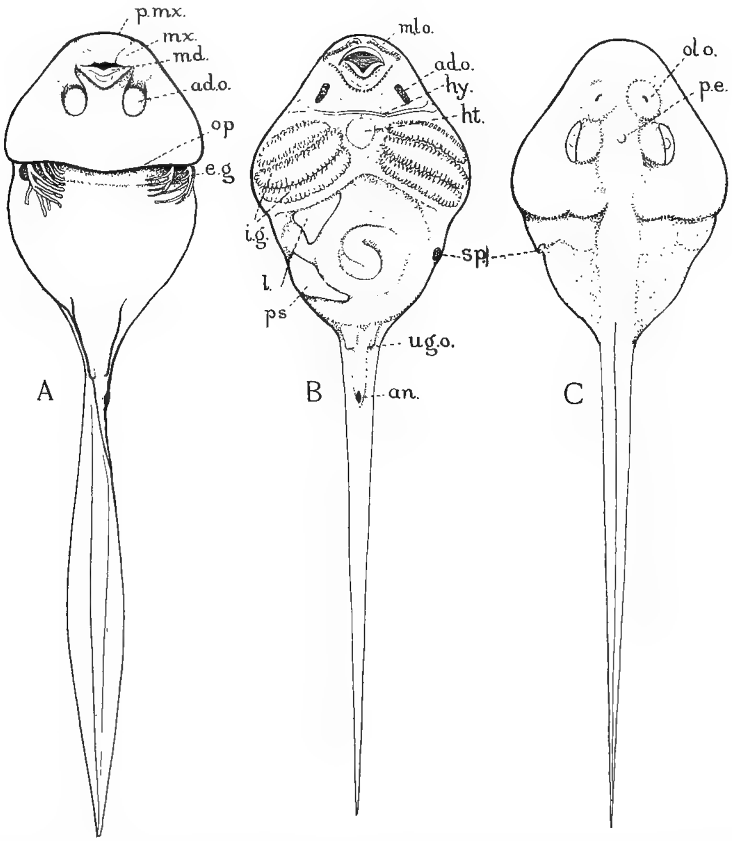


Fig. 167.—Tadpole of frog. *A*, Hæmal surface; *B*, older stage, seen from the hæmal surface as a semi-transparent object, and showing the relations of the oral, respiratory, and digestive orgas; *C*, same specimen from the neural surface. Figs. 164 to 167 show frog tadpoles in the ostracoderm stages.

Without going any further into the discussion of the infinite variety of arthropod respiratory appendages, these facts stand out clearly, namely: 1. there is a tendency to restrict the respiratory function to a small group of metameres, four or five in number, more or less, following the oral or locomotor ones; 2. that in the true respiratory appendages, the non-respiratory part is often rudimentary or absent; and 3, that in the higher forms of arachnids, the respiratory part of the appendage is deeply infolded to form the walls of a gill sac.

We conclude from the above facts that approximately the same group of appendages, which in the arachnids have become partly or wholly infolded to form the respiratory sacs, have retained that function in primitive vertebrates, and have given rise to the ectodermic portion of the visceral clefts, or branchial chambers. We also conclude that no vertebrate, however primitive, ever possessed

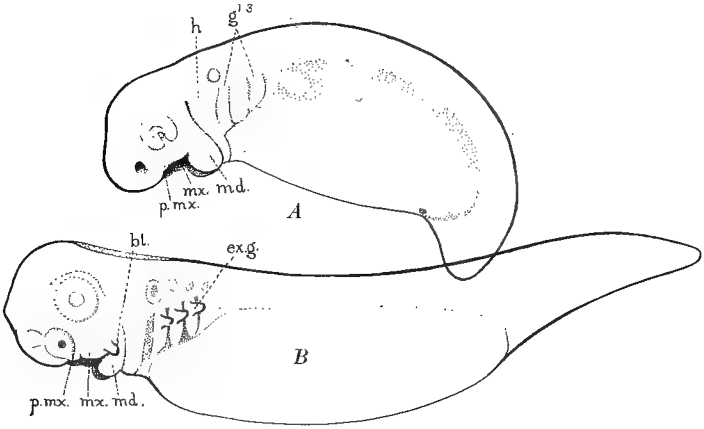


FIG. 168.—Amblystoma larvæ, showing the vestigeal cephalic appendages in the form of external gills, or the "balancers" of the oral arches.

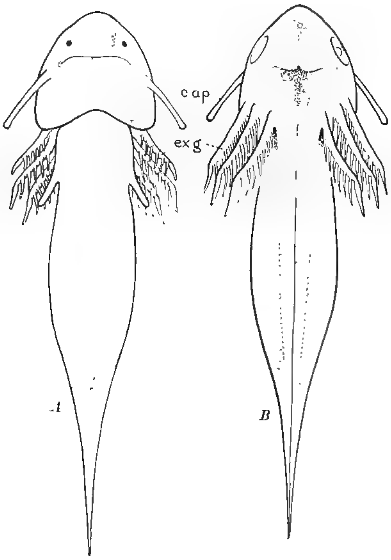


FIG. 169.—Amblystoma tadpole, showing the balancers," *c.a.p.*, at the height of their development.

functional gill-clefts in front of the hyoid arch metamere or any considerable distance back of the metameres which are now provided with gills in typical fishes.

VI. The Gut Pouches.

The midgut of the arthropods, in its typical condition, may be regarded as a straight tube with lateral diverticula, or pouches segmentally arranged. In primitive crustacea there may be either a single unbranched diverticulum directed forward and hæmally from the anterior end of the gut, cladocera (Fig. 9); or one or more pairs of branching lobes, as in phyllopods (Fig. 273), and many cirripeds. (Fig. 275.)

In the arachnids the gut pouches of the thoracic and abdominal regions become very highly developed, forming one of the most conspicuous features of their internal structure. Their structure and development is clearly seen in Limulus. Here the cephalothoracic yolk mass gradually breaks up into six pairs of lateral lobes. (Figs. 149, 150, *lv.l*$^{1-6}$.) The five anterior pairs form a group by themselves and open into the midgut by a single channel. The sixth pair may be distinguished from the others by its larger size, the absence of enclosed cells derived from the hæmal blastoderm and by the fact that it opens into the gut by a separate channel. (Fig. 151 *lv.l*^{6}.)

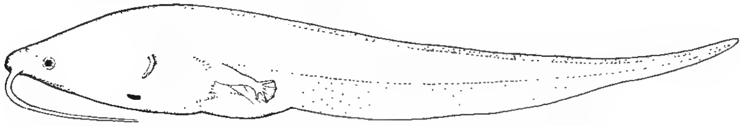
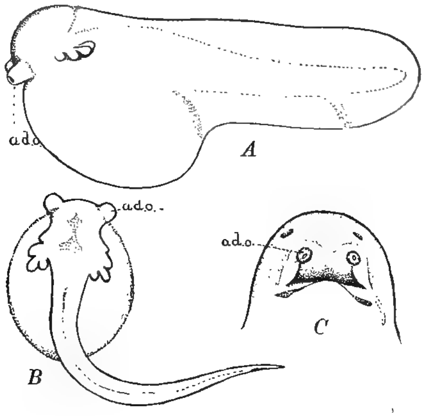


FIG. 170.—Tadpole larva of Zenopus lævis, Daud. After Bles. 60mm. long.

In the later stages, a pair of lobes develop from its hæmal surface and extend forward and backward, forming the anlage of a special system of hæmal gut tubes. (Figs. 151, 154 *a.b.*) In the adult, the extensive ramifications of the lateral tubes fill the greater part of the cephalothorax, the branches of the posterior hæmal tubes, *b*, being apparently the only ones that extend into the abdomen. In the young scorpion, a similar arrangement is seen. (Fig. 179.) The sixth pair, the so-called salivary glands, *l.t.l.*, are large and open, as in Limulus, by separate ducts. The five anterior pairs *a.t.l.*, are reduced to small blind pockets. The hæmal lobes *h.t.l.*, are well developed, the large anterior horns extending forward, over the hæmal surface of the forebrain. (Fig. 43.) In the branchial region, there are six pairs of pouches, the first corresponding to the comb segment, the next four to the lung books, and the sixth extending backward into the last mesothoracic segment. (Figs. 43, 179.)

In the pedipalpi, the large hæmal lobes of the thorax are united by a transverse anastomosis. In the pycnogonida and in the spiders, the long thoracic diverticulas are unbranched, and may extend a considerable distance into the base of the legs. (Fig. 180.) In the spiders, there are also four pairs of abdominal pouches.

In primitive vertebrates, a variable number of lateral gut pouches are formed belonging to the postoral group of metameres. They unite with the adjacent gill pockets, and thus establish a communication between the gut and the exterior, via the enteric diverticula and the ancestral gill pockets.



171

172

FIG. 171, 172.—Larva of Polypterus senegalus, showing rudimentary maxillary appendages, or adhesive papillæ. After Budgett.

What caused the opening of one organ into the other in ancestral vertebrates we do not know, any more than we know why it actually takes place now in the embryos of modern vertebrates. For our present purpose, it is sufficient to show that in the arachnid ancestors of the vertebrates the gill pockets and enteric diverticula stand in the same relation to each other and to the rest of the head that they now do in vertebrate embryos before the perforation takes place. We are here dealing with one of those cases where there are no intermediate stages between two very different conditions, for either the gut tubes open into the gill chamber, or they do not; if they do, we are dealing with animals of the vertebrate type; if not, with those of the invertebrate type.

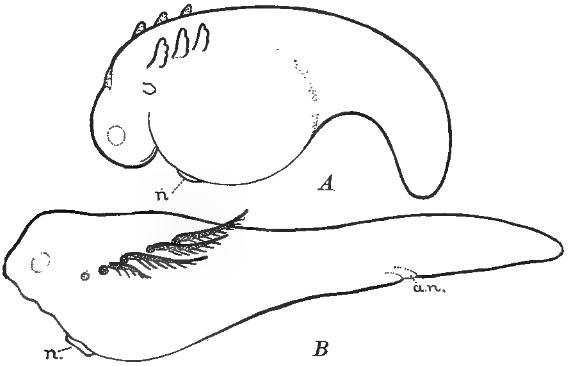


FIG. 173.—Larvæ of Protopterus annectens, showing the highly developed external gills. *A*, Seventh day embyro; *B*, tenth day. After Budgett.

The most anterior of the lateral gut pouches in the vertebrates correspond with those of the locomotor appendages of the arachnids. They probably atrophied in the immediate ancestors of the vertebrates, neither communicating with the exterior, nor leaving any definite organs behind.[1] The paired hæmal outgrowth of the thoracic gut probably persists as the thyroid gland, with which it agrees in position and direction of growth. (Figs. 43, 44, 308.)

In the arachnids the free ends of the lateral and of the hæmal enteric pouches of the thorax are usually branched, or lobular, or racemous, the subdivisions consisting of a single layer of cylindrical secreting cells that suggest, in their general appearance, the condition presented by the thyroid in vertebrates, and by those organs resembling the thyroids that arise from the walls of the visceral clefts.

The thymus probably represents a modification of the several pairs of thoracic coxal glands that occur in the arachnids.

The postbranchial outgrowths of the vertebrate mesenteron, *i.e.*, the lungs, liver, and pancreas may be regarded as local specializations of enteric diverticula comparable with the endodermic portions of the visceral clefts. (Figs. 181, 182.)

VII. The Locomotor Appendages.

A. The Cephalic Appendages.—In the higher arthropods, locomotion is effected by several pairs of jointed appendages arranged in strictly segmental order, and usually located anterior to the respiratory region. (Figs. 3, 4, 5.) In true vertebrates the locomotor appendages are always situated behind the gills; there are never more than two pairs; and they have no fixed relation to the metameres. (Fig. 4, *B* and *C*.)

The meaning of this sharp contrast will appear after a more careful examination of their structure and serial location in the two groups, and in the intermediate one formed by the ostracoderms.

In free swimming phyllopods and arachnids, there may be one pair of large oar-like appendages that arise from the anterior end of the thorax, as for example the antennæ of many cladocera and entomostraca, or the elongated cheliceræ of Pterygotus. Or such a pair may arise from the posterior part of the thorax, as in Eurypterus. (Fig. 5.) In all these cases the locomotor appendages lie in front of the respiratory region.

In typical vertebrates the paired locomotor appendages, if present, consist primarily of two lateral folds that extend from the postbranchial to the precaudal region. The pectoral and pelvic fins are local expansions of these folds. The paired fins are not definite segmental structures, for they consist of muscle buds and cartilages derived from a large and varying number of metameres.

As there are approximately sixteen or more metameres in the vertebrate head,

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[1] Possibly they may be represented by the "lateral thyroids" and by the diverticula leading into the cement glands of amphibia.

it is clear that the paired fins of vertebrates cannot represent any arthropod appendages in front of the sixteenth pair.

The clue to the whole problem of vertebrate and arthropod locomotor appendages will be found in the ostracoderms, where both cephalic appendages of the arthropod type, and lateral folds of the trunk, like those in true vertebrates, are present.

In Bothriolepis oar-like cephalic appendages are present that clearly belong to the anterior division of the head, for they lie immediately behind the oral arches and in front of the gills. (Fig. 4, *A*, 247.) In Cephalaspis the large paddle-shaped appendages are of the same general nature and lie in a similar position. (Fig. 232, 234.) In Tremataspis portions of armored appendages have been found similar to those in Bothriolepis, that fit into the most anterior of a series of nine pairs of notches, or openings. The eight posterior pairs served either for the attachment of smaller appendages, comparable with external gills, or as openings to respiratory chambers containing the internal gills. (Fig. 236.) In Cyathaspis, Drepanaspis, Palæaspis, and Pteraspis, there are indications of external cephalic appendages in the form of armored "oars" like those in Bothriolepis, or in the form of naked tentacles. (Figs. 244–246.)

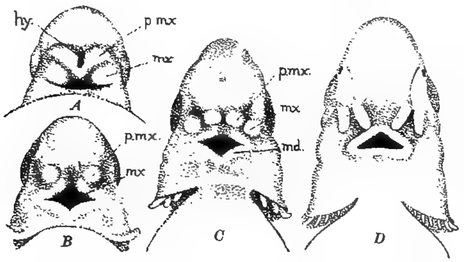

FIG. 174

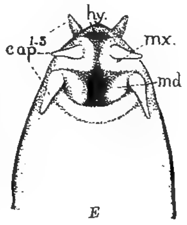

FIG. 175

FIG. 174.—Embryos of the sturgeon; showing the rudimentary cephalic appendages of the oral arches. After Salensky.

FIG. 175.—Oral region of an adult Cyclostome (Bdellostoma) showing three pairs of rudimentary oral-arch appendages. Compare with the oral arches of an amphibian embryo, Fig. 161.

The cephalic appendages of the ostracoderms no doubt represent the same kind of organs as the external gills, the balancers, and the oral arch tentacles of primitive vertebrate embryos, and all these structures probably represent various modifications of the cephalothoracic appendages of the arachnids.

B. The Fringing Processes and the Lateral Fold.—In those ostracoderms that are well enough preserved to show the shape of the body, the postcephalic portion has a triangular outline in cross-section, with either a series of distinct separately movable plates of peculiar structure on either margin, or a continuous membranous fold, with or without, supporting specules or minute ossicles.

In Bothriolepis the trunk was practically naked and was provided with two narrow membranous folds projecting freely from the hæmo-lateral margins. The folds extended from the root of the trunk backward, uniting with each other on the hæmal surface at the base of the caudal fin. (Fig. 248.) This fold is usually sharply defined and shows no trace of subdivisions or of supporting rays.

In a small undescribed species of Cephalaspis from Dalhousie, N.B., a similar fold is present, but it appears to be strengthened by minute, ill-defined spicules. (Fig. 234.)

In the larger species, like C. lyellii and C. murchsonii, in place of a membranous fold, there is a series of separately movable processes, segmentally arranged and covered with a dermal skeleton having the same surface ornamentation as that on the rest of the body. There is nothing in true fishes exactly comparable with these remarkable structures.

In C. lyellii (Fig. 232), the fringing processes hang freely away from the trunk, in a nearly vertical position, with their distal ends bending backward in graceful curves. Each process has a slender neck and rounded head that fits into a cup-like depression on the posterior ventral margin of the large dorso-lateral trunk scales. (Fig. 233, *C.*) There are from twenty to thirty pairs, beginning just back of the cephalic shield and gradually decreasing in size from that point toward the tail end. The most posterior ones are reduced to mere spines or rhomboidal plates, loosely articulated to the lateral trunk scales.

In C. murchisonii the fringe plates are distinctly lobed, and overlap one another so that their flattened surfaces are directed diagonally forward and outward. (Fig. 233, *D.*) In Cephalaspis pagei they appear to have a similar shape and arrangement, but are armed with coarse projecting spines that give them a decidedly arthropod appearance. (Fig. 233, *E.*)

There can be no doubt that the fringing processes represent an initial stage in the formation of a lateral fold like that in the embryos of true fishes. They may be regarded as small segmentally arranged locomotor appendages comparable with arthropod abdominal appendages, but belonging to metameres lying farther back than any that occur in that class of animals. An alternative interpretation would be to regard them as a series of overhanging pleurites like those in the trilobites and in many other arthropods.

We may therefore conclude that the oral arches, gill arches, external gills, "balancers," the lateral folds of vertebrate embryos, the cephalic oars and fringing processes of the ostracoderms, are various local modifications of one set of serially homologous structures, that are in turn comparable with the segmental appendages of arthropods. The pectoral and pelvic fins of true vertebrates are to be regarded as comparatively recent modifications of the lateral folds, and as containing the remnants of a large and varying number of such appendages.

This interpretation of the origin of the paired appendages gives us precisely what Gegenbaur claims has heretofore been lacking in the lateral fold theory, namely: 1. a reason for the existence of the primary fold of ectoderm that initiates the formation of the lateral fold; 2. a reason for the migration into it of segmental detachments of muscle, nerve, and cartilage; and 3. a primary function for the lateral fold, out of which a set of locomotor organs could be logically developed.

Conclusion.—A general survey of the appendages throughout the arthropod-vertebrate stock reveals a steady and logical progress in their specialization. Sensation, feeding, locomotion, respiration, and reproduction are alike essential functions, but they do not make their local appearance at the same time phylogenetically or ontogenetically; or make the same demands for space or for special locations. Sensory and feeding appendages, for example, must be located near the mouth, which is the oldest organ of the body, and the first one to be formed. Locomotor appendages must be located where they can raise and move the primitive head, or in the later phases of evolution, lift the whole body and support it in a properly balanced position. Respiration, circulation, excretion, and reproduction make no such imperative demands for special locations or for early development.

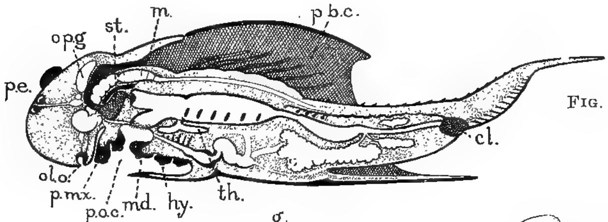

FIG. 176.

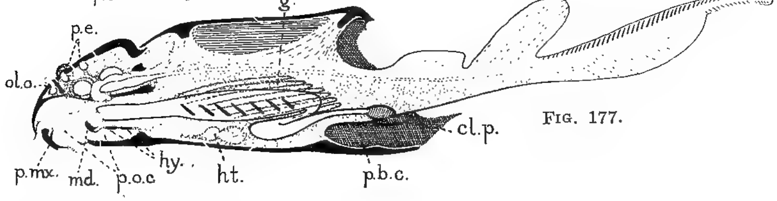

FIG. 177.

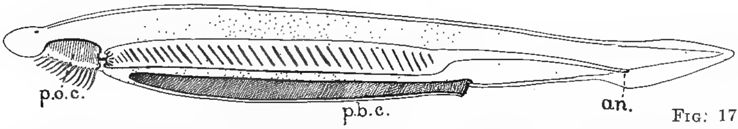

FIG. 178.

FIGS. 176 TO 178.—*A*, Hypothetical form in median section, indicating the probable arrangement of organs in an intermediate condition between that in an arachnid and an ostracoderm; *B*, median section of an ostracoderm (Bothriolepis) showing the arrangement of the internal organs; in part, hypothetical; *C*, Amphioxus, in median section. Diagrammatic.

Thus there is established in the appendages, at a very early period, a definite linear sequence of functions that coincides with the sequence in the historical evolution of the functional demands made upon them.

In other words, the oldest organs phylogenetically, and those first in demand ontogenetically, are laid down first in time, and consequently at the head end of the series, because growth in segmental animals always takes place by a process of addition at the tail end. Those organs that make no special demand for location or for prior use, even though they may have an equally long pedigree with the rest, are gradually relegated to the more recently added territory in the posterior part of the body.

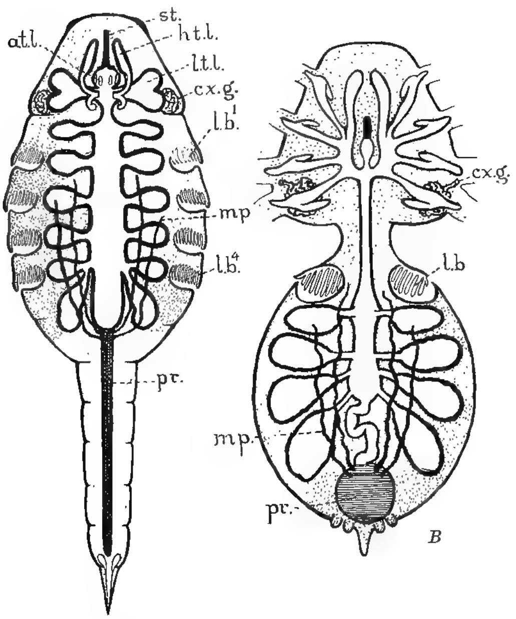

Fig. 179. Fig. 180.

Figs. 179 and 180.—Diagrams showing the location of the principal viscera, such as the enteric pouches, coxal glands, malpighian tubules, lung books and gills. *A*, Scorpion; *B*, spider.

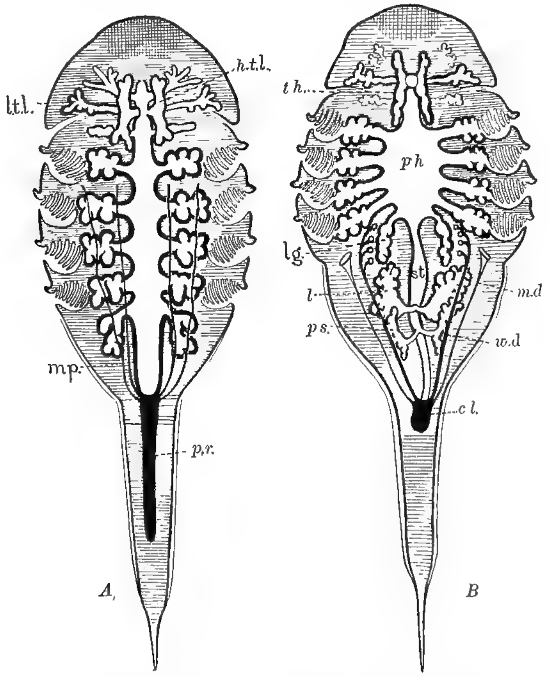

Fig. 181. Fig. 182.

Figs. 181 and 182.—Hypothetical forms leading to the condition in vertebrates.

In accordance with these principles, the linear distribution of functions in the following order: sensory, feeding, respiratory, and reproductive, becomes very early established, and thereafter suffers but minor modifications throughout the entire range of the arthropod-vertebrate series. For example, in the arachnids the procephalic appendages are mainly sensory, the dicephalic, masticatory, the mesocephalic, locomotor, and the metacephalic, respiratory and reproductive. The boundaries to these divisions are not always sharply defined, and there may be some overlapping of functions, but not enough to invalidate the general law.

One of the more recent changes in this primitive distribution of functions to the appendages was the transfer of the locomotor organs to a postcephalic position, owing largely to the increased number of metameres and the consequent shifting of the center of balance backward.

CHAPTER XV.

VARIATION AND MONSTROSITIES.

The study of variation is an important aid to phylogeny, for with the ever shifting conditions within and around a center of life, that which is now an occasional phenomenon, or "abnormality," may under other conditions become a "normal" or constant result. Thus the abnormal of to-day may have been the normal of yesterday, or the normal of to-day the abnormal of tomorrow.

The minute variations expressed toward the close of development, and which at most are only productive of new species, or even genera, are not likely to be the sources of those fundamental changes which give rise to new classes. In our problem, therefore, we should consider those early embryonic variations in vertebrates that are likely to reveal the structure of their remote ancestors; or failing that, we should seek for embryonic variations in arthropods that might have produced a vertebrate; for if we know the broad limitations to the range of variation in a given animal, we may feel a reasonable confidence that we can roughly define all the principal forms in which the ancestors or the descendants of such animals could be expressed.

To begin such a study, it is necessary to have an inexhaustible supply of embryonic material that is easy to prepare, easy to observe, and easy to separate the abnormal from the normal. I know no other animal in which these conditions are so happily fulfilled as in Limulus. The eggs may be obtained in hundreds of thousands and when properly prepared, the checkerboard arrangement of organs can be easily observed in their normal and abnormal conditions. The abnormal embryos may be obtained in great numbers by placing the eggs from many different nests in running water. In due time, eight to ten weeks, the normal eggs hatch and the free swimming larvæ are carried off in the waste. The five or ten per cent. that remain are apparently sound and healthy, but among them will be found all the different phases of abnormality likely to occur. There are pygmies and giants, in early and late stages; some are legless, others headless, or tailess, or consist of fractional parts, such as halves, quarters and smaller divisions, in endless combination and variety. Then there are doublets and triplets in various stages of progressive or regressive growth.

As all the eggs develop under similar conditions, the cause of these various abnormal forms must be referred not to the unusual environment of a modern hatching jar, but to variable conditions in the eggs themselves, that were probably as frequent millions of years ago as they are to-day.

These variations are much greater and more numerous than one might have expected in such an ancient type as Limulus, although there is no reason to believe that the range of variation in Limulus is exceptional.

Our observations show that there is a very small range in the kind of variation, for it is of a plus or minus nature in practically all cases. They also show that the normal forms follow a set course; extreme divergence from it leads to complete extinction by a process of degeneration that is the reverse of the process of generation, the various organs disappearing in the same order in which they made their appearance.

I. Invaginated Appendages.

This common abnormality consists in the transformation of the usual outgrowing appendages, in whole or in part, into ingrowing pockets.

The infolding may take place in the comparatively late stages of its development, only the tip of a well developed leg being infolded (Fig. 183, *C.*); or the entire leg may, from the beginning of its development, grow inward instead of outward) forming a deep pocket opening outwardly by a transverse slit. (Fig. 183, *B.*,

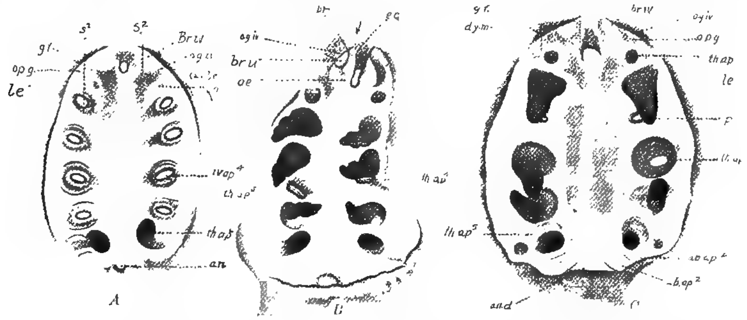

Fig. 183.—Three Limulus embryos in about the same stage of development (stage G-H) and drawn to the same scale. They show the variations in the size of the appendages, and of the embryos as a whole; also the varying extent to which the appendages are infolded. *A*, All the thoracic appendages are invaginated, except the first and last pairs; *B*, the fourth pair completely invaginated; *C*, the third pair completely invaginated, and the tip of the fourth appendage of the right side. Camera.

Any thoracic appendage, except possibly the first, may be invaginated. In a given embyro the infolding may affect one appendage, or a pair, or several appendages on one, or on both sides. Infolded legs are found in otherwise normal embryos, or in those presenting other abnormalities; never in the adult.

The conditions under which they occur clearly show that they are in all probability produced by some special condition within the appendage itself, not by local pressure, or by any other external cause.

The frequent occurrence of invaginated appendages in Limulus embryos is an important fact. We may infer that similar "abnormalities" occurred in other arachnids and for some unknown reason became "fixed" or " normal," giving rise to the infolded abdominal appendages which form the basis of the lung books. In the tunicates, in Balanoglossus, and in vertebrates, similar respiratory pouches or ingrowths occur, but in these cases they have become perforate at their inner ends, and open into the cephalic diverticula of the alimentary canal.

II. ASYMMETRY.

It has been shown that in typically segmented animals the organs are arranged symmetrically, in checkerboard fashion, on either side of a median line. (Fig. 157.) Asymmetry occurs when any of these paired organs differs in form from its mate on the opposite side. If this local variation occurs, all the other parts of the body respond to it by a change in position or form. A common form of asymmetry is the reduction in size, or the absence of certain organs on one side of the median line. In such cases the opposite half of the body tends to form a spiral or circle, with the defective area as its center.

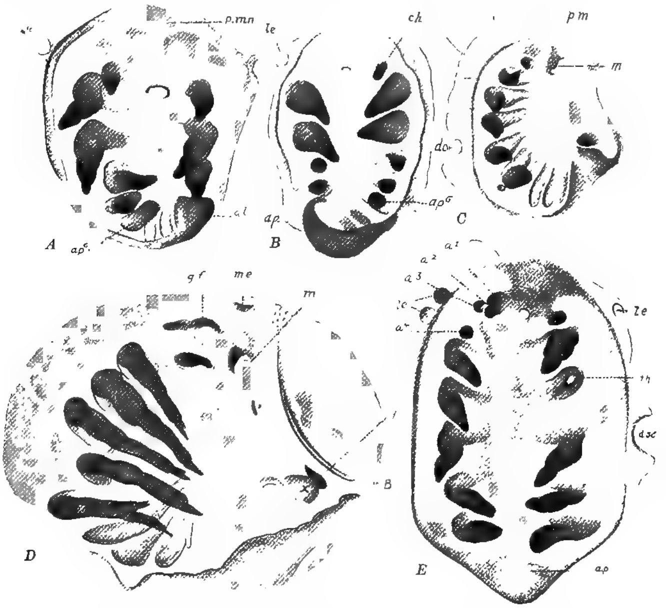

FIG. 184.—Limulus embryos of different ages, showing various forms of asymmetry, due either to the absence of organs usually present, or to the presence of extra organs on one side of the median line. *A*, The right side of the abdomen and the right half of the last three thoracic metameres, absent. ×30 *B*, Left half of abdomen and left chelicera absent; posterior thoracic appendages abnormally small; cam. ×30. *C*, Right half, except the sixth thoracic appendage, absent; cam. ×16 1/2. *D*, Stage L. M. (about ready to hatch). Right half of nerve cord is present but all the other structures of the right side are absent, except traces of third(?) and sixth thoracic appendages, and the margin of the thoracic and abdominal shield; cam. ×30. *E*, Stage G. H. There are two lateral eyes and four chelicerae on the left. The apex of the third thoracic appendage on the right is invaginated; cam. ×30.

It is generally assumed that the morphological unit of segmented animals is the metamere or a complete transverse row of organs. But it appears that in Limulus, and no doubt it is true of other animals also, the right and left halves of a metamere attain a higher stage of organic unity, are more variable than the metameres themselves, and should be regarded as the true morphological units.

Asymmetery is a common abnormality in Limulus and is expressed in a variety of ways. It is most easily observed in the appendages, but in most cases, apparently, changes in them are accompanied by similar ones in the corresponding half neuromeres, the somites, and sense organs.

A. Multiple Organs.—Asymmetry due to the presence of extra organs on one side is very rare. A good illustration is seen in Fig. 184, *E.*, where the first thoracic half metamere has divided twice, giving rise to two half neuromeres, two left lateral eyes, and four imperfectly divided left chelicerae.

B. Defective Organs.—Asymmetry due to the absence, or reduction of appendages is very common, and apparently occurs as frequently on the right side as on the left, and as frequently in the thorax as the abdomen. (Fig. 184.) But half embryos like that in Fig. 184, *C.*, are very rare. Here all the organs on the right side, except what appears to be the sixth leg, are absent; the left side appears perfectly normal except for its curvature toward the right.

Asymmetry similar to that seen in Limulus has become a fixed character in certain groups of arthropods, *e.g.* hermit crabs and bopyridæ. The radial symmetry of the echinoderms was brought about by the loss of one side of the body probably in some arthropod-like ancestor. The remaining side taking the form of a closed ring established a successful organic union and laid the foundations for a new type of radiate structure and a new class of animals. See Chapter XXIII, p. 421.

III. DEGENERATION.

A. **Median Fusion and Antero-posterior Degeneration.**—This remarkable phenomenon is so common, and has been observed in so many different stages, that there can be no doubt of the manner in which it takes place. The process starts in the anterior metameres and is taken up by the following ones in numerical order. In the typical cases, each organ unites with its fellow of the opposite side to form an unpaired organ, which then disappears. Those nearest the median line unite first, and after they degenerate those lateral to them unite and degenerate in the order of their position, till the whole of the metamere has disappeared. As the process in one metamere is always a step in advance of that in the next posterior metamere, A-shaped embryos are produced showing various stages in the progress of degeneration. The successive steps are most clearly shown by the appendages, the dorsal organs, and the nerve cords. The other paired organs probably fuse and degenerate in the same manner, but their history is not so easily followed. Toward the close of degeneration we may find, at what was the posterior end of the embryo, either a median row of unpaired organs, or an exhausted mass of cells, and finally they may in their turn disappear, leaving no trace of the embryo behind.

An examination of the different stages of the process (Figs. 185, 189) shows that as the neuromere disappears, the corresponding appendages approach each other and unite, fusing at the base first and at the tip last. The large unpaired leg thus formed first becomes long, slender, and often coiled and twisted; later, it shortens, becomes smaller and smaller, and finally disappears.

The process of degeneration may be best understood by a consideration of the normal structure of bilaterally symmetrical animals and the way in which it is produced. This may be illustrated by a diagrammatic mercator projection of its superficial organs. (Fig. 192, *A.*) Here the line, *A.P.*, represents the cephalo-caudal neural line; each lettered square represents a paired segmental organ, and each transverse row a metamere. The middle section shows five body metameres with the typical arrangement of segmental organs, from the neural series, *a.a.*, to the hæmal series, *e.e.*

The apex of the figure, *m.A.n.*, illustrates the progressive elimination of lateral segmental organs in the head region, and the predominance of the neural ones. The lower part, *L.P.R.*, shows the order in which the organs arise by apical growth. In this process we may recognize two distinct factors, or two different kinds of growth. One gives rise to a longitudinal series of similar metameres, the new ones always appearing just in front of the apex and behind the one previously formed. The other produces a transverse row of unlike organs, *i.e.*, neuromere, ganglion, leg, sense organ, nephridia, heart, etc., extending from the median line outward, the most highly specialized ones being at the median end of each row.

The relative age of each organ, and its degree of specialization is therefore a function of its position in relation to these two axes of growth.

Degeneration takes place in the following manner: the most median organs of the first metamere, *a* and *a*, unite to form an unpaired organ, *A*, which then disappears, followed in the same way by *c. d.* and *e.* The same thing takes place in all the following metameres, the process in the second metamere being one step ahead of that in the third, and so on.

If the process proceeds till the first two *e's* of Fig. 192, *A.*, are united, all the organs within the area, *a.m.A.n.a.*, will have disappeared, and those that were on the margins of this area will form a median row of unpaired, unlike organs, *E.A.*, arranged from before backward in the reverse order of that on the half metamere. (Fig. 192, *B.*) Embryos in which this condition is approximately realized are shown in Figs. 185 and 189. The condition is shown in diagrammatic form in Fig. 191.

This mode of degeneration, therefore, takes place according to a definite law, and creates an entirely new, heretofore unrecognized architectural type. This type is fleetingly represented in degenerating Limulus embryos, and probably in many other segmented animals also. The animals in which this condition became established in the adults would form a new class.

* * * * * * * * *

B. **Hour-Glass Embryos.**—Precisely the same kind of median fusion and degeneration may appear at other points in the body, forming marked transverse constrictions, or even complete fission. A common condition is where the constriction appears in the middle of the thorax forming the hour-glass embryos, as in Fig. 189.

Several other minor zones of transverse constrictions may be recognized. They are formed at the points where a reduction in the size of organs and a tendency to undergo median fusion takes place in the adults of other groups of arthropods. They divide the body more sharply than usual into cephalic lobes, oral, thoracic, vagal, and abdominal regions. Each of these regions, or tagmata, may show traces of degeneration from before backward, independently of the others, and in the same manner that we have seen in the whole embryo.

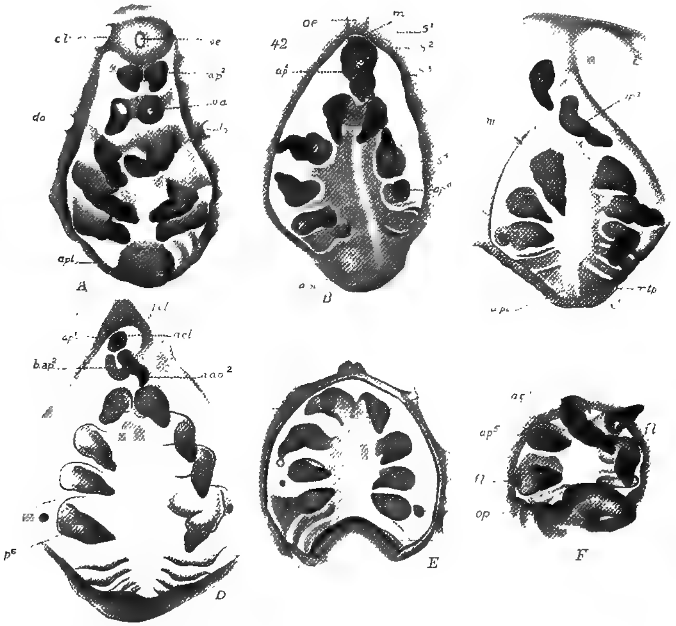

FIG. 185.—Limulus embryos in various stages of degeneration; all drawn to the same scale. The process consists in the union in the median line, and the subsequent degeneration, of the right and left organs of each metamere. The organs nearest the median line are the first to unite, forming a single extra large organ having the characteristic features of each member of the pair. The unpaired organ then decreases in size till it completely disappears. In its place the organs lateral to it, on the same metamere, unite, and in turn degenerate; and so on till the whole metamere has disappeared. The process begins in the most anterior metameres, and progresses in a cephalo-caudal direction. In typical cases, as soon as the first unpaired organ formed in, say, the first thoracic metamere, has disappeared, the same organ is found unpaired in the second metamere; and by the time that has disappeared, the unpaired condition of that organ obtains in the next following metamere; and so on, till every paired organ has become median and unpaired, and then disappeared. In the later phases of the process, nothing is left of the embryo but the mesodermic area and a posterior unpaired process, representing either the last thoracic appendage, or the tail lobe; and these in turn finally disappear.

In very rare cases, one of the posterior pair of appendages may fuse in the median line, without any indication of fusion in front of that point. But there is no evidence of a progressive median fusion and degeneration extending toward the anterior end. Camera × 30.

It would appear, therefore, that the broad subdivisions of the arthropod body, which constitute the very foundation of arthropod morphology, are the varying results of apical growth, locally checked by median fusion and degeneration.

C. **Acephalic and Acaudal Embryos.**—A common abnormality consists in the extensive reduction of the anterior or posterior metameres, or of both, leaving only the middle portion of the trunk intact. It is not clear whether this result is brought about by median fusion or not.

It is a common thing to find embryos without the cephalic lobes; or without cephalic lobes and the first three pairs of thoracic appendages; or the abdomen alone may be present, without the head and thorax. The most common form consists of little more than the three posterior thoracic metameres. Such embryos may have a deceptive resemblance to a crustacean nauplius. (Fig. 186, *B*.)

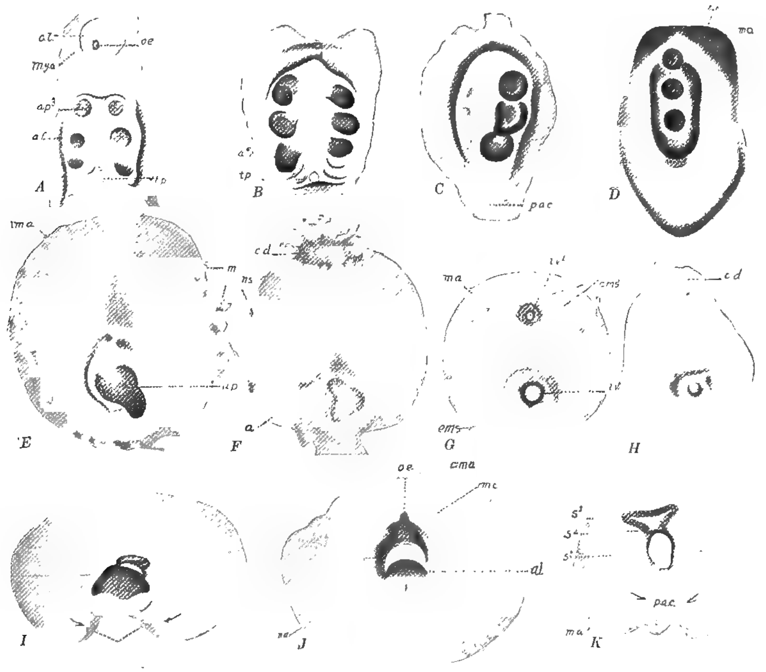

FIG. 186.—Limulus embryos in advanced stages of degeneration. *A*, Stage G. The anterior half of the thorax is absent and the isolated procephalic lobes are reduced to a thin depressed plate, with an underlying mass of yolk cells. Cam. ×30. *B*, Stage G. Anterior half of thorax absent, and the greatly reduced cephalic lobes covered by a thick fold of ectoderm. Cam. ×30. *C*, Stage G. The abdomen and the anterior half of the thorax absent. Last three thoracic appendages on the left, reduced to shallow pits; cam. ×30. *D*, Germinal disc, with three unpaired thoracic appendages; cam. ×30. *E*, Remnants of an embryo, probably in stage G; only the tip of the abdomen, or the unpaired remnants of one of the more posterior pairs of appendages, projects above the surface of the faint embryonic area; cam. ×60. *F-K*, Similar embryos in more advanced stages of degeneration.

Such cases as these, and the hour-glass type, show that certain groups of metameres have an organic unity that enables them to survive, at least for a certain period, independently of other parts of the body. It suggests the phenomena of transverse division in the annelids; the remarkable process in cirripeds (Sacculina) by which the abdomen is cast off, leaving only the thorax to complete the life cycle;

and the amputation of the head, in larval star-fishes, leaving only the posterior part to complete its development.

D. **Final Stages of Degeneration.**—The vast majority of all abnormal embryos, whether single, doublets, or triplets, continue to degenerate by gradually cutting off the more anterior segments, or by some modification of the process of median fusion and antero-posterior degeneration. The details of the final stages cannot be followed, but the general nature of the process and the final results are readily observed. In the class of cases we shall now consider, after the disappearance of all the appendages, the embryo may be reduced to a mere pit or sac, yet preserving certain features, such as concrescing mesodermic areas and protruding tail lobe, which show clearly the advanced stage of development in which the whole embryo would have been, had no degeneration taken place. (Fig. 186, *J.K.*)

Some embryos may consist of two pits, or two groups of cells, like two primitive cumuli, one corresponding to the head and the other to the tail end of the body. (Fig. 186, *G.H.*) Finally these sac-like remnants are reduced to faint clouds of scattered cells, or nuclei, which in turn disappear, leaving no trace of living substance in the yolk.

The conditions we have just described are important in that they give us a glimpse of the negative processes of life, side by side with the positive ones. They afford us a new picture of death, unlike the one with which we are most familiar. In these embryos cell production, cell specialization, and cell decay proceed side by side, for in every part of the body karyokinetic figures and the fragments of decaying nuclei are found. The result depends on the relative intensity of these three factors. The embryos apparently dwindle in size because the death rate of the cells is greater than the birth rate. Nerve centers, sense organs and appendages disappear because the specialization of individual cells ceases and only the simplest kinds remain.

The process of degeneration is never exactly the same, but if completed it invariably carries the organism back, in the main, over the old lines of progressive development till it is reduced to its primitive condition, namely, a small community of similiar, unspecialized cells which disappears with the death of the last survivor.

This may be called the true natural death of an organism, all others are more or less catastrophic, and are due to the increasing lack of coordination and of adjustment to the new conditions that have been created by growth.

IV. Double Embryos.

We may distinguish two kinds of fission, transverse and longitudinal.

1. Transverse fission divides the embryo into anterior and posterior portions, the point where the division most frequently occurs being between the third and fourth thoracic appendages, or between the abdomen and thorax. The steps leading up to this form have been described under the preceding sections.

2. Longitudinal fission is radically different from transverse fission, for the latter is the result of a local concrescence and degeneration of segmental organs, while longitudinal fission consists in the formation of two new halves of an embryo along the median line of one already existing. The formation of the new halves begins at the anterior end and extends gradually backward. The old halves are thus thrust apart and each old half, together with the adjacent new half, makes a new embryo.

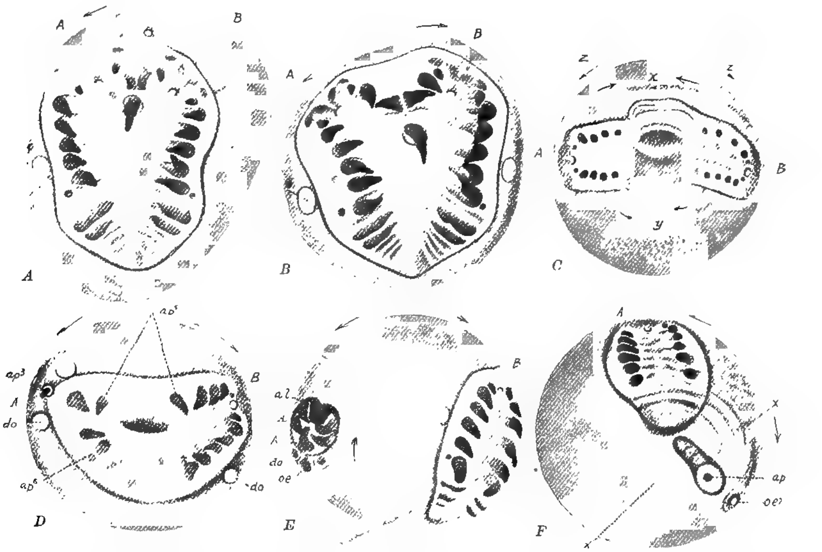

FIG. 187.—Limulus embryos, stage H, showing various steps in the formation of double embryos. Double embryos are formed, in all the observed cases, by the generation, beginning at the anterior end, of two new halves between the old ones. If there are five paired organs on each segment, and *a* is median and *e* lateral, then *a* will be the first new organ to appear, and it will appear in the median line of the first segment as an unpaired organ. It divides, and in its place in the same segment will be found an unpaired organ, like organ *b*. But at the same time a new, unpaired organ, like *a*, will be formed in the median line of segment number two. At the next division, organ *a* will be produced in the median line of the third segment, *b* in the second, and *c* in the first; organs *a* and *b* being now completely formed in pairs in the first segment, and organs *b* in the second. This process goes on till two complete new halves are wedged in between the old, and two new individuals are produced, each individual consisting of an old and a new half.

A, and *B*, Early stages in the formation of the new halves; cam. ×16. *C*, Later stage; cam. ×15. *D*, The left-hand embryo has begun to disappear by median fusion and progressive cephalo-caudad degeneration; cam. ×16 1/2. *E*, The two embryos have completely separated and the one on the left is disappearing by the characteristic method of degeneration; cam. ×16 1/2. *F*, One embryo normal; the other reduced to a single appendage, and a narrow embryonic area; cam. ×16. Stage H.

This process may be repeated a second time in one of the new embryos, thus producing three embryos tail to tail, consisting of the two original halves plus four new ones.

All multiple embryos in Limulus are formed in the above manner, never by the partial union of embryos originally separate. This is shown by the fact that in all these cases the embryos match each other exactly, and always in the same way, which could hardly be the case if two separate embryos had united through accidental contact.

Where do the new halves come from, and by what processes of growth are they formed? There is no evidence of the existence of special formative material along the median line where the new parts are forming. This is especially clear when the process begins at a late period. The old halves are then quite distinct from the new, and there seems to be no way open to explain the origin of the new half of a segment by lateral budding, or by regeneration, or by growth from the corresponding old one. We might perhaps infer that the new neuromeres in Fig. 187, *A.B.* come from a kind of regeneration of the old one, but that could not possibly be the case with any of the new organs lateral to the neuromere, such as the appendages, sense organs, and the margin of the mesodermic area.

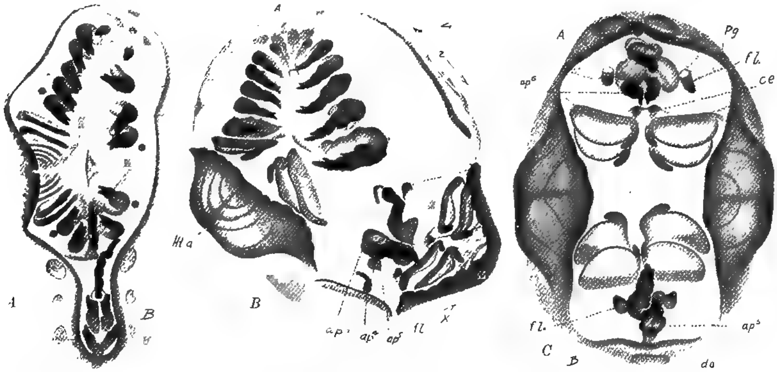

FIG. 188.—Double embryos of Limulus, accompanied by median fusion and cephalo-cauded degeneration; cam ×16 1/2.

A comparison of double embryos in various stages shows that the sequence in the production of new organs is as follows: The most anterior metameres are formed first. Each new organ of a metamere first appears as a single organ common to both embryos and having a normal position for each. Additional organs are formed in the same way, in the order of their arrangement on the metamere. For example, the organ nearest the median line is formed first; this then divides into two, and the one lateral to it appears between them as a single organ common to both embryos; this divides, and the next one appears in the same place, till all the organs of a given metamere are formed. (Fig. 187, *A.B.*) The same process takes place in the next posterior metamere, but it is always one step behind that in the metamere in front of it.

An embryo that has nearly completed its division, as shown in the diagram (Fig. 190), presents a row of median unpaired organs which follow the same order in a cephalic direction that they do in a lateral direction on the metamere, namely *a.b.c.d.e.*

The successive eruption of new organs along this median line, and the manner in which they divide and move away from it to right and left, is so entirely different from what we have been accustomed to see that it is very impressive.

New organs make their first appearance in the same stage of development as the corresponding old ones. Each newly formed median appendage first attains a considerable size, then divides at the apex, the separation gradually extending toward the base. This, it will be observed, is the exact reverse of what occurs when degenerating appendages of the right and left sides unite to form a single median one.

During the later stages of double embryos the growth of the new halves forces the old ones apart, and the two embryos then swing into a straight line, tail to tail. (Fig. 187, *C.*) They may then separate, moving tail first in opposite directions till they lie on opposite sides of the egg. (Fig. 187, *E.*)

At any stage in this process of division, one or both embryos may undergo the typical median fusion and antero-posterior degeneration. The process may go on in one embryo quite independently of that in its mate, but always in the typical manner described for the single embryos. (Figs. 187, 188.)

V. TRIPLE EMBRYOS.

Triple embryos are very rare. Their mode of origin is shown by the accompanying diagram. (Fig. 190, *B.*) It is assumed that in the beginning a single normal embryo, in the manner already described, gives rise to two embryos, of

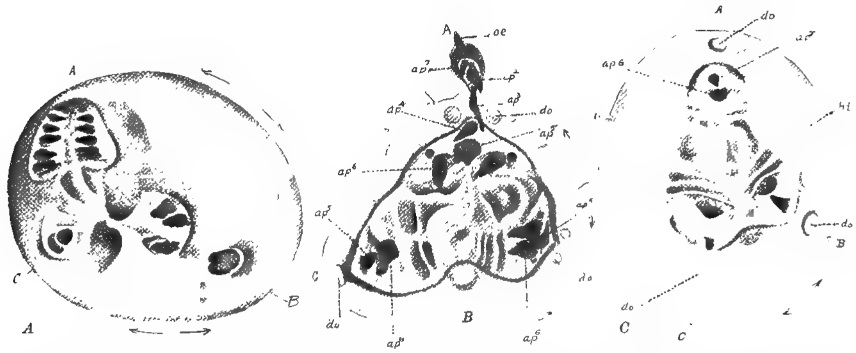

FIG. 189.—Triple embryos of Limulus, showing extensive median fusion and cephalo-caudad degeneration.

A. Of the three embryos in this egg, *A* is normal and perfect in everything except the abdomen. *B* has undergone median fusion and degeneration, and transverse fission. The cephalic lobes and first four segments have disappeared, except two incompletely fused appendages. The abdomen and the posterior part of the thorax persists. The latter is bounded in front of the fifth pair of appendages by a great fold that extends completely across the median line. The nerve-cord in this posterior remnant of an embryo forms a conspicuous, unpaired ridge. Embryo *C* has undergone extensive fusion and antero-posterior degeneration, nothing remaining but the fused appendages of the sixth segment, and a rudimentary abdomen. It is probable that the original embryo divided lengthwise, giving rise to *A* and *BC*, and the latter then divided, giving rise to *B* and *C*. Cam. ×15.

B. Embryo *A* has undergone median fusion and transverse fission. The fused appendages of the first four segments are arranged in a single row. The cephalic lobes are narrowed, and covered by a hood-like fold of ectoderm, through which one sees the œsophagus. The marginal fold has grown across the median line in front of the fourth pair of appendages. In front of this fold, and near the median line, are the dorsal organs. Embryo *B* has degenerated completely in front of the fused fifth pair of appendages, with the exception of the dorsal organs, which have almost reached the median line. In embryo *C*, the median fusion and degeneration has progressed still farther, or the dorsal organs have fused and also the six pairs of appendages. At the central ends of all three embryos, are paired and unpaired ridges, representing abdominal appendages. Mercator projection; cam. ×15.

C. A triple embryo in which each individual is reduced to an unpaired dorsal organ, to the last thoracic and first branchial appendages. There are faint indications of cardiomeres and of caudal segments; cam. ×16 1/2.

which one is *A*, the other occupying the position of *B*. The right hand embryo then divides again, forming embryos *B*. and *C*. Thus two new generations of halves are produced, *II* and *III*, each consisting of an embryo with inverted

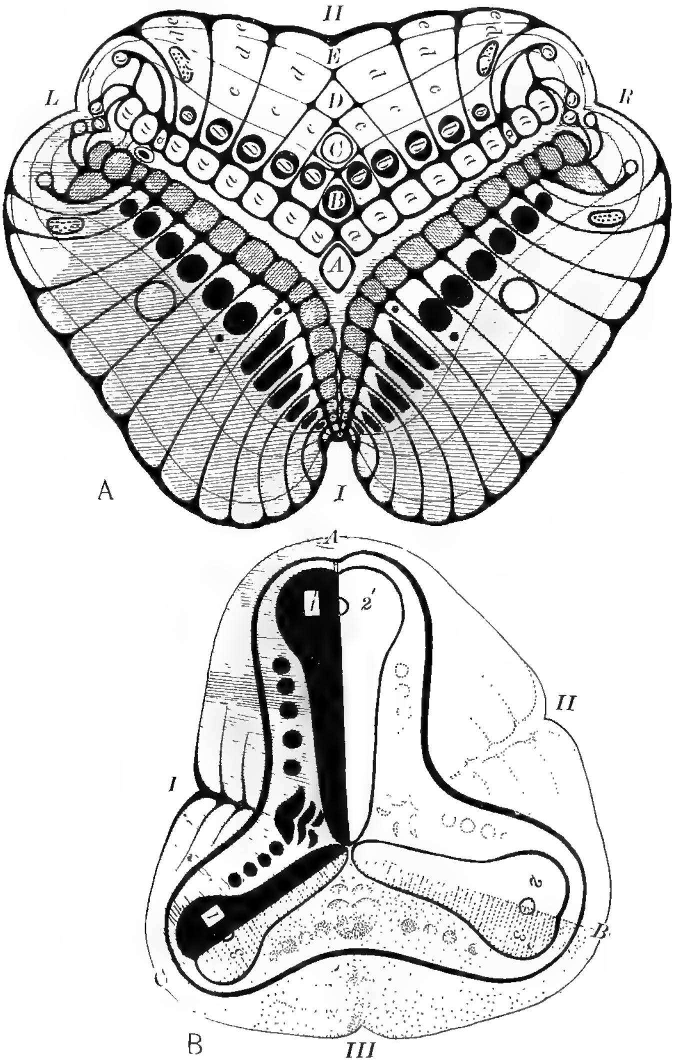

FIG. 190.—Diagrams illustrating the mode of growth of double and triple embryos.

A. Diagram of a dividing limulus embryo showing the sequence in which the organs, *a-e*, of the two new halves are generated. The newly formed, unpaired organs are in capitals; the organs formed by their division are in corresponding small letters. The old halves shaded, new halves unshaded; see also explanation of Fig. 187.

B. Diagram of a triple embryo. First generation of metameres, black and shaded; second, blank; third, dotted.

right and left sides. The three generations now form a tri-radiate figure, with the new and old halves making three apparently normal embryos, *A*. *B*. and *C*. But the halves of the original embryo are now separated by an angle of about

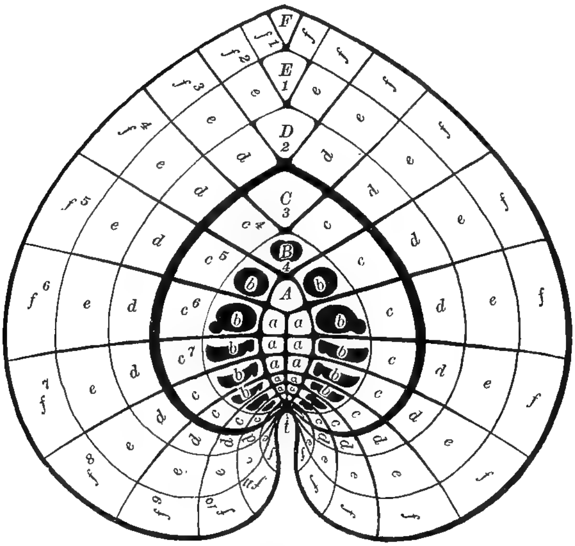

FIG. 191.—Diagram of a degenerating limulus embryo, showing the order in which the paired organs unite in the middle line and then disappear. Organs formed by normal apical growth are represented by small letters; the unpaired organs formed by their union, and which are about to disappear, are in capitals.

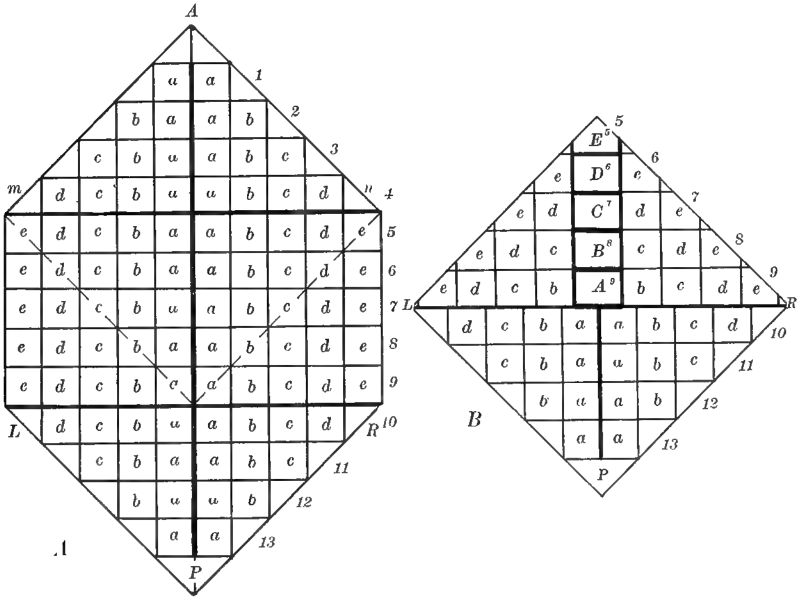

FIG. 192.—Diagram illustrating the law of growth and degeneration of segmented, bilaterally symmetrical animals.

A. The segmental organs, seen in mercator projection from the neural surface, are represented by letters, and the metameres by numbers. *A-P*, The principal, or neural axis; *A*, cephalic; *P*, caudal end. *A*, *m.n.*, area of initial growth; *m.L.R.n*, area of multiple growth; *L.R.P.*, area of diminishing growth.

B. The arrangement of organs after the degeneration of the area in figure *A*, enclosed by the lines *A.m.* $a.n.^4$ With the disappearance of this area, the lines $m.a.^9$ and $a.n.^4$ unite to form the line of unpaired organs *E-A*.

240°; and embryo *A*. consists of a mother and a daughter half; *B*. of a daughter and a grand-daughter half, and *C*. of a granddaughter and a mother half.

Some of the conditions that are actually realized are shown in Fig. 189. In all these cases, median fusion and degeneration accompanies, or follows the formation of triplets.

In Fig. 189, A, embryo *A*. is practically normal; embryo *B*. has undergone median fusion and degeneration, almost resulting in transverse fission at the fourth segment. The abdomen and last two thoracic appendages are practically normal, while the anterior part of the thorax and cephalic lobes has disappeared, except one pair of fused appendages. In embryo *C*. median fusion and degeneration have obliterated all but the abdomen and the last pair of fused thoracic appendages.

In another triplet (Fig. 189, *B*), embryo *A* has undergone median fusion and degeneration, forming a good example of an hour-glass embryo. The same process has affected embryo *B*, entirely obliterating the cephalic lobes and the anterior portion of the thorax; the dorsal organs, however, are not quite fused in the median line. But this has taken place in embryo *C*, and in other respects the degeneration is carried farther than in *B*.

In still another triplet (Fig. 189, *C*), all three embryos are reduced by antero-posterior fusion and degeneration nearly to the same level; each one retains an unpaired sixth thoracic appendage, a remnant of the abdomen, and an unpaired dorsal organ.

Multiple embryos, therefore, are formed by the appearance of new halves between the old, the various organs being formed in a definite and orderly manner. After a time degeneration begins, the organs disappearing by a method and in an order that are the reverse of those in which they were generated.

VI. Summary and Conclusion.

1. The variations here described are primarily due to structural variations resident in the ovum, and not to differences in the environment.

2. There is a great difference in the growth rate, under apparently the same conditions.

3. There is a great difference in size, some embryos of the same stage being much larger than others.

4. Certain organs or regions of the body may be entirely absent, and are not subsequently restored.

5. When organs disappear it is usually by median fusion and degeneration, in the reverse order of their age and specialization.

6. Multiple embryos are produced by the formation of new halves between the old, the process beginning at the head end. The new organs are produced in the reverse order to that in which they are formed by normal apical growth, that is, the lateral ones before the median ones. The arrangement is also reversed, the

hæmal organs lying in the axis of growth and the neural ones on the margins. The way in which the new organs make their appearance is the reverse of that by which organs disappear by median fusion and degeneration.

7. Multiple embryos thus formed disappear again by median fusion and anteroposterior degeneration.

8. Variation in Limulus is primarily of a plus or minus nature. The endless variety of results attained is due to the presence of a larger or smaller number of organs. We are apparently always dealing with the same things and with the same kind of stuff. When an unusual form of the aggregate appears, as in the semicircular form of a half embryo, it is the indirect result of the absence of some other part. In no case does a new organ or a new part appear that is different in kind from those already existing; in no case is an organ out of place in reference to others; in all cases the organs come and go in a definite orderly sequence.

The organs of the embryo, crystal-like, are always expressed in approximately the same forms and in similar geometrical aggregates. The successive steps in apical growth, in degeneration, in twin formation, and again in degeneration, are minutely graded transitional phases in which the living substance in the egg of Limulus finds formal expression.

9. The parallel rise and fall, or the opening and closing of the checker-board pattern, is a fundamental attribute of organic growth, and is a basic factor in the morphogenesis of all segmented animals. The laws of differential apical growth, and of the reverse process, or degeneration, are the keys to their morphology, accounting for their bodily subdivisions, and for the unequal growth, specialization, and union of their various organs.

CHAPTER XVI.

THE DERMAL SKELETON.

We recognize four distinct structures in the skeleton of primitive vertebrates: 1. The dermal skeleton, consisting of bony plates more or less intimately united to form a continuous external armor for the head and trunk; 2. the primordial endocranium, consisting of a broad unsegmented plate of fibrocartilage lying on the hæmal side of the brain; 3. the gill-bars, segmentally arranged cartilage bars lying in the visceral arches; 4. the notochord; 5. neural arches, segmentally arranged blocks, or half-rings of cartilage distributed along the sides of the nerve cord and notochord. These structures differ from one another in their chemical and histological composition, and in their origin. The general trend in the evolution of the vertebrate skeleton is toward the elimination of the two oldest constituents, the dermal skeleton and the notochord, and the union of the remaining elements, without distinction of origin, structure, or previous function, into a common axial skeleton.

These five sets of skeletal structures are already established in the arachnids, viz: 1. The external chitenous armor with its primordial canaliculi and lacunæ. 2. the fibrocartilaginous endocranium or plastron; 3. the cartilaginous bars supporting the branchial appendages; 4. the middle cord, or lemmatochord, and 5. the segmentally arranged cartilages over the spinal cord. Nothing resembling this assemblage of skeletogenous tissues is found in any other animals outside the vertebrates and arachnids.

I. The Dermal Skeleton of Vertebrates.

The dermal skeleton of primitive vertebrates consists of a series of bony plates, not preformed in cartilage, arising in or beneath the epidermis. It has been generally assumed that the most primitive dermal skeleton is one consisting of small isolated placoid scales, similar to those in the elasmobranchs; and that the larger plates seen in the ganoids, dipnoi, and ostracoderms were formed by the secondary union of such scales. This assumption is based on the prevalent belief that the elasmobranchs and cyclostomes are the most primitive vertebrates, and that the above mentioned heavily armored forms were derived from them. This view is untenable, since it takes no account of the fact that the ostracoderms, which are the oldest known, and the most primitive fish-like vertebrates, were pre-eminently heavily armored forms.

We shall reverse the usual way of approaching this question and start with the assumption that the most primitive vertebrate dermal armor is like that of the

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ostracoderms, and consists of a practically continuous bony envelop for the head and gill region, with segmentally arranged plates, loosely articulated, covering the joints of the trunk and tail. Such an exoskeleton resembles that of the marine arachnids, the hypothetical ancestors of the vertebrates.

It is assumed that the cephalic buckler of the ostracoderms corresponds to the cephalothoracic shield of the merostomes and arachnids generally, *i.e.*, the primitive head, the first six thoracic, and the vagus segments. The buckler of such forms as Pteraspis, Tremataspis and Bothriolepis also includes the abdominal or respiratory segments.

The line of union between the thoracic and branchial regions is clearly indicated in Bothriolepis by the hinge-like joint separating the cephalic buckler from the respiratory chamber. (Fig. 247.) Just in front of this joint are two pores leading into the interior of the shell. Two similar pores are found in Tremataspis (Fig. 236), and just back of these pores is probably the dividing line between the cephalic and branchial regions in these animals.

In Cephalaspis and Tremataspis, the trunk region is covered with segmentally arranged dermal plates corresponding with the plates covering the neural surface of the post-branchial region in arthropods. Only a few of the more anterior segmental plates of the ostracoderms are represented in the arthropods, the more posterior ones being new formations added after the separation of the vertebrate from the arthropod stock had taken place.

In Bothriolepsis, and in a small undescribed species of Cephalaspis from Dalhousie (Fig. 234), the trunk and tail are naked, save for a few minute, irregularly distributed ossicles near the anterior end of the trunk.

In Pterichthys and Pteraspis, the trunk appears to have been covered with rounded or polygonal scales, probably formed by the breaking up of larger segmental scales like those of Trematapsis.

The Minute Structure of the Dermal Bones of the Ostracoderms.

The structure of the dermal bones of Tremataspis, Pteraspis, and Bothriolepis has been studied with special care, and some observations were made on the dermal skeleton of Cephalaspis and Tolypaspis, but they are incomplete, owing to the lack of adequate material.

It is surprising how beautifully the details of the minute structure of these ancient fish bones is preserved. When properly prepared, the color and the minutest details may occasionally be seen as clearly as though the animals had been dead a few weeks only, instead of a few million years.

Tremataspis.

In Tremataspis the outer surface of the shell generally has a light yellowish-brown color. It is beautifully polished and under the lens appears to be ornamented with low winding ridges and mounds, similar to those of Bothriolepis, but much fainter. The surface is dotted with minute circular openings arranged in irregular rows that usually correspond with the meshes of the underlying canals.

The shell is about 0.3 mm. thick. The inner portion consists of horizontal lamellæ of uniform width, interrrupted by large irregular chambers. (Fig. 193.) The lamellæ appear to have consisted originally of fibrous strands arranged with great regularity into parallel bundles, those in adjacent layers running at right angles to one another. Viewed from the inner surface of the shell the strands of the lamellæ look like the warp and woof of a coarse cloth (Fig. 194). Between the layers are flattened lacunæ, sometimes filled with a reddish-brown substance that gives them a very striking resemblance to living pigment cells. Canaliculi radiate from the lacunæ and anastomose with those in the layers of bone above and below.

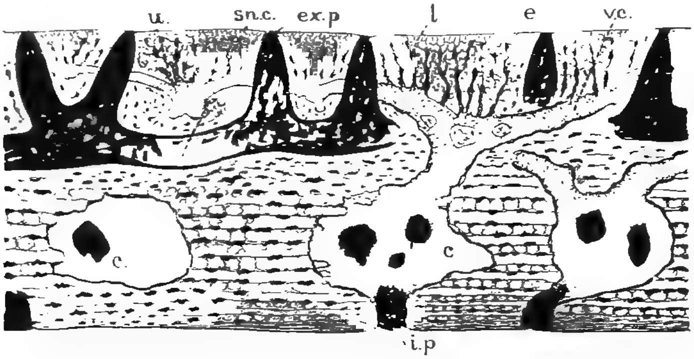

FIG. 193.—Cross section of the exoskeleton of Tremataspis.

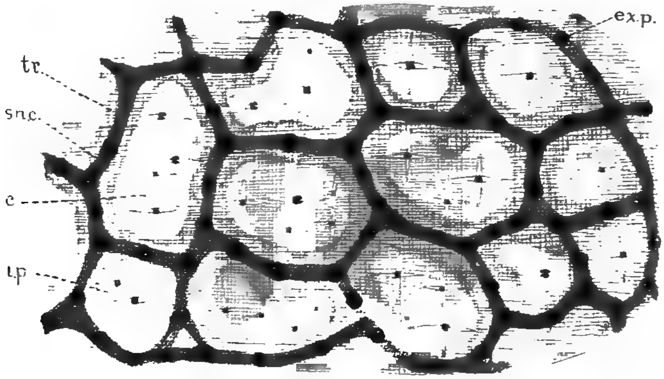

FIG. 194.—Exoskeleton of Tremataspis, seen from the inner surface. Enough of the outer surface has been removed to make the remainder semi-transparent.

The substance of the shell is penetrated by two sets of canals. The deeper set forms a horizontal meshwork of uniform caliber, opening to the outer surface at frequent intervals by short conical chimneys. (Fig. 193, *sn.c.*) This system of canals is generally filled with a peculiar matrix that is either colorless and similar to that outside the shell, or impregnated with a dark red or black substance. The walls of these canals, which appear to have contained sense organs and mucous glands, are very sharply defined. Bone lacunæ do not open into them, and they lead only at irregular intervals, if at all, into the other system of canals, or into the cancellæ. They appear to be uniformly distributed in the shell, throughout all parts of the buckler. When the outermost layers are removed and the shell is viewed as a semi-transparent object from its inner surface, the sensory canals are seen to overlie the partition separating the cancellæ. (Fig. 194.)

The canals belonging to the outer set are smaller and much fainter than the ones just described, and never contain pigment, or foreign materials derived from the surrounding matrix. They form a horizontal polygonal mesh network of slender irregular vascular canals, *v.c.*, that open by larger ones into the summit of the cancellæ, *c*, and hence through the floor of the cancellæ into the interior, *i.p.*

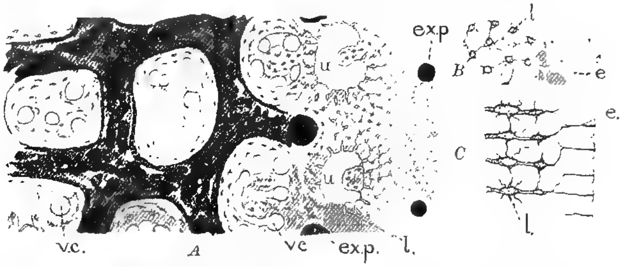

Fig. 195.—*A*, Tangential section of the outer layers of the exoskeleton of Tremataspis; *B*, outermost layer, in surface view, more highly magnified; *C*, same in cross-section.

Several strands of the arching horizontal canals lead into irregular spaces lying in the center of the areas enclosed by the chimney pores. From the floor of these spaces, numerous irregularly looped canals arise that project inward, forming ill-defined tufts of vascular canals (Fig. 195, *v.c.*), on about the same level with the large sensory canals. Some of these canals appear to open occasionally into the floor of the sensory canals.

From the roof and sides of all the outermost vascular canals, and from their points of union with one another, arise numerous tapering vertical canals, the osteo-dentinal canals. They are larger than the ordinary canaliculi, especially at their proximal ends, and after expanding into a row of three or four overlying lacunæ, open into innumerable anastomosing canaliculæ. The main axial canal terminates in a single minute canaliculus, that runs through a faintly defined cylinder to the outer surface. (Figs. 193, 195, *e*.)

The layer of prisms with their axial pore canals make up the glassy outer surface of the shell; the layer of osteo-dentinal canals forms the dentinal layer.

The bone cells, or lacunæ, lying in the spaces between the vascular and sensory canals are smaller than the ones just described and are more like the typical bone lacunæ. They appear to lie between the concentric bone lamellæ surrounding the canals.

Pteraspis.

Of the genus Pteraspis only a part of the cephalic armor and a few scale-like structures belonging to the anterior part of the trunk are known.

The boat-shaped dorsal shield (Fig. 245), is composed of seven portions, marked off on the outer surface of the shield by furrows, and on the inner surface by ridges. In young specimens the rostrum and the central disc may be found separately. In each piece the ornamental surface ridges and furrows, which look much like the wavy lines on the finger tips, are arranged in concentric lines parallel with its margins. This fact, together with other considerations, led Lankester to believe that each piece ossified from a separate center, and that their complete anchylosis occurred only in the adult.

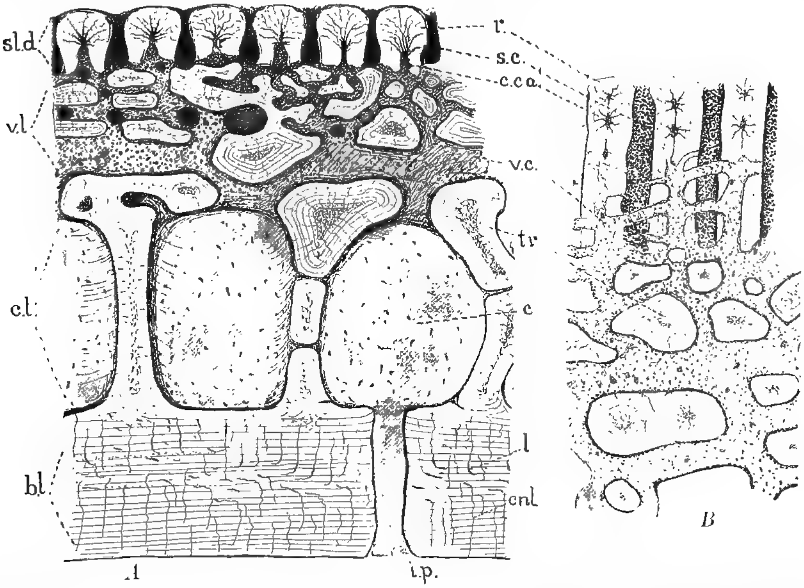

FIG. 196.—*A*, Cross-section of the shield of Pteraspis, at right angles to the surface ridges; *B*, Tangential section through the outer layers, and nearly parallel with the outer surface.

Along the lateral margins of the shield, in the rostrum, and near the posterior dorsal spine, the shell is greatly thickened, and consists of a network of bony trabeculæ with irregular spaces between. In the median portions it is of a more uniform thickness, about 0.6 to 0.8 mm.

In sections across the ridges (Fig. 196, *A*), the shell is seen to consist of four principal layers: 1. A thick inner wall, *b.l.*, composed of many parallel layers of uniform thickness, perforated here and there by openings that lead from the interior of the head into the overlying cancellous spaces. 2. A cancellated layer, *c.l.*, consisting of polygonal chambers, *c.*, separated by thin vertical walls that are perforated here and there by narrow lateral passages. 3. Three or four layers of canals, *v.l.*, each layer forming a close four-sided meshwork from which vertical canals connect with the layer above and below. The diameter of the canals in the inner layer is the largest and the main canals of this layer run at right angles to the surface ridges. (Fig. 196, *B.*) The diameter of the canals in the several layers diminishes toward the outer surface; at the same time the apparent trend of the main canals of a layer gradually shifts, so that in the outermost one the main horizontal canals run parallel with the surface ridges, one canal running lengthwise along the basal portion of each ridge. In sections parallel to the outer surface as well as in cross-section, it is readily seen that each ridge canal opens right and left into the bottom of the grooves, *s.c.*, between the ridges, and at pretty regular intervals sends a short loop upward into the ridge itself, *c.ca.* From the summit of these ridge-loops arise the radiating dentinal canals of the ridges. These terminal canals resemble those of Tremataspis, but they do not contain any lacuna-like dilatations. 4. The layer of surface ridges and the intervening grooves form the fourth or outer layer of the shield.

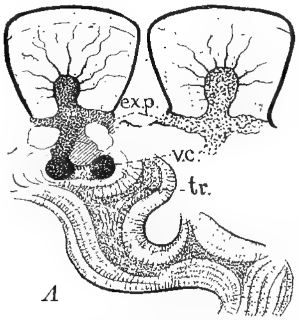

FIG. 197.

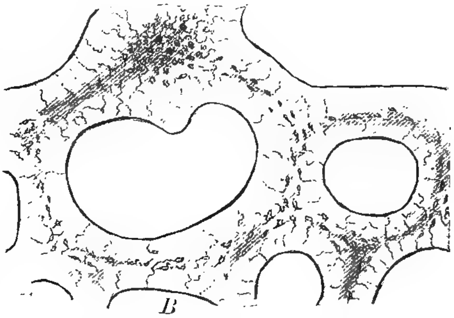

FIG. 198.

FIG. 197.—Cross-section of a small portion of a shield especially well preserved, and probably belonging to Pteraspis; highly magnified, showing the axial core and the sharply laminated structure of the trabeculæ.

FIG. 198.—Trabeculæ of Ateleaspis.

The substance of the shell consists of a series of plates and trabeculæ; the cut surfaces of the latter present a very distinct concentric lamination that is precisely like the laminated trabeculæ in Limulus. In each plate or bar there is an axial core of a darker, yellowish-brown color; it is also distinguished by a change in the distinctness of the lamination. The outermost laminæ are crossed by innumerable fine lines that produce the appearance shown in Fig. 197. In other specimens that have been preserved in a little different manner, some of the canals are filled with air so that they become very distinct, like the pore canals of Limulus, or the air-filled canaliculi of typical bone cells.

These canaliculi begin at the surface of the trabeculi and extend at right angles to the lamellæ into the axial core. There they bend nearly at right angles and some of them terminate in slender, spindle-shaped, or elongated dilatations, the long axis of which generally lies parallel with the long axis of the core. These terminal dilations or primitive lacunæ are readily seen with a magnification of about 600 diameters. The same kind of unbranched canaliculi and terminal lacunæ are seen, often with great distinctness, in the basal layers. (Fig. 196, *Al.*)

It has been generally assumed that in the pteraspids true lacunæ are absent. It will be seen from the above account that they possess a primitive form of lacunæ that are similar to those in Limulus. They differ from typical bone lacunæ in their small size and in the absence of radiating canaliculi.

Ateleaspis.

In a specimen of Ateleaspis from Scaumenac Bay (Fig. 198), the shell in tangential sections forms a continuous network of trabeculæ. They are not as distinctly laminated as in Pteraspis, although there is a dark brown axial core in which most of the lacunæ are located. The lacunæ are spindle-shaped, with more than one canaliculus, some of which can be traced to the outer surface of the trabeculæ.

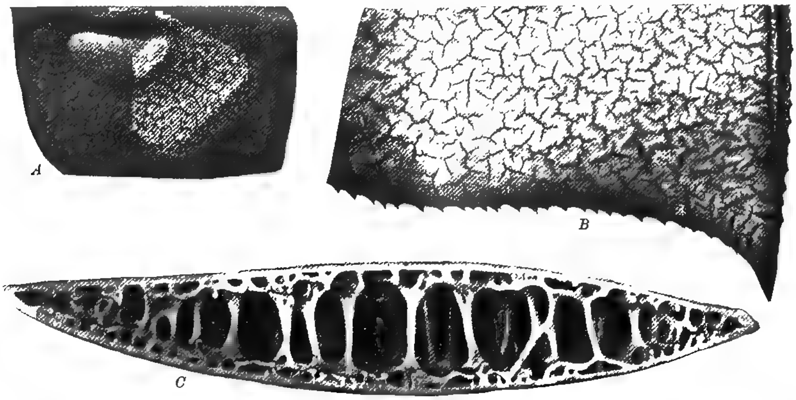

FIG. 199.—*A*. Surface ornamentation of the thoracic shield of Limulus, near the lateral eyes. *B*. Same on the hæmal surface of one of the cornua. *C*. Cross-section of one of the cornua.

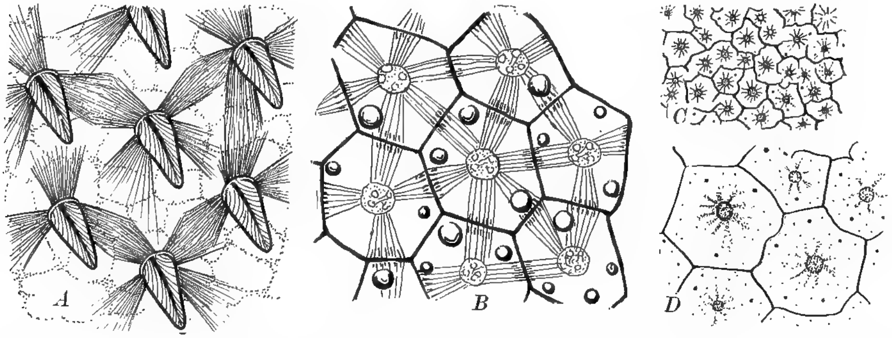

FIG. 200.—*A*, Surface view of semi-transparent exoskeleton of Limulus, from the flexible portion in the olfactory region. It shows the peculiar groups of pore canals, lyng just below the surface, and radiating from the base of the denticle-like spines; also the polygonal network of low ridges, or trabeculæ, projecting from the inner surface of the exoskeleton. *B*, Surface view of thoracic shield of an ostracoderm (Ateleaspis, sp?) showing the polygonal areas, surface tubercles, and the peculiar grouping of canals lying just below the surface. *C*, Surface ornamentation from the hæmal surface of thoracic shield of Limulus. *D*, Same, more highly magnified.

II. Dermal Skeleton of Limulus.

We shall describe in some detail the dermal skeleton of Limulus because it has the usual arthropod characters, and at the same time several other very important ones that are not found in any other animal, so far as I know, outside the vertebrates.

The outer surface of the shell of half grown Limuli (Fig. 199, *B.*) is marked by broad zig-zag ridges separated by shallow grooves. In some places, notably in the region about the lateral eyes, the ridges break up into polygonal areas, each of which contains a crater-like depression with radiating grooves extending toward the base of the cone, Fig. 200, *D*. The distinctness of the ornamentation is accentuated by the deeper color and other optical properties of the matrix in the grooves and craters; but the same figures can be obtained in wax impressions of the outer surface, except that they are fainter.

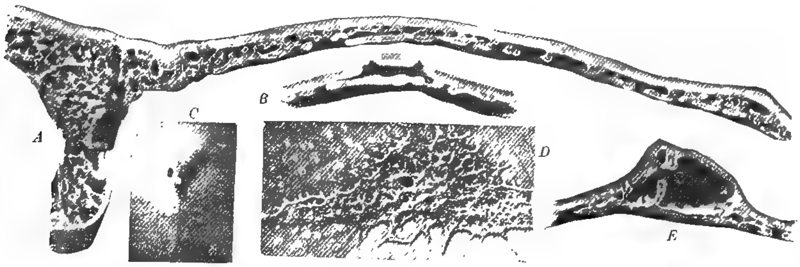

FIG. 201.—Dermal skeleton of Limulus. *A*, Cross-section through the posterior median portion of the thoracic shield; *B*, through the pineal eye chamber; *C*, surface view of the trioculate parietal eye; *D*, bony trabeculæ on the inner surface of the shield, in the lateral eye region; *E*, Cross-section of the lateral eye chamber.

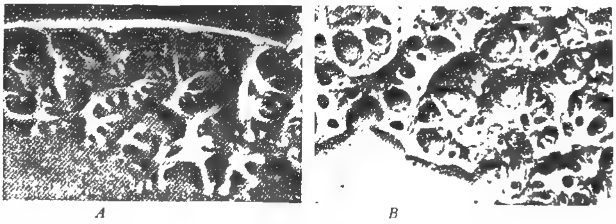

FIG. 202.—*A*, Inside margin of the thoracic shield, showing the mode of growth of the trabeculæ; *B*, mass of bony trabeculæ from the inner surface of the thoracic shield.

The inner surface of the shell at certain places gives rise to great masses of interwoven chitenous bars, or trabeculæ, separated by irregular spaces filled with loose connective tissue, blood-vessels and nerves. (Figs. 203, 204.)

The bars are concentrically laminated and contain numerous fine canals and spindle-shaped cavities, so that the whole mass of tissue resembles in a very striking way the cancellous bony tissue of vetebrates.

The trabeculæ are most highly developed along the lateral margins of the thoracic and branchial shields, and in the cornua. In these places the spaces between the dorsal and ventral walls are filled with dense masses of this tissue. (Fig. 199 *C*.) In the cornua the trabecular network of each wall is united to the other by long columns with branching ends. (Fig. 199, *C*.)

In the margins of the thoracic shield (Fig. 202, *A*) one sees how the new trabeculæ arise at separate points, unite, and later form new supports which gradually lift the older bars off the surface.

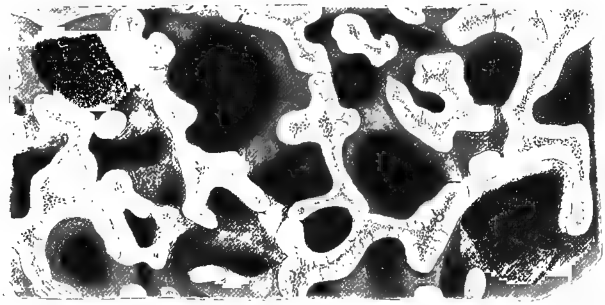

FIG. 203.—Section of the dermal skeleton of Limulus, tangential to the surface, showing the cancellous spaces, and the axial location of the lacunæ in the trabeculæ. Margin of thoracic shield.

There are similar deposits of this tissue under the lateral eyes, enclosing each eye within a bony orbit (Fig. 201, *D*, *E*), another beneath the median eyes (Fig. 201, *B*), and six or seven pairs of irregular patches arranged symetrically on the dorsal wall of the abdomen along the median margin of the six pairs of entapophyses. (Fig. 205.)

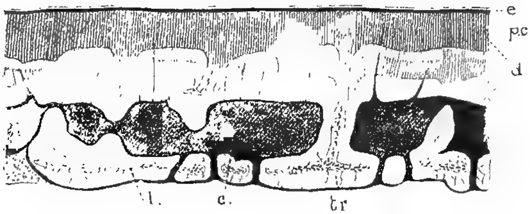

FIG. 204.—Cross-section of the dermal skeleton of Limulus. Margin of thoracic shield.

Minute Structure.—The chitenous trabeculæ often form a nearly continuous sheet spread out over the inner surface of the shell, and differing from it to a very marked degree, in color, texture, and general appearance. (Figs. 201, *A* and 204.)

The shell, in such places, is divided into several layers:

1. The outer layer is strongly laminated, and traversed by two or three kinds of rather large canals, which contain ducts of mucous glands, or nerve fibers, and other tissue. All these canals reach the outer surface, and either open freely to the exterior, or lead into spines or hairs of various shapes. Between them are

innumerable canaliculæ (pore canals of authors). They are extremely minute and extend in straight lines or in finely wound spirals almost to the outer surface, *p.c.* The most superficial layer, *e*, is thin, colorless, vitreous, and devoid of canaliculi. Although very hard and polished, it is easily destroyed under some conditions. In surface views it is seen to be divided by shallow grooves into polygonal facets or zigzag ridges. (Fig. 200; *D.*)

2. The middle layer consists of broad cancellous spaces separated by irregular vertical partitions. The cancellæ are filled with loose connective tissue, through which ramify nerves and blood-vessels.

3. The third, or inner, layer is composed of trabeculæ arranged parallel to the outer surface. It is horizontally laminated, and is pierced with large irregular openings, through which nerves and blood-vessels pass to the cancellated layer.

Each bar, or trabecula, is covered by a thin layer of pigmented ectoderm continuous with that underlying the outer layer, and that secretes, or produces by the periodic transformation of its own substance, the chitenous lamellæ of the shell. The lamellæ are generally grouped in bands which differ in their color and in their chemical reaction. The older, outer layers of the shield are dark brown, and a band of this colored chiten extends into the axis of each trabecula. The deeper lamellæ of the outer layer, and the outer lamellæ of the trabeculæ, are transparent and nearly colorless.

The axial core of the trabeculæ stains deeply in hæmatoxylin and in acetic acid carmine, the outer layers remaining colorless. This fact is important, as it indicates some preliminary chemical change in the axis of the bars, where the bone cells later appear.

In the oldest crabs, the axis of each bar is densely crowded with spindle-shaped cavities, or lacunæ. Their long axes are parallel to the long axis of the bar, and, under favorable conditions, we can see that many of them are connected at one end with a very fine tubule, or canaliculus, which runs radially toward the periphery. The largest lacunæ are nearest the center of the trabeculæ. (Fig. 206, *A*.)

If a section of the bone is dried in the air and then mounted in balsam or glycerine, the lacunæ and canaliculi appear black in transmitted light, and silvery-white in reflected light, showing that by the drying up of their semi-fluid contents they have become filled with air. Old fragments of bone that have dried in the sun for an indefinite period, when softened and sectioned, show the same structure. Caustic potash dissolves the granular contents of the lacunæ, but does not otherwise affect them.

Stained sections, quickly transferred to balsam, have many of the lacunæ and canaliculi injected with the stain, which generally disappears when the sections are well washed. But even after long washing with acidulated alcohol, some of the larger lacunæ show a characteristic color due to the presence of a faintly stained granular substance, and a small darker colored body.

All these facts show that we are dealing with actual cavities and canals in the chiten, some of which are filled with nucleated protoplasm.

The lacunæ are best seen in old crabs where several trabeculæ unite. At such points they are very numerous and apparently vary a good deal in shape. (Fig. 206, *B.*) This is largely due to the fact that they are turned in various directions, so that some are cut crosswise, others lengthwise. The lacunæ are usually filled with air and appear jet black. As the canaliculi enter the darker axial core (Fig. 206, *B.a.b.*), they become sinuous, and many side branches arise which terminate in minute lacunæ. Some of the latter appear to increase in size and

Fig. 205.—Inner surface of the shield of Limulus, showing the muscle markings and the distribution of the bony trabeculæ, the entapophyses, and the principal muscle markings.

to separate from the main canal, ultimately opening directly to the exterior by a single canaliculus.

At *d*, large elongated lacunæ are seen, some of them constricted transversely as though about to form several smaller lacunæ, although this appearance is not as common as the branched one described above. At *e*, are a few lacunæ belonging to a trabecula running at right angles to the plane of the paper.

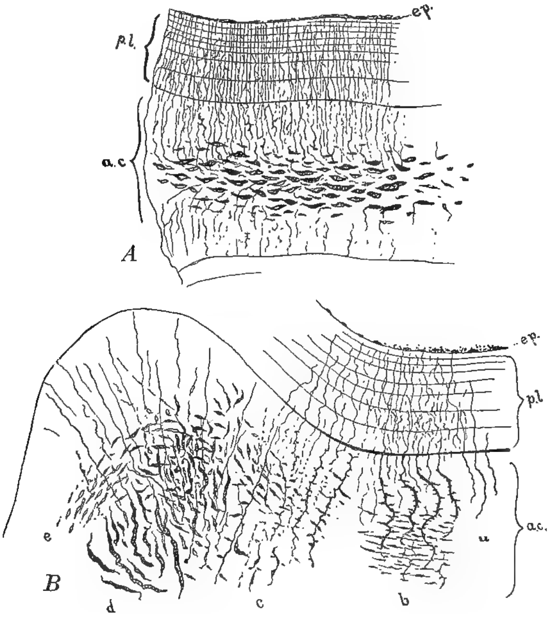

FIG. 206.—Section of bony trabeculæ from the shield of an old Limulus, showing the shape and arrangement of the lacunæ and canaliculi; highly magnified.

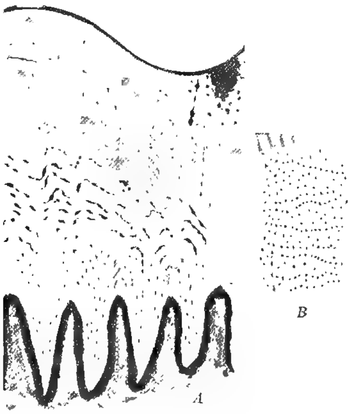

FIG. 207.—*A*, Section of the chitenous investment of the œsophagus of Limulus, showing the deeply stained chains of spindle-shaped bodies between the chitenous lamellæ. Delafield's hæmatoxylin. *B*, Section of the flexible chiten in the olfactory region, showing the minute, deeply stained, nuclear-like bodies in the pire canals. Hæmatoxylin.

The dermal bone tissue varies considerably in extent in different individuals. It is not visible in specimens less than eight inches long and probably does not make its appearance till the animal is full grown. Even when it is largely developed, the characteristic lacunæ in the chitenous bars may be absent. This shows, I believe, that the lacunæ are not fully developed till long after maturity is reached, for it was in the very oldest individuals, with much scarred and worn armor, that I found them best developed.

It is difficult to determine how the nuclei get into the lacunæ. They appear to migrate into them from the surface epithelium through the canaliculi. The following observations lend some support to this view. In the region of the olfactory organ, the chiten is soft and flexible and the bone cells are absent. When stained with the ordinary nuclear stains, the whole thickness of the wall is seen to be filled with minute sharply stained, nuclear-like bodies of uniform size, arranged with considerable regularity in the pore canals. (Fig. 207, *B*.)

In sections of the adult oesophagus (Fig. 207, *A*), the chiten is seen to be filled with bodies that also take a nuclear stain. Here they are of varying sizes; some are minute dots, others much larger, and spindle-shaped, and arranged in rows that follow the undulations of the lamellæ. The rows of spindle-shaped, or bead-like bodies are often united by delicate threads, as though they had multiplied by division and were still imperfectly separated from each other.

It is possible that some of these bodies are bacteria, or the spores of a parasitic fungus, or the products of some degenerative process. That is a point upon which I have not been able to satisfy myself, one way or the other. It is certain that a species of fungus, Macrocystis, does grow in the chiten of Limulus. Fragments of the skin, stained with methylene blue, often show the deeply stained hyphæ ramifying in all directions through the substance of the chitenous covering of the gills, or in the chiten surrounding the olfactory organ. They appear to dissolve out channels in the chiten, which are then completely filled by the growing hyphæ. The characteristic spores of Macrocystis have been found in abundance on the outer surface of the chiten in the olfactory region of dried shells. There is, however, no suggestion of any connection between this fungus and the nuclear bodies just described.

* * * * * * * * *

The continuous external armor of arthropods must be shed at regular intervals, to make room for growth, and the shedding of the old shell is always a difficult and dangerous process. In Limulus we see the beginning of a new type of exoskeleton, one that is subdermal and discontinuous, that need not be, and never is cast off after it is once formed. Indeed, Limulus could no more shed its dermal bones than a vertebrate could shed its cartilage cranium or its vertebral column. Limulus has therefore solved the problem for arthropods, of getting rid of an impractical external covering, a covering which has become too cumbersome and too impermeable for physiological purposes, which prohibits growth if retained, and which it is a menace to remove. In its place, it is producing an armor that is permeable, capable of indefinite expansion, and one that cannot, and need not, be shed at frequent intervals.

The new conditions under which this skeleton is developed, and especially its permanent retention within the foreign mesodermic tissues, were no doubt important factors in bringing about a permanent change in its chemical composition.

III. Summary and Comparison.

I. We have shown that Limulus possesses a remarkable dermal skeleton, and that in either coarse or minute structure there is nothing resembling it known in any other invertebrate. The nearest approach to it is found in the pteraspidian division of the ostracoderms. No other known animal, vertebrate or invertebrate, resembles Pteraspis in the structure of its exoskeleton so closely as Limulus. If Limulus were an extinct animal, it would be exceedingly difficult to discover any differences between the minute structure of its deeper lying exoskeleton and that of Pteraspis.

II. The surface ornamentation of the exoskeleton of the ostracoderms may be resolved into a series of alternating ridges and grooves that are either very uniform in size and nearly parallel, as in Pteraspis; or sinuous and with a tendency to break up into rows of tubercles, as in Bothriolepis; or finally forming tuberculate polygonal areas, as in Cephalaspis.

III. The outer surface is also marked by a special series of shallow grooves in Bothriolepis (Fig. 247), Ateleaspis (Fig. 242), and Tremataspis (Fig. 236), that probably mark the location of rows of sensory organs.

Another set of deep lying canals, probably representing enclosed surface grooves, are present in Pteraspis and Tremataspis. They are of even caliber and open outward by narrow slits, or pores, or by very short, chimney-like canals, (Figs. 193, 196, *s.c.*) that probably contained sensory organs or mucous glands. They differ from the vascular canals in that they are generally filled with a matrix like that outside the shell, showing that they communicated freely with the outside, while the vascular canals and even the cancellæ, may be quite empty.

IV. The surface ornamentation of the exoskeleton of the ostracoderms may be regarded as a further specialization of the ridges and grooves seen on the outer surface of the exoskeleton in the marine arachnids. It would require but a slight modification of the scale-like markings in Pterygotus, or of the zigzag ridges and grooves, or the polygonal areas, in Limulus, to produce the characteristic markings of Pteraspis, Bothriolepis, or Cephalaspis.

V. The surface ornamentation of the cephalic buckler in both arachnids and ostracoderms may be regarded as the external expression of internal irregularities in growth which ultimately lead to the breaking up of the continuous shell into separate plates.

VI. From a vertebrate standpoint, the continuous dermal armor of the ostracoderms appears to be a very primitive exoskeleton, and one from which that of the true fishes has been produced by breaking up the surface ornamentation into isolated dermal denticles and bony plates. From the invertebrate standpoint, the ostracoderm skeleton is a highly specialized one, produced by an exaggeration of the type of exoskeleton seen in Limulus.

VII. It may be urged that the bony plates of the ostracoderms are mesodermal in origin, while those of Limulus are epidermal. But we have no means of knowing whether the bony plates of the ostracoderms were developed entirely inside, or outside the ectoderm, and we cannot class them as subdermal, or mesodermal, unless we beg the whole question and assume that the ostracoderms are typical fishes.

VIII. The structure of the exoskeleton of the ostracoderms is as much like that of Limulus as that of vertebrates. The dermal skeleton of vertebrates can be derived as readily from that of Limulus as from that of the ostracoderms. To do this, for example, we need only to assume that the outer layer of the shell of Limulus has been reduced to a thin cuticular layer and is cut off entirely from the underlying trabeculæ. The skin and the skeletal parts derived from it would then appear to be formed of two layers, a continuous outer layer, and an inner one composed of more or less isolated fragments formed by local ingrowths from the outer layer.

The two kinds of exoskeleton, epidermal and subdermal, would then be present at the same time, as indeed they are in Limulus. But in Limulus the subdermal skeleton is in its initial stages, and the epidermal is the more voluminous. In primitive vertebrates the epidermal skeleton is about to disappear, being represented solely by the enamel layer, and possibly the dentine, while the subdermal layer has attained its maximum development. The distinction between the epidermal skeleton of the arachnids, and the dermal one in vertebrates is, therefore, only one of degree, not of kind.

In the embryonic development of dermal bones in vertebrates, the arachnid process of separating bony trabeculæ from the inner surface of the ectoderm is apparently greatly abbreviated, but indications of it have been observed in the development of certain cranial bones. These observations, therefore, need not be looked upon with suspicion, or, if accepted, taken as evidence of the untrustworthiness of the germ layer theories. They should be regarded rather as the naturally to be expected embryological indication of the derivation of the vertebrate dermal skeleton from the epidermal armor of arachnid ancestors.

IX. The dermal denticles are the oldest parts of the dermal skeleton of vertebrates, and they naturally still retain the clearest indications of their derivation from an arthropod exoskeleton.

The chiten of arachnids, and the enamel and dentine of the dermal bones of primitive vertebrates have essentially the same structure and mode of growth, as shown by their pronounced laminæ and the minute parallel canals that run at right angles to them. The differences are mainly ones of degree, *i.e.*, the number and size of the canals, and the density and composition of the matrix.

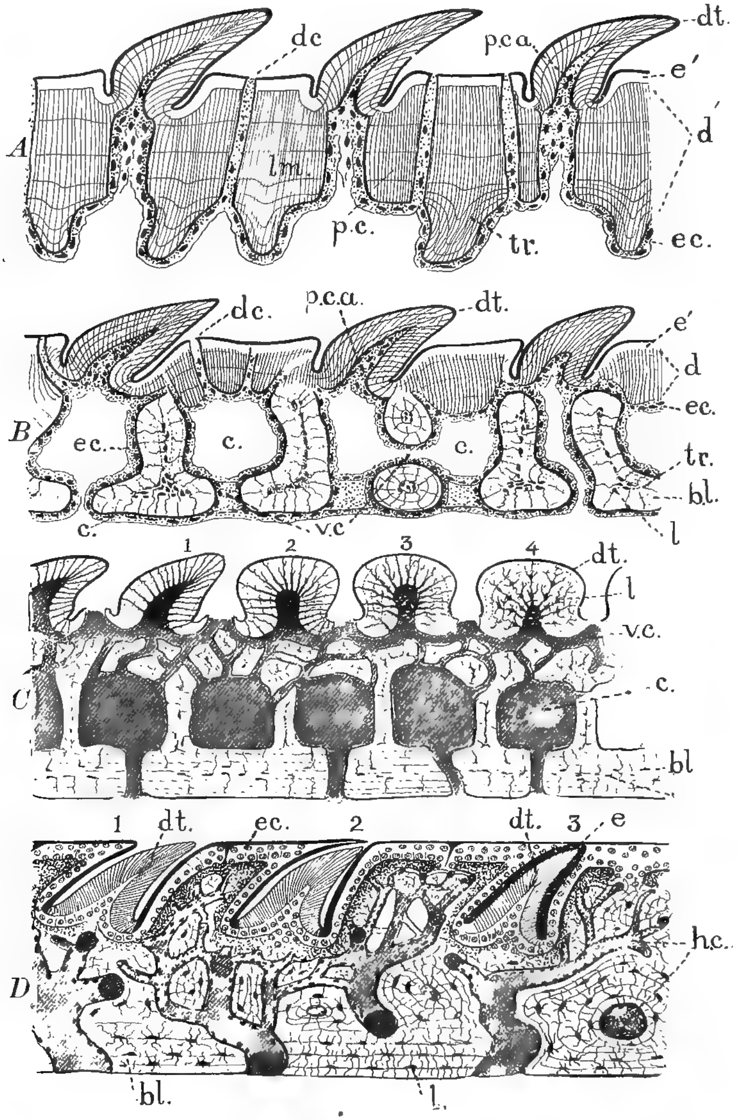

FIG. 208—Semi-diagrammatic sections illustrating the evolution of the chitenous epidermal exoskeleton of arachnids into the bony sub-dermal exoskeleton of vertebrates. *A*, Exoskeleton of immature Limulus showing the beginning of the trabecular ingrowths; *B*, mature Limulus, showing the cancellated exoskeleton; the trabeculæ, with their axial lacunæ; and the dentine-like chitenous matrix, with its parallel pore canals and concentric lamellæ; *C*, the exoskeleton of an ostracoderm, consisting of dentinal, vascular, cancellous, and basal layers. In the outer layer are shown several forms of tubercles, denticles, and dentinal ridges, with various forms of dentinal canals; *D*, the final stages showing the conversion of the vascular, cancellous, and basal layers into subdermal bone; and the conversion of the isolated remnants of the primitive epidermal skeleton, into dermal denticles.

When two such similar structures as enamel and dentine appear to arise, one from the mesoderm, the other from the ectoderm, it probably means that either there is no real distinction between the two layers, or else that both structures arise from the same layer. As there is no doubt about the origin of the enamel layer, and as there is no conclusive evidence that the odontoblasts have not arisen at a very early period from the ectoderm, it may be assumed that both enamel cells and odontoblasts were primarily derived from the ectoderm.

We may, therefore, regard the dermal skeleton of primitive vertebrates as consisting of two parts, viz. 1. the subdermal trabeculæ that develop into the characteristic bony plates, and that consist of concentric lamellæ, true bone corpuscles, and vascular chambers, or canals; and 2. the more superficial skeleton, that arises either from the outer surface of the ectoderm, or from cells in intimate relation with it, and that consists of parts having a chitenoid, enamel-like, or dentine-like structure.

X. The general nature of the process by which the continuous epidermal armor of the arachnids becomes fragmented and divided into two overlying systems, and the method of substituting the inner system for the outer, is shown in a diagrammatic way in Fig. 208.

The ostracoderm skeleton, *C*, clearly represents a transitional stage between the vertebrate and the arachnid type. In the vertebrates themselves, the principal events in the evolution of the dermal skeleton are the gradual elimination of the epidermal structures, except those retained in the teeth; the reduction of the subdermal bones to relative insignificance; and the substitution for them of an endoskeleton of true mesodermal origin.

CHAPTER XVII.

THE ENDOCRANIUM, BRANCHIAL AND NEURAL CARTILAGES.

I. The Endoskeleton of Arachnids.

Many arthropods are provided with an elaborate system of ectodermic infoldings, lined with chiten, that serve for the attachment of muscles and in some cases as a supporting framework for the anterior part of the nervous system. They may be segmentally arranged, and in some cases appear to be the modified remains of duct-like infoldings that originally served some other purpose than for the attachment of muscles. There are no indications that these structures are represented in vertebrates, and we merely refer to them here in order to emphasize the distinction between them and the true endoskeleton we shall describe in the following pages.

The endoskeleton of arachnids (Limulus) consists of four distinct parts, their relation to the corresponding parts in the vertebrate skeleton being sufficiently indicated by their names. They are: *a.* the neural arches; *b.* the branchial cartilages; *c.* the endocranium; *d.* the notochord. (Fig. 209.)

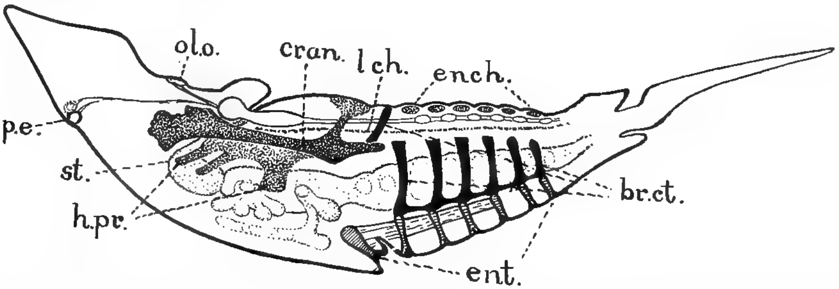

FIG. 209.—Diagram of the endoskeleton of a marine arachnid (based on Limulus) showing the locations of the lemmatochord, endocranium, neural arches (dotted), branchial cartilages (black), and the chitenous entapophyses (shaded).

With the exception of the notochord, these structures are primarily mesodermic in origin; they serve for the attachment of muscles, and with the possible exception of the branchial cartilages, their origin and development was determined by the development of the muscles now associated with them. They have the same general form, location, consistency, and chemical reaction that the corresponding cartilages have in vertebrates.

The arthropod notochord is a modification of the middle cord and is primarily ectodermic in origin. The median nerve derived from it degenerates and the remnants become invested with a thick envelop of neuroglia-like tissue that may serve for the attachment of segmental muscles. At no time in its phyllogenetic history has it any functional connection, or relation to the endoderm, or to the alimentary canal.

II. THE NEURAL ARCHES. (Figs. 70, 75, 78, 209.)

The neural arches (endochondrites of Lankester) are six small plates of fibro-cartilage. They lie on the neural surface of the cord beneath the integument, to which they are attached near the base of each pair of gills. Each arch is concave on its inner surface and partly surrounds the nerve cord, holding it firmly in place. (Figs. 70, 75, 78.) The opercular neural plate is typical; it is rectangular, and its flat neural surface is indented by two pits, from which arise a pair of muscles attached to the inside of the operculum. A pair of anterior and posterior processes serve for the attachment of strands from the longitudinal muscles of the abdomen. On the sides of the arch is a pair of processes which project hæmally and a little outward and backward, one on each side of the ventral cord. They furnish attachment for a pair of hæmo-neural muscles that are inserted on the hæmal side of the carapace, just median to the entopophyses.

The neural arches of Limulus may be regarded as the precursors of the neural arches of vertebrates, with which they agree in location, and in their general form and function. No other invertebrate is known to have neural plates of this character.

III. BRANCHIAL CARTILAGES. (Figs. 78, 209, 210, 211.)

There are seven pairs of branchial cartilages in Limulus. The most anterior pair are two small bars arising from the inner surface of the chilaria, and attached to the posterior margin of the endocranium. (Fig. 215.) The remaining six pairs arise from the base of the abdominal appendages, and go to the corresponding entopophyses. (Fig. 209.)

The branchial cartilages arise at an early embryonic period as clearly defined outgrowths of the walls of the mesoblastic somites. (Fig. 210.) Their union with the epidermis is secondary, and they are in nowise derived from chitenous ingrowths of the epidermis.

The branchial bars serve for the attachment of the flexor and extensor muscles of the gills, and for a small muscle, the internal branchial, arising from the corresponding neural plate. The opercular bar is the largest. In a small male, it is about 25 mm. long, oval in cross-section, and about 6 mm. by 3 mm. in diameter. The remaining bars decrease gradually in size to the posterior end of the series.

A band of cartilage, similar histologically to that of the branchial cartilages, extends from the distal end of one entopophysis to the next, uniting the hæmal ends of the gill bars. (Fig. 209.)

The branchial bars are hard and elastic, and have the general appearance and consistency of hyaline vertebrate cartilage. Chemically and histologically, they are quite different from the fibro-cartilage of the endocranium, or of the neural plates. There is apparently no invertebrate, outside of the arachnids, that has a tissue comparable with it. The nearest approach to it, chemically and histologically, is the muco-cartilage in Petromyzon. The branchial bars of Limulus correspond to the gill bars of the post auditory region of vertebrates, as we first indicated in 1889. In 1893, we called attention to the surprising histological resemblance between these cartilages and those of Petromyzon, and still later, 1896, it was shown that in abnormal Limulus embryos, one or more pairs of appendages were invaginated, forming transverse slits along the sides of the head, that resemble vertebrate gill slits or the lung books of the arachnids. (Fig. 183, *A*.)

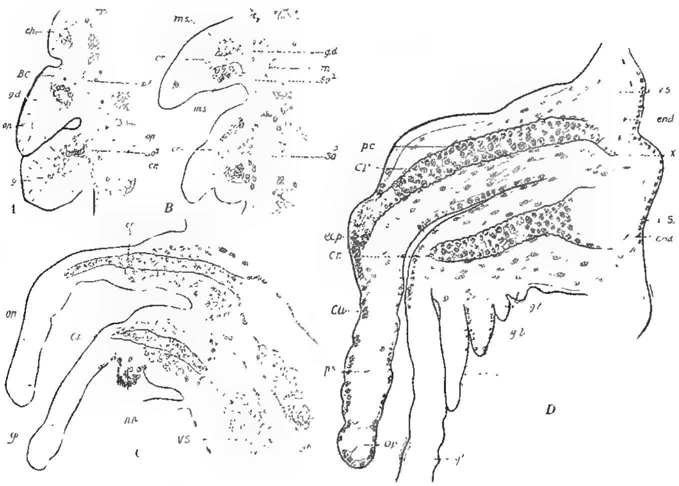

FIG. 210.—Sagittal sections of Limulus embryos, showing successive stages in the development of the branchial cartilages. After Patten and Hazen.

Development of the Branchial Cartilages in Limulus.—The following description is based, in the main, on what takes place in the operculum. The cartilages in the other abdominal appendages develop somewhat later, but in a very similar manner.

In an embryo of three abdominal segments, there is no trace of the opercular cartilage. (Fig. 210, *A*.) By the time five abdominal segments are developed, the outer wall of the somite forms a thick ring of mesoderm around the base of the appendage. The opercular cartilage makes its appearance as a transverse plate of cells subtending the ring, with its distal end projecting into the cavity of the appendage. (Fig. 210, *B*.)

In the next stage, *C*, where one gill leaf is developed on the first branchial appendage, the cartilages have increased in size and now show the features that characterize them so clearly in the later stages; viz: 1, the cartilage cells are larger than the surrounding mesoderm cells, and have distinct cell walls; 2, they are arranged in rather regular order; and 3, the protoplasm stains very lightly in borax carmine.

In the next stage, with three gill leaves on the first branchial appendage (Fig. 210, *D*), the cartilages form long flat plates that extend some distance beyond the ring of mesoderm into the appendage. The cartilage of the first gill is attached to the anterior wall of its appendage, and extends from there to the corresponding somite, which has now become a venous sinus bounded by a thin membrane.

A perichondrium is now visible, composed of a layer of spindle-shaped cells, apparently derived from the breaking up of the mesodermic ring, and not from a transformation of the peripheral cartilage cells. The latter, as we have shown, are formed from the mesothelium of the somatic walls.

The ends of the branchial cartilages finally fuse with the ectoderm on the anterior wall of the appendages and with the hæmal wall of the abdomen. At these points the cartilage and ectoderm are so completely united that their original boundaries cannot be distinguished.

The spaces in the distal ends of the gills are crossed by fibrous columns arising from the ectodermic walls. At the base of each column are several nuclei, as though the columns were formed by the union of several cells. At this stage no mesoderm extends into the appendages beyond the distal ends of the cartilages.

In the early trilobite stage the branchial cartilages differ but little, except in size, from those in the adult.

Minute Structure of Branchial Cartilage.—During the late larval period, each cartilage cell develops on its outer surface a cartilage-like matrix that envelops and isolates each cell. This is the primary capsule. It gradually increases in size, forming a large thin-walled chamber, within which the cell continues to divide in the three planes of space, each division plane being generally at right angles to the preceding one. After each division the daughter cells form new capsules inside the old ones. As there is little or no shifting of the cells after each division, the shape and position of the primary, secondary and tertiary, etc., capsules show pretty clearly the history of the previous divisions.

The cluster of cells and capsules enclosed in the primary capsule constitutes a cartilage nest. The nests are largest in the axis of the gill bar; the periphery of the bar consists of small cells not clearly grouped into nests. The cartilage tissue terminates abruptly under the perichondrium. The two tissues are different chemically and ontogenetically and there are no indications of intermediate stages between them, although occasionally one finds a small cluster of cartilage cells enclosed like a foreign body, in the perichondrium, or in the fibrous tissue connecting the inner ends of the entopophyses. Similar nests of capsuligenous cartilage are said to occur in the endocranium of Mygale (Lankester) and Telephonous (Gaskell).

When the gill bars with their adhering fibrous and muscular tissue are boiled for a short time in caustic potash, the perichondrium and muscles are at once dissolved, leaving the cartilage bar clean and free from all other tissues. The cartilage swells and turns yellow and transparent, but otherwise appears to be unchanged. After prolonged boiling it breaks down and disappears.

Thin sections of the gill bars, boiled in potash till the perichondrium is completely dissolved, show under the microscope irregular crevasses and spaces around the central cell nests, indicating that the clear matrix, or cement, surrounding them has been dissolved out. The capsules themselves are swollen, and their walls appear much more distinctly laminated than before. On further boiling, the axial portion of the section drops out, indicating that the nests have been completely isolated; when boiled still longer, the peripheral portion breaks down also.

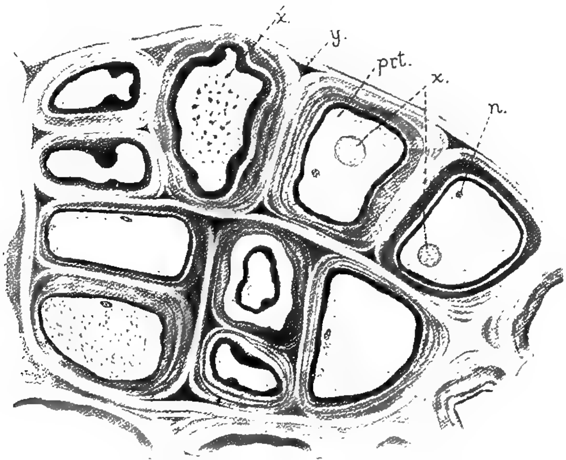

FIG. 211.—Section of the branchial cartilage, in an adult Limulus, highly magnified, showing a single nest of cartilage cells. The arrangement of the concentric layers of differently colored chondrin indicates the successive generations of cartilage cells. Stained in thionin and picric acid.

When free hand sections of alcoholic material are treated with thionin, complicated color reactions take place that vary with the thinness of the section, strength of the solution, and apparently with the exposure to air and duration of the staining. The reactions may be studied under the microscope in a watch glass. If the stained sections are mounted in glycerine, it will be seen that the lacunæ are lined with a finely granular protoplasm, with one or more small nuclei on the periphery. (Fig. 211, *n.*) The center is filled with a fluid, containing in some cases coarse granules of a deep reddish-violet, x', in others, large spherules of a faint yellow color, x. In most cases the central portion appears to be empty, and if the sections are carelessly handled they may contain large air bubbles.

The capsules consist of alternating red, or violet, and blue laminæ. The red bands vary greatly in thickness and in the intensity of the color in different capsules. The innermost one is deep red, with a rough irregular inner surface, the larger protuberances probably marking the beginning of a new partition. Just outside this layer there may be a very sharp, thin, blue band, or a broad red band of a lighter color. The most intense and widest blue bands form the middle layer in the partitions between two cells, or between two groups of cells, or in the layers surrounding the whole nest.

In some instances, after staining a short time only, these reactions seem to be reversed, the violet bands appearing blue and the blue ones violet. The violet bands are the first to stain, the blue ones appearing much later; they show most clearly after the sections have been partially decolorized in glycerine. Similar color bands are seen after staining with hæmatoxylin, except that the bands are of different shades of purple.

If thionin sections are treated with weak picric acid, the blue bands become intense green, and later bright yellow, while the violet bands are affected but little. These preparations are most brilliant and are the ones from which the drawing was made.

In the axial portions of the gill bars, the cell nests in some cases, are separated by considerable areas of a nearly homogeneous matrix, some parts being blue, others violet. The perichondrium stains a bright characteristic violet, and the muscles blue.

The probable explanation of these complicated color reactions is that the walls of each capsule consist of a graded series of different chemical substances arranged in concentric layers, the substance giving the red reaction being the most abundant in the inner protoplasmic layers of the capsules, and that giving the blue reaction being more abundant on the periphery, with intermediate transitional compounds between; and that the blue material is formed by a gradual modification of the red.

The gill bars of Limulus are exceedingly interesting histologically, and deserve a more careful and detailed description than we can give them here. The main points we desire to establish now are that they contain true cartilage of a very primitive type, and that this cartilage is quite different, chemically and histologically, from that found elsewhere in Limulus.

The reaction of the gill cartilages to thionin and hæmatoxylin indicates that they contain, besides other substances, a considerable amount of mucin. This fact, together with their remarkable histological structure, emphasizes still more strongly the resemblance between the gill bars of Limulus and those of Petromyzon. Moreover, the extraordinary difference between the capsuligenous cartilage and the fibro-cartilage of the endocranium in Limulus is paralleled by the fact that there is a corresponding difference between gill cartilage and cranial cartilage in the cyclostomes.

The fibro-cartilage of the arachnids appears to have arisen by the gradual transformation of fixed muscle ends into sinews or tendons, in proportion as the corresponding muscles become more active and voluminous. The capsuligenous cartilage appears to arise "de novo," making its appearance as an entirely different looking material from that in which it is imbedded. The gill bars for example are well developed at a very early embryonic period, and appear to be quite out of proportion to the volume and functional importance of the surrounding muscles. Moreover isolated and highly developed cartilage cells, or cell nest, may be seen in adult crabs lodged in the perichondrium of the gill bars, or at the ends of the entopophyses and in other places where they appear quite foreign to the surrounding tissues, and with nothing to suggest the reason for their presence in such unusual surroundings.

IV. The Endocranium.

The endocranium, variously named prosomatic endosternite, cartilaginous sternum, or plastron, has been found in many of the arachnids and in the phyllopods. In 1889, I figured and described the endocranium of the scorpion, and compared the endocrania of the scorpion and Limulus with the primordial cranium of vertebrates. In 1899, in collaboration with Mr. Redenbaugh, a graduate student in Dartmouth College, the endocrania of Apus, Mygale, and Limulus were described and illustrated in more detail.

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The endocranium of arachnids is a broad plate of fibro-cartilage lying on the hæmal side of the brain. It serves primarily for the attachment of the muscles that move the oral appendages, and for the flexor muscles that move the cephalo-thorax on the branchial section of the body. In scorpions and in Limulus a complete occipital ring is formed about the spinal cord, near its union with the brain.

The floor of the endocranium is a continuous structure and there are no indications that it consists of originally separate pieces; the supra-occipital plate, when present, may be regarded as a modified neural arch belonging to the vagus segments. We recognize in the higher arachnids three principal parts, viz. two lateral bars; a broad median plate that unites the posterior ends of the bars; and a bridge of cartilage on the neural side of the nervous system, which together with the above mentioned parts forms a closed ring about the anterior end of the spinal cord.

The endocranium has a true cartilaginous consistency, and is composed of a mass of interwoven fibers and a dense matrix containing stellate lacunæ united by anastomosing canaliculi. In the living cartilage, the canaliculi contain minute branching processes of the cartilage cells situated in the lacunæ.

The endocranium of arachnids, as I first pointed out in 1889, represents the ancestral stage in the evolution of the primordial cranium of vertebrates, the lateral bars, the transverse plate, and the neural arch of the arachnid cranium corresponding respectively to the trabeculæ, the parachordals, and the occipital ring of the vertebrates.

The Endocranium of Apus. (Fig. 212.)—In Apus the endocranium is a thick plate of fibro-cartilage, without an occipital ring, located just behind the mouth, between the central nervous system and the intestine. The body of the endocranium is elongated in a transverse direction, its flaring ends giving attachment to the powerful adductor muscles of the mandibles.

A pair of chitenous apodemes, *apo.*, project into the posterior side of the endocranium. They are ectodermic invaginations lined with chitin, formed between the bases of the first and the second pair of appendages. From the inner ends of the apodemes, a pair of tendenous cords run directly through the body of the endocranium, at right angles to its fibers, emerging on the anterior side as the anterior cornua, *ac.*

The endocranium terminates posteriorly in a thin membrane *w*, which is attached to the integument between the nerve cords.

Longitudinal muscles of the abdomen are attached to the posterior sides of the apodemes and to the endocranium itself. A process on the neural side of each apodeme serves for the attachment of muscle strands going to the inside of the second pair of maxillæ, *x.* Hæmo-neural muscles are attached to the hæmal sides of the apodemes, and a pair of muscles, inserted on the posterior neural portion of the endocranium, *y.*, pass between the nerve cords to the integument just back of the first cross commissures.

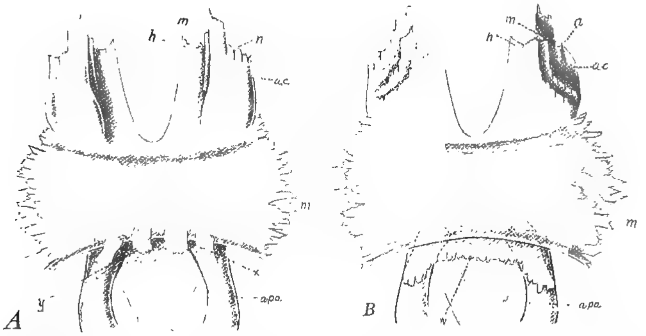

FIG. 212.—Endocranium of Apus; *A*, Neural surface; *B*, hæmal surface. The mandibular muscles are attached to the large transverse processes, *m*; maxillary muscles to the small processes, *x*. A pair of chitenous entopophyses, *apa.*, are imbedded in the posterior side of the endocranium. × 27 1/2. After Patten and Redenbaugh.

Endocranium of Mygale (Fig. 213.)—The endocranium of Mygale is a large oval plate of fibro-cartilage with crenate margins; like that of Apus, it lies between the alimentary canal and the central nervous system.

The neural surface is concave and provided with paired, plate-shaped processes, *A*, *n.pl.* From about the middle of the large anterior cornua, arise a pair of neural processes, *n.pr′*, which bend around the brain and attach themselves to the integument close together on the neural side. They probably represent the lateral portion of the occipital ring of Limulus.

On the hæmal side, *B*, two high, flaring ridges converge toward the posterior end of the endocranium, forming a deep gully in which lies the alimentary tract.

The hæmal ridges are split up into five pairs of hæmal processes, *h.pr.*$^{1-5}$, of unequal length. The endocranium ends posteriorly in a short median process. From nearly the whole of the neural surface muscles go to the base of the legs. Hæmo-neural muscles are attached to the hæmal processes, and longitudinal muscles to the posterior process.

The œsophagus passes through the brain, between the anterior cornua, to the sucking stomach which lies in the groove on the hæmal side of the endocranium. Muscle strands run from the stomach to the walls of the groove.

Endocranium of Limulus (Figs. 2, 70, 75, 78, 209, 214, 215).—The endocranium of Limulus is the largest of any living arachnid. It is a rectangular plate of fibro-cartilage, about three inches long, two and one-half inches wide, and from one-eighth to one-half an inch thick on the margins. It lies near the center of the cephalothorax, with its anterior margin about opposite the cheliceræ, and its posterior one opposite the chilaria. It serves as a center of attachment for the more important muscles of the thorax. The mouth is located a little anterior to the center of the endocranium. From it the œsophagus passes forward, through the brain, and between the anterior cornua to the mesenteron. (Figs. 78–209.) The latter begins a short distance in front of the endocranium and extends straight backward close to its hæmal side.

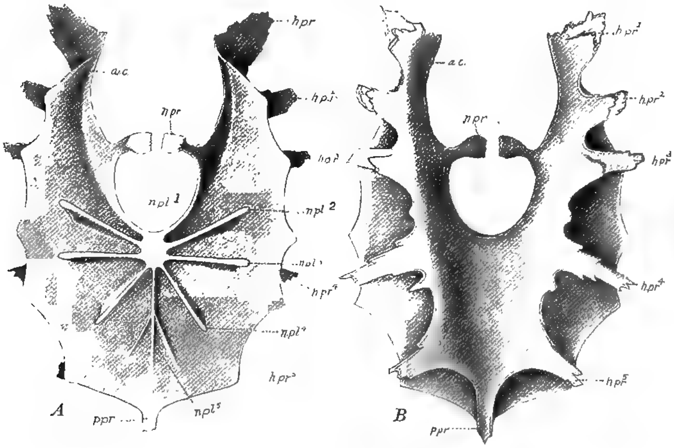

FIG. 213.—Endocranium of Mygale. *A*, Neural surface; *B*, hæmal surface. ×5. After Patten and Redenbaugh.

The neural surface of the endocranium is nearly flat and bounded on either side by a sharp ridge or lateral wall. The anterior ends of the wall are much higher and generally slope inward. (Fig. 215, *A*.) The posterior ends also increase in height, turn inward and become continuous with the plate of cartilage that forms the roof of the occipital region. The endocranium thus forms a shallow box, with low vertical walls along the sides and along a part of its posterior end. There is no transverse anterior wall and no covering, or roof, except at the posterior end. The brain lies on the floor of this box, the ventral cord and several pairs of nerves extending backward through the large occipital foramen in the posterior wall. (Fig. 214.)

We may recognize the following parts, viz. *The anterior cornua, a.c.*, a pair of stout, transversely flattened processes formed by the forward prolongation of the thickened lateral margins. From each process arise three muscles, the opposite ends of which are attached to the hæmal side of the carapace (Fig. 75); one is directed forward from the extremity of the cornua, one perpendicularly from its inner surface, and one obliquely forward from its hæmal margin.

The neural margins of the cornua and the entire lateral portions of the endocranium, including the posterior lateral processes, give attachment to the plastro-coxal muscles of the second to the sixth pair of thoracic appendages. (Fig. 75.)

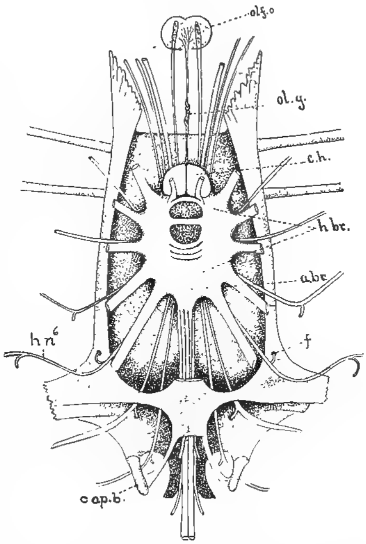

FIG. 214.—Endocranium of Limulus, seen from the neural side, with the brain in place.

Anteriorly, the muscles do not cover the neural surface of the endocranium, but posteriorly the muscles increase in size with the increase in size of the appendages, and encroach upon the neural surface even to the median line. There is therefore on the anterior neural surface of the endocranium a triangular space which, except for a few loose strands (plastro-buccal muscles going to the œsophagus) is free from muscles and comparatively smooth. (Fig. 215, *A*.)

The anterior hæmal processes, l.c., arise from the anterior hæmal side of the endocranium. They consist of two pairs of long and slender processes each one attached by a short muscle to the hæmal side of the carapace, close to the origins of the tergo-coxal muscles.

The posterior hæmal processes, h.pr., lie on the hæmal side near the lateral edge of the endocranium. They incline slightly outward, and each gives attachment to two muscles: one going from the extremity of the process to the carapace, and the other from the posterior margin of the process to the first entapophysis. (Fig. 75.)

The posterior lateral processes, lp.pr., are flattened expansions of the posterior portion of the endocranium. Along the posterior margin of each process, on the neural side, is a sharp transverse ridge which, toward the median line, unites with the lateral ridge and with the base of the occipital ring. The posterior-lateral processes give attachment to some of the plastro-coxal muscles of the sixth pair of legs, which are the most powerful appendages of the animal.

The posterior median process, p.pr., or basioccipital, begins as a median ridge on the hæmal side of the endocranium, between the hæmal processes. It increases in thickness posteriorly, ending in a bifid process, each division of which is deeply grooved on the hæmal side. Along the whole hæmal side of the process are attached two large muscles that go to the first pair of entapophyses. To the body of the endocranium, on both sides of the basioccipital, are attached longitudinal abdominal muscles. Their attachments extend a little anterior to the hæmal processes. In front of this, the body of the endocranium is destitute of muscles on the hæmal side. A pair of small chilarial muscles are attached to the hæmal side of the extremity of the basioccipital.

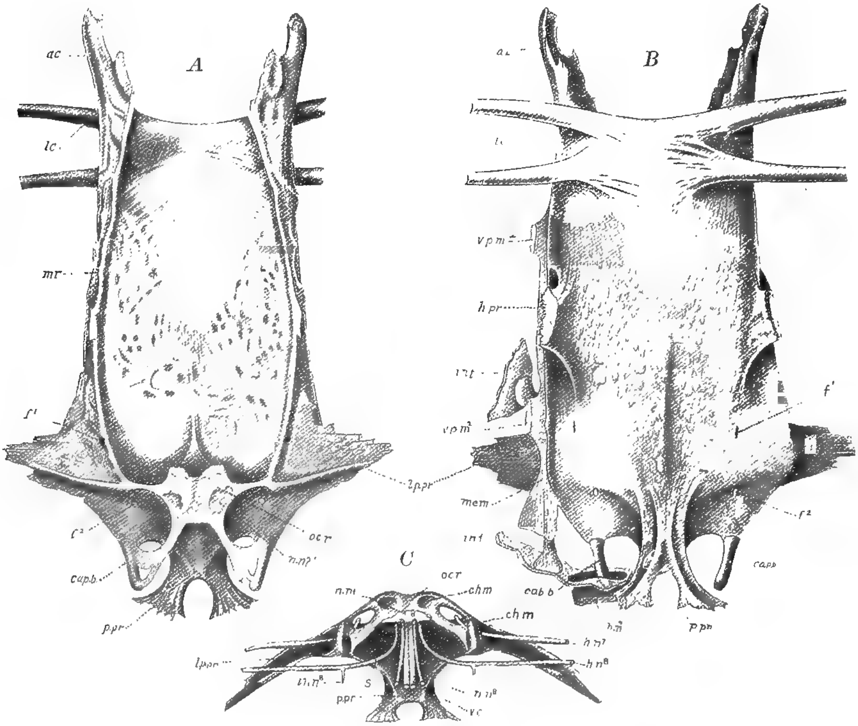

FIG. 215.—Endocranium of Limulus. *A*, Seen from the neural surface; *B*, from the hæmal surface; *C*, from the caudal end.

The occipital ring, *oc.r.*, begins at the points where the marginal walls meet the posterior-lateral processes. Here two vertical outgrowths are formed which unite with each other on the neural side of the ventral cord. At their bases the processes are slender, but distally they enlarge and thicken, forming a polygonal, supraoccipital plate that is joined to the capsuliginous bars, *B*, by strands of connective tissue. Upon the neural surface of the supraoccipital plate are two depressions, to which are attached a pair of muscles going to the insides of the chilaria, *ch.m.* From the anterior edge of the plate, muscle strands pass forward to the integument immediately behind the mouth.

The capsuliginous bars, *B*, arise from the thin posterior margin of the endocranium, bend neurally and slightly toward the median line, and are attached to the posterior sides of the bases of the chilaria. A small transverse muscle joins the distal ends of the two bars. Two other small muscles run to the chilaria from the thin portions of the endocranium, near the bases of the bars.

It is especially noteworthy that the body of the endocranium is composed of fibroid cartilage, while the bars just described are of capsuliginous cartilage, exactly like that found in the abdominal appendages. The development of the bars shows that they represent a pair of gill bars belonging to the chilaria, that have been secondarily united with the cranidium.

Foramina.—There are two pairs of foramina for the passage of nerves. One pair lies just outside the marginal wall, appearing on the hæmal side of the endocranium, a little posterior to the hæmal processes, f^1. The intestinal branches of the hæmal nerves belonging to the sixth thoracic neuromere pass through this pair. (Fig. 214, $h.n^6$.) The intestinal branch of the chilarial hæmal nerve passes through the second foramen, f^2

The occipital foramen is the large canal enclosed by the basioccipital and the supraoccipital plates. Through it passes the spinal cord, the chelarial and opercular nerves.

Endocranium of the Scorpion (Figs. 43, 216, 217, 218).—The endocranium of a small American scorpion, probably Buthus carolinianus, was reconstructed, by plotting serial sections of the whole thorax. The endocranium of the large African scorpion was dissected out and the drawings and measurements were made under the simple microscope.

In the American scorpion, Fig. 216, the endocranium consists of two nearly parallel plates of fibro-cartilage, or trabeculæ; they are united at their posterior ends by a broad basilar plate, which extends laterally into wing-like, posterior-lateral processes, *l.p.*, and backward in two long posterior processes, *p.p.* The thickened median portion forms the basioccipital. The trabeculæ are united in front of the basioccipital by a thick membrane, on the neural surface of which lies the enlarged anterior end of the bothroidal cord, *m.c.* Opposite the ends of the membrane, are two plate-like hæmal processes, directed hæmally and laterally. The middle portion of the trabeculæ are thin, nearly horizontal plates. The anterior ends are greatly thickened and end in two pointed processes.

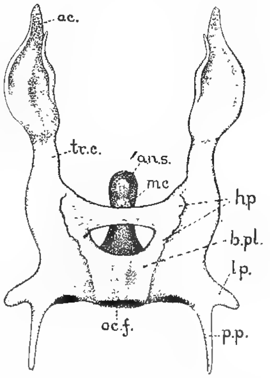

FIG. 216.—Endocranium of an American scorpion (Buthus) seen from the hæmal surface. Reconstructed from sections and dissections.

There is a distinct occipital ring enclosing the posterior part of the brain.

In the large African scorpion (Figs. 217, 218), the endocranium is heavy and well developed and in its general form resembles the one just described. The neural surface of the diverging trabeculæ is flat and their united posterior ends form a thick basilar plate from which spring, right and left, the broad vertical plates representing the posterior lateral processes, *l.p.* The supraoccipital, *oc.p.*, is a thick triangular plate with clean cut, beveled edges. The apex extends forward as two diverging tendons, *an.s.*, and the posterior angles extend backward over the occipitals as diverging crests that become continuous with the ragged flaring plates that represent the posterior processes, *p.p.* A small vertical process arises from the middle of the posterior margin of the supraoccipital. (Fig. 218, *n.p.*)

When seen from behind, the occipital ring presents a very striking resemblance to the occipital region of a vertebrate cranium. (Fig. 218, *B.*) The exoccipital region is heavily reinforced, and on each side a ridge extends laterally from the posterior face of the exoccipitals along the posterior process.

The hæmal plates are two deep, flaring plates extending along the hæmal surface of the trabeculæ and basilar plate. The posterior hæmal processes, *h.p.*, may be regarded as a local specialization of the hæmal plates, corresponding to the posterior pair of hæmal processes in the endocranium of mygale. They are long narrow plates arising about opposite the anterior margin of the occipitals. The anterior hæmal process, *a.h.p.*, is a thin, irregular prolongation of the anterior margin of the hæmal plate. It is of uncertain form, since its margins are easily injured in the dissection.

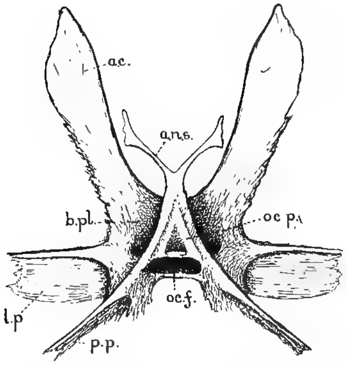

FIG. 217.—Endocranium of a large African scorpion, seen from the neural surface. Cam. outline. ×7.

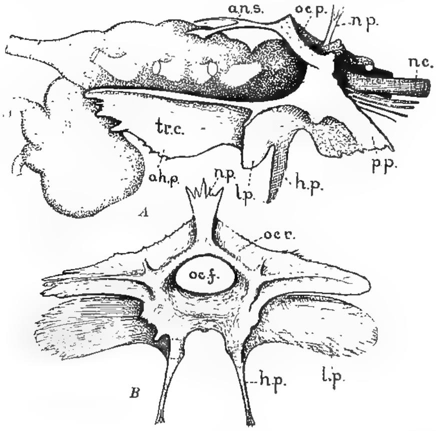

FIG. 218.—Endocranium, same as in preceding figure. *A*. Seen from the side; *B*, the occipital portion, seen from the caudal end. ×7.

The hæmal plates converge posteriorly, following the general direction of the trabeculæ. The anterior ends flare outward; the posterior ends are nearly vertical, and form the lateral walls of a deep sub-cranial channel in which lies the posterior portion of the stomodæum and the anterior end of the gut. In Fig. 218, *A*, the brain and endocranium are shown from the side in their proper relations. The anterior ends of the trabeculæ reach almost to the anterior surface of the bent over forebrain. The neural surface of the trabeculæ forms two horizontal shelves on either side of the hindbrain, the four posterior thoracic neuromeres sending their nerves laterally over the neural surface of the shelf.

The supraoccipital forms an arching roof over the posterior thoracic and vagus neuromeres. The thoracic nerves pass out of the endocranium through the wide open sides, while the nerves of the four vagus neuromeres, together with the nerve cords, pass backward and out of the cranium through the foramen magnum.

Telyphonus.—The endocranium of Telyphonus (Fig. 219), can be readily reduced to the type of those described above.

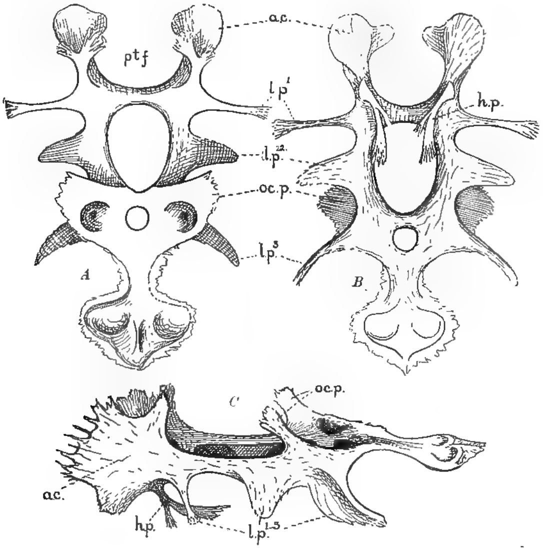

FIG. 219.—Endocranium of Telyphonus. *A*, Neural surface; *B*, hæmal; *C*, side. × 5 1/3.

V. SUMMARY AND COMPARISON.

I. Endocranium.

1. A cartilaginous endocranium is eminently characteristic of the phyllopod-arachnid-vertebrate stock. It appears to be absent in the insects, myriapods and crustacea. Its simplest adult condition is seen in Apus and Branchipus where it is an unpaired, unsegmented basilar plate of fibrocartilage, with thickened margins and projecting cornua. This is also its early embryonic condition in Limulus.

2. The evolution of the form, location, and mode of growth of the endocranium was determined primarily by the size and functional activity of the muscles and appendages with which it was associated.

3. The basilar plate served primarily for the attachment of muscles arising from the bases of the mandibles, or of the anterior thoracic appendages. It is first seen in the anterior midbrain region as a thickened horizontal membrane, lying between the nerve cord and the alimentary canal and extending across the median line from the base of one appendage to its mate.

In Apus and Branchipus it is confined to the mandibular metamere; in

Limulus and other arachnids, it arises from all the thoracic and first vagus metameres, and in the adult it may cover a much wider territory than the entire brain.

4. The extension backward of the basilar plate in the arachnids, and the increased volume of its posterior portion, was due to the diminished size of the anterior thoracic appendages and the increase in size of the posterior ones. Also to the fact that as the thoracic metameres united more intimately with each other and with the forehead, the posterior portion of the basilar plate served as a more and more important point of attachment for those voluminous longitudinal trunk muscles that helped to move the whole cephalothorax on its hinge-like joint. Another factor that aided in the development of the occipital region was the crowding forward of the neural arches of the vagus segments to form the supraoccipital plate, and the union of the latter with the underlying basilar plate to form the occipital ring. The occipital region was also reinforced by the addition of the branchial bars of the rudimentary vagus appendages to the posterior part of the basilar plate.

5. The basilar plate is anchored to the hæmal wall of the cranium by the powerful plastro-tergal muscles that arise from the keel-like hæmal plates. The size of these plates, their form, and the direction of their fibrous constituents, is determined by the amount and direction of the strain on them, and hence is determined indirectly by the same factors that control the form and development of the basilar plate and the occipital ring.

6. Thus the evolution of the arachnid endocranium becomes intelligible. Its four main axes, or planes, of growth that have given rise to the transverse basilar plate, the longitudinal trabeculæ, the vertical hæmal plates, and the heavy occipital ring, are due more remotely to those causes controlling the concrescence of the cephalic metameres, and more directly to the nature of the three axes of muscular strain, transverse, longitudinal, and vertical, that have acted upon it. It will be observed that owing to the relation of the endocranium to the mouth, brain, stomodæum, and intestine, the framework of the endocranium could not be constructed along any other lines than those indicated. (Fig. 220.)

7. There is no reason to doubt that the conditions prevailing in living arachnids, also obtained in the trilobites and merostomata. In the gigantic eurypterids, with powerful, oar-like appendages and movable head, the endocranium probably reached a higher grade of development than in any of their living representatives.

8. The fully developed arachnid endocranium is in every essential respect a duplicate of the primordial cranium of a primitive vertebrate embryo. They agree: *a.* In their position relative to the brain; *b.* in their general form; *c.* in their mesodermic origin and histological structure; *d.* in their absence of segmentation, although spreading over several metameres; *e.* in their great size compared with the brain; and *f.* which is the most important agreement of all, they agree in their four axes, or planes of growth; namely, the transverse growth of the basilar

plate, the longitudinal growth of the trabeculæ, the overarching growth of the occipitals, and the longitudinal vertical growth of the hæmal plates or palato-pterygo-quadrate arcade. (Compare Fig. 220.)

9. The endocranium has developed along these lines primarily in response to muscular strain, and its principal axes of growth, therefore, coincide with the axes of strain. But after it has become established phylogenetically, as in the vertebrates, it acquires a new moment of growth that is independent of the direction or location of the muscular strains brought to bear upon it.

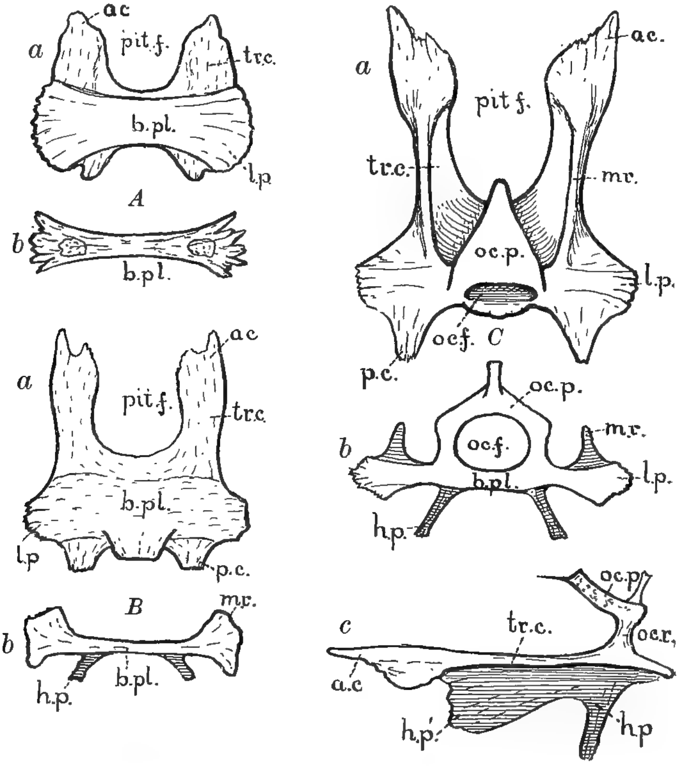

FIG. 220.—Diagrams illustrating three stages in the evolution of the arachnid endocranium. *A*, Phyllopod stage, seen from the neural surface, and in transverse section. The endocranium consists of a flattened basilar plate, located in the region of the oral appendages (mandibles and maxillæ) and composed of a thickened transverse bar, and two longitudinal ones. *B*, Primitive arachnid stage; the endocranium extends over the whole of the thoracic region, and shows the beginning of the anterior and posterior cornua, *a.c.* and *p.c.*, lateral and haemal processes, *l.p.* and *h.p.*, and marginal ridges. *m.r.* *C*, Arachnid stage, showing the fully developed arachnid endocranium, and the principal axes of growth.

10. The vertebrate embryo picks up the growth of the endocranium at about the highest stage reached in the arachnids. If the growth of the arachnid endocranium advanced still farther along the lines it has already established, it would follow very nearly the later embryonic development of the vertebrate cranium. For example, *a.* the upward growth of the lateral walls of the trabeculæ; *b.* the forward growth of the supraoccipital; *c.* the forward growth of the trabeculæ and the

union of their anterior ends; *d.* the closing up of the pituitary foramen; and *e.* the separation of a part of the hæmal arcade from the basilar plate to form the pterygo-quadrate arcade.

II. Branchial Skeleton.

1. *a.* In Limulus the first six pairs of appendages, *i.e.*, those belonging to the same metameres as the endocranium, never develop appendicular cartilages. In the seven following appendages, the bars are present; they are therefore post-cranial in origin, although the first pair (chilarial) is firmly attached to the posterior end of the basilar plate. *b.* The hæmal ends of the branchial bars, except the first pair, are united by a longitudinal band of cartilage. *c.* The gill bars and the longitudinal band are composed of capsuliginous mucoid cartilage, quite different chemically and histologically from the cartilage of the endocranium; and *d.* The three pairs of hæmal processes in Limulus have a superficial resemblance to the gill bars in position and direction, but they are of a different nature in structure and origin, and belong primarily to the endocranium.

2. Similar conditions prevail in vertebrates: *a.* The true branchial bars are independent, post-cranial structures, the anterior pairs being joined secondarily with the cranium. *b.* The segmentally arranged gill bars may be united by continuous longitudinal bands. *c.* The gill bars and bands are composed of muco-cartilage differing chemically and histologically from the fibro-cartilage of the endocranium. *d.* The four or five preauditory metameres (excluding the forebrain region) never give rise either to typical or fully developed gills, or to gill bars. *e.* The proximal portion of the palato-pterygo-quadrate-hyomandibular arcade does not represent modified gill arches. It belonged originally to the primordial cranium and represents in part the hæmal plate arcade of the arachnid endocranium. (Fig. 220.)

III. Neural Arches.

The neural arches of Limulus represent the initial stages in the formation of a vertebral column. Their contour is due to the direction and intensity of the muscular strain acting on them, and they agree in general form and in the direction of their processes, with the neural arches of vertebrates.

CHAPTER XVIII.

THE MIDDLE CORD THE LEMMATOCHORD AND THE NOTOCHORD.

The failure to recognize the notochord in invertebrates has been due to the prolonged domination of the annelid and gastrula theories.

It has been generally assumed that the notochord is found only in the vertebrates because no one could find one in the invertebrate midgut where the gastrula theory proclaims it ought to be located if present. So long as it was confidently assumed that the "archenteron" of vertebrates was the ontogenetic repetition of an ancestral midgut, and that its associated parts, mesoderm and notochord, were necessarily entodermic in origin, no one ventured to look for the notochord elsewhere than in the midgut of an annelid, or in some other worm-like invertebrate. It is not surprising then that almost any unpaired enteric outgrowth has been called, at one time or another, a notochord, thus giving a pseudo-respectability to such morphological curiosities as diplochorda, adelochorda, hemichordata, etc. On the other hand, any organ not entodermic in origin was thereby branded as illegitimate and excluded from further consideration.

One misinterpretation led to another, till the original theory became so deeply buried that embryologists appeared to forget that the whole superstructure rested on the extremely doubtful assumption that certain stages of vertebrate embryos were to be interpreted in terms of adult jelly-fishes.

The fact that there was little or no evidence that the archenteron really represents a primitive gut, or that the notochord ever had any other function than it has at present, was persistently ignored.

As I stated in my earliest paper on this subject, 1889, p. 351: "There is nothing in the embryology of the vertebrates to show to what germ layer the notochord belongs. It is never continuous with functional endoderm; there is no evidence that it ever exercised, itself, any alimentary functions; or that it is ever connected in any way with an alimentary canal." The only thing vertebrate embryology tells us about the notochord is that it has its origin, like the axial mesoderm, the nerve cord, and the entoderm, in the common mass of growing cells at the tail end of the embryo. As to the original function of the notochord, or its relation to germ layers, vertebrate morphology has, as yet, had nothing conclusive to say.

We must, therefore, first identify the representative of the notochord in the invertebrates before we can safely interpret its morphology in vertebrates. This we can do readily enough as soon as we eliminate the misconceptions of the gastrula and annelid theories, for the main facts in the development of the vertebrate and invertebrate notochord are sufficiently clear. The beginning of the notochord may be recognized in practically all segmented invertebrates, as the so-called middle cord, or median nerve, and in its derivative, the lemmatochord. This structure forms a fundamental part of the body in all segmented invertebrates. It undergoes many modifications, but its location, function, mode of growth, and its development, are in all cases essentially the same, and leave no reasonable doubt that it is indeed the long looked for notochord of the invertebrates.

I. The Middle Cord of Insects.

Acilius (Figs. 221, 222).—The middle cord arises at a very early embryonic stage as a median longitudinal groove that extends from the posterior margin of the stomodæum to the posterior end of the body. It should not be confused with the so-called primitive groove of arthropods, or with the neural groove of vertebrates.

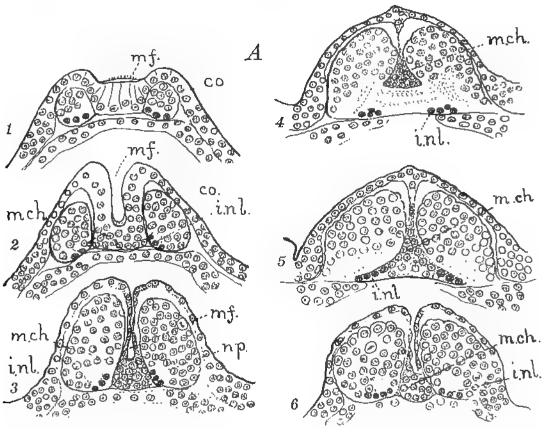

FIG. 221.—The second pedal neuromere of an embryo of Acilius; serial sections showing the development of the middle cord, and its relation to the cross commissures, inner neurilemma, or neuroglia, and median nerve.

The walls of the groove, in the interganglionic portions, give rise either to thickenings to which muscles are attached (thoracic region) or to the median nerve (abdominal region). The walls of the intra-ganglionic groove give rise to nerve cells that form a part of the ganglia, and to the neuroglia.

The early conditions are shown in a series of sections of the nerve cord of Acilius opposite the second pair of legs, during the formation of the dorsal organ. (Fig. 221.)

The groove deepens in front of the second pedal neuromere and its nuclei become darker colored, A^3. In the middle of the neuromere, the outer walls of the groove have almost disappeared, while the floor forms a solid triangular block of cells overlying the cross commissures, A^4. A few nuclei, like those in the middle cord, lie underneath the lateral ends of the cross commissures, *inl.* On the posterior margin of the neuromere, A^5, the middle cord is still a solid triangular block of cells, with its deep lateral angles spreading outward underneath the longitudinal connectives. Still farther back, A^6, the middle cord is again a deep groove, open at the surface, and with thin lateral walls. The sections show that the floor of the intra-ganglionic middle cord is raised over the cross commissures, and that the cells at the deep angles of the middle cord are spreading forward and backward around the cross commissures and longitudinal connectives. These cells form the so-called inner neurilemma, or neuroglia. There is nothing to indicate that the cross commissures arise from the intraganglionic cells of the middle cord, as is claimed by many authors. They appear to be outgrowths from the ganglion cells of the lateral nerve cords.

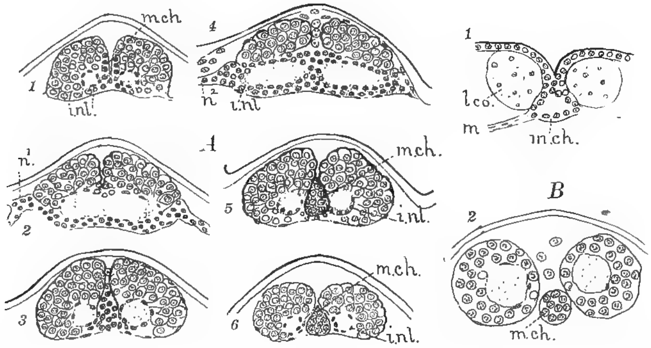

FIG. 222. —Nerve cord of an embryo of Acilius. A, $^{1-6}$, serial sections of an abdominal neuromere showing a later stage in the development of the neuroglia and middle cord (median nerve); B^1, inter-ganglionic infolding of middle cord of the thorax in a newly hatched larva of Acilius, showing modifications of middle cord for the attachment of muscles; B^2, section in same stage of an inter-ganglionic space of the abdomen, showing the middle cord as the ganglion of the median nerve.

In one of the next stages, a series of sections beginning at the anterior margin of the second pedal neuromere, shows that the middle cord has now lost its connection with the surface ectoderm. (Fig. 222.). In the center of the neuromere, A^4, its cells have multiplied and form a thick neuroglia investment around the cross and longitudinal connectives. At the posterior end of the neuromere, A^6, the middle cord assumes its characteristic cell structure, and gradually merges into the interganglionic cord.

In the later stages, at the time of hatching, the interganglionic segments of the thoracic middle cord are still in connection with the ectoderm, as they are through life, and wing-like bundles of muscles are attached to their sides, B^1. The interganglionic segments in the abdomen become completely separated from the ectoderm, forming a cylinder of nerve cells like those of the lateral cords, B^2 At each end the cord merges into the central tissues of the neuromeres. The chain of abdominal interganglionic segments of the middle cord may now be recognized as the median nerve of the adult.

Thus the thoracic furcæ for the attachment of muscles, the median nerve, and the neuroglia are but different stages, or modifications, of a single structure.

We may conclude from the wide distribution of the middle cord in the arthropods, and from the important part it plays in the early embryonic stages: 1. That the central nervous system of primitive arthropods consisted of three parallel, longitudinal bands that were divided into similar segments; 2. that the neuromeres of the middle cord fused with those of the lateral cords, and that the longitudinal connectives remained separate; and 3. that there has been a progressive degeneration, or modification, or specialization, of the intra- and interganglionic segments of the middle cord from the head end backward into non-nervous structures; while the lateral cords have increased in the specialization of nervous tissues from behind forward.

The Lemmatochord of Lepidoptera (Figs. 223, 224).—The lemmatochord of lepidoptera, or Leydig's cord, is a large, irregular, cylindrical rod of elastic, semi-gelatinous tissue extending along the hæmal side of the nerve cord from the thoracic neuromeres to the posterior end of the cord. It serves as a support to the nerve cord and for the attachment of lateral sheets of muscle fibers, the ends of which are imbedded in the substance of the cord. (Fig. 224, *B.*) It resembles the notochord of vertebrates in its position, its consistency and general histological structure; and in its function. Morphologically it represents the interganglionic segments of the abdominal middle cord, enveloped in the thickened neurilemma of the median nerve and that of the adjacent lateral cords. It makes its appearance during the metamorphosis of the larvæ into the imago.

* * * * * * * * *

The following observations refer to the development of the lemmatochord of Cecropia and Sphinx.

At the close of the larval period, the lateral and median cords are surrounded by two membranes, an inner, distinctly cellular layer, *i.sh.*, and an outer one, *o.sh.*, that forms a thick hyaline membrane. During the early pupal stages, large polygonal, or oval cells, with clear protoplasm and small nuclei, make their appearance between the inner membrane and the nerve cord. (Fig. 223, *A.*) In some places they are isolated and imbedded in a darker plasma. In others they are crowded together and appear to have thick, but not sharply defined walls.

At this time the outer hyaline membrane, *o.sh.*, also increases greatly in thickness and becomes distinctly laminated. Here and there small flattened nuclei are seen, and in some places clusters of thick-walled chorda cells, *B.* These changes take place in the membranes surrounding the ganglia, the longitudinal connectives, and the median nerve.

During the subsequent period, the distinction between the two investing membranes disappears, owing to the conversion of the flattened cells of the laminated membrane into the characteristic, thick-walled chorda cells, and to its invasion by chorda cells formed from the inner membrane. The chorda cells develop most rapidly along the hæmal surface of the lateral cords, and around the median nerve; they thus form three large irregular bands of chorda cells, roughly triangular in cross-section. The two lateral bands finally crowd the median one inward, and unite with it to form a single cylindrical cord, in which the arrangement of the chorda cells may still indicate the separate origin of peripheral and axial cells. (Fig. 224, *A*. *s.mn.* and *s.l.c.*) Meantime the median nerve has disappeared, or at least no traces of it can be seen, except where it rises to the surface of the chorda to enter the ganglion, *m.n.*

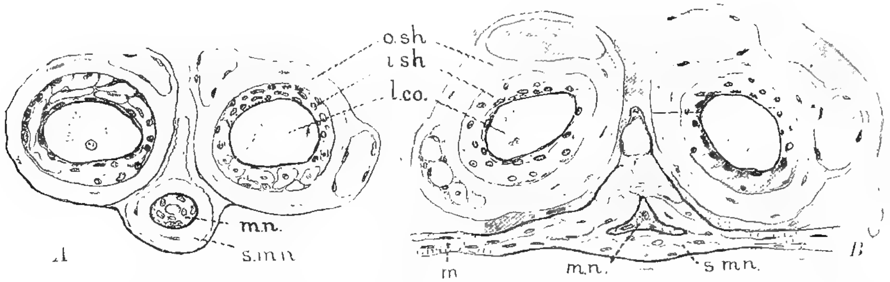

FIG. 223.—Sections through the abdominal nerve cord of Cecropia, early pupal stage, showing the greatly thickened sheaths of the median and lateral nerve cords. *A*, Midway between two neuromeres; *B*, near the posterior side of a neuromere.

At the close of the metamorphosis, the cord has become irregularly oval, the walls of the chorda cells have disappeared, and their nuclei have become irregular in shape and size. (Fig. 224, *B*.) As the chorda assumes its final form, a thick hyaline sheath forms around it, except along its hæmal side where the muscle cells are attached.

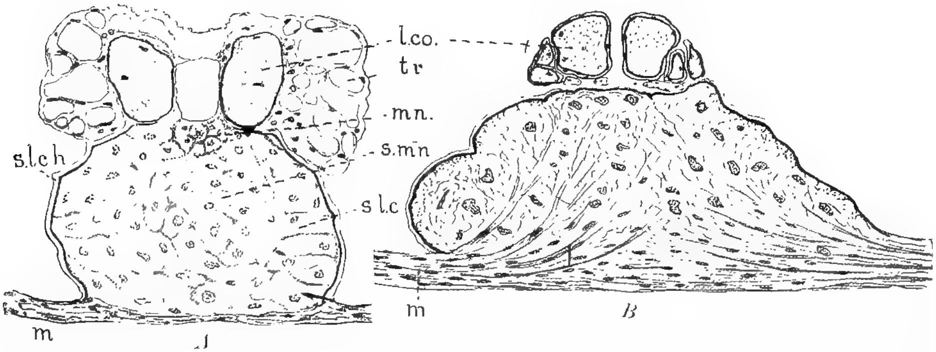

FIG. 224.—Nerve cords and lemmatochord of Cecropia. *A*, Late pupal stage showing the fully formed lemmatochord, derived from the condensed sheaths of the median and lateral cords; also remnants of the median nerve; *B*, adult Cecropia. The tissue of the lemmatochord has undergone degenerative changes, and at this point is invaded by the ends of the attached muscle cells.

At the beginning of the pupal period the thickened neurilemma on the neural side of the lateral cords becomes inflated with a network of trachea, *tr.*, which later disappears, leaving the cords again surrounded by a thin double layered membrane.

The chorda muscles appear at the close of the larval period, just in front of each neuromere, and close to the lateral branches of the median nerve, as a thin, dark, nucleated band, extending across the hæmal surface of the median nerve.

In the young pupæ the band expands very rapidly, forming in front of each neuromere a transverse muscular sheet, broad over the median line and tapering to a point at either side. They ultimately form a continuous sheet beneath the cord. In the adult, the ends of many of the muscle fibers spread out in fanshaped masses of fibers that penetrate the substance of the cord in all directions. (Fig. 224, *B*, *m*.)

II. THE MIDDLE CORD OF THE SCORPION. (Figs. 15, 16, 43, 71, 225 to 230.)

The middle cord and associated parts are in some respects imperfectly developed in the scorpion, so that it is difficult to follow their local modifications; but the conditions appear to be essentially the same as those we have described in embryos of Acilius, and in the larvæ of Cecropia.

In the scorpion, the median nerve itself is hardly recognizable; its neurilemma forms in part the walls of a blood sinus. The neurilemmas of the median and lateral cords form the bothroidal cord of the abdomen and the merochord of the posterior thoracic neuromeres. Chiten-lined neural apodemes are absent.

A. **Neural Sinus, Merochord and Bothroidal Cord of the Adult.** In the adult scorpion a large blood vessel extends along the hæmal side of the nerve cord, exclusive of the brain. In the abdomen and tail it opens into vertical channels which, behind each neuromere, pass between the connectives to the skin on the neural surface of the body. There are also in each segment two lateral branches which follow pretty closely the course of the spinal nerves. Between the successive neuromeres the vessel is much enlarged, and is either round or triangular in section. (Fig. 225^3.) Beneath each neuromere it is much flattened and in some cases hardly visible. (Fig. 225^2.) The walls of the sinus consist of an inner epithelial layer of clear cells, sharply contrasted with the dark coagulum in the sinus.

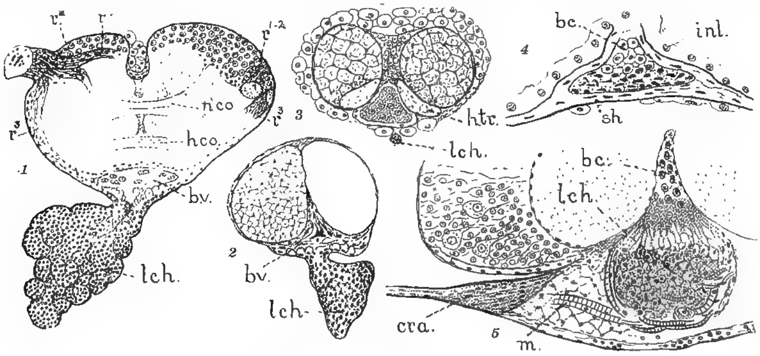

FIG. 225.—Cross-sections of the nerve cord of an adult scorpion. No. 1, Section through the posterior portion of the first free abdominal neuromere; No. 2, section between the vagus and abdominal neuromeres, showing the very thick walls and small lumen to the neural sinus; No. 3, section just in front of the second free abdominal neuromere, showing the conspicuous hæmal tracts; No. 4, section through the anterior half of the last caudal neuromere, showing the solid cord of cells derived from the middle cord and continuous with the neural artery; No. 5, section just in front of the anterior vagus neuromeres showing the merochord.

The outer layer is denser, contains a few small dark nuclei and scattering bundles of longitudinal and circular fibers; it appears to be continuous with the inner fibrous layer of the neurilemma. The sinus and the whole spinal cord is surrounded by a layer of large granular cells which vary greatly in number and arrangement in different parts of the body.

The Bothroidal Cord or Lemmatochord.—Along the hæmal surface of the neural sinus is an elongated, lobular organ extending the whole length of the abdomen. At irregular intervals it forms large, spindle-shaped bothroidal masses that are united with each other by a very delicate hyaline fiber. (Figs. 71, 72). The masses vary in number and size; in three different specimens I have counted 4, 7, and 9 of them. In sections they have a lymphoid appearance, and are seen to consist of dense, indistinctly fibrous masses crowded with minute, deeply stained nuclei. (Fig. 225, *l.ch.)* They are united here and there with the neural sinus by short stalks. In one specimen there were ten attachments of the cord to the sinus, six of which were hollow and opened into the neural sinus.

In the embryos the tissue from which the bothroidal cord arises extends forward into the thorax, where it forms segmental thickenings between the successive neuromeres. All these thoracic thickenings disappear, with the exception of the one beneath the connectives of the fifth and sixth thoracic neuromeres. This one becomes the merochord. It lies on the neural surface of the endocranium near the anterior edge of the cross bar. (Fig. 71.) The adult merochord (Fig. 225^5) is a large rounded body containing a few clear cells, many small dark nuclei, and irregularly coiled muscle strands.

The overlying interganglionic space is closed and is filled with a dark coagulum connected with the merochord by an irregular reticulum.

B. **Development of the Lemmatochord.**—The lemmatochord arises, in part, as an axial cord of cells extending forward from the primitive streak. In stage *A*, Fig. 15, the primitive streak is seen as a large median mass of polygonal cells near the posterior end of the embryo. In sections the cord appears to form as an inward proliferation of the surface cells, but without the surface infolding seen in Limulus. (Fig. 226^1.) From the point of proliferation, covering but one or two sections, the cord extends forward a short distance as a well defined cylinder. In stage *B*, it is greatly reduced in thickness and forms a broad lenticular band with the edges thinned out to a single layer of cells, not sharply marked off from either mesoderm or endoderm. It is largest just in front of the base of the tail lobe, and extends forward, becoming less and less distinct, as far as the third abdominal neuromere. It does not extend into the tail lobe.

In the following stages, up to stage *G*, the primitive streak forms lens-shaped thickenings beneath the 3, 4, 5, 6, and 7 interganglionic spaces of the abdomen. It is easy enough to distinguish these thickenings at this stage, but difficult to determine their lateral boundaries. A fairly defined layer of flattened cells separates them from the yolk. (Fig. 228.)

In stage *K*, Fig. 229, the primitive streak has definitely split along its whole length into two layers, the under one being the anlage of the sexual organs, *g.c.*, the upper one, the lemmatochord, *l.ch.* In a series of cross-sections of this stage, beginning at the posterior end of the abdomen, the lemmatochord is first seen just back of the sixth abdominal ganglion, as a dark lenticular thickening. (Fig. 230^1.) The cord has the same flattened appearance in all the sections until we reach the vagus neuromeres, when it suddenly enlarges and assumes more of its future appearance. (Fig. $229,^{4-7}$.) The anterior end of the lemmatochord is seen between the second and third vagus neuromeres. (Fig. 229^2.)

From this stage up to the time of hatching, the genital cells gradually separate from the lemmatochord, and the latter separates from the neural sinus, except at certain places where it remains permanently attached to the neurilemma of the middle cord. By the time the body pigment is well developed, the lemmatochord of the first free abdominal ganglion appears as in Fig. 230^4. In this figure we can see indications of the passageway into the sinus. The lemmatochord, just behind the third vagus neuromere, is reduced to a slender fiber. (Fig. 230^6.) At the posterior end of the abdomen it decreases in size and disappears, apparently running directly into the thickened wall of the neural sinus. (Fig. 230^5.)

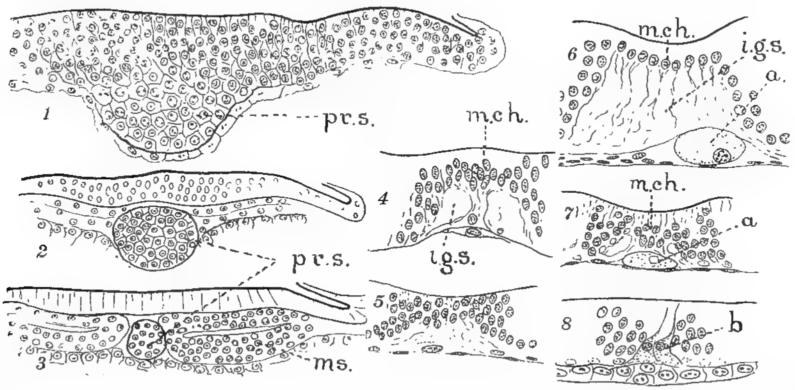

FIG. 226.—Embryo scorpion (Buthus carolinianus). No. 1, 2, 3, Sections through the posterior end of the embryo, stage *A*; No. 4, 5, 6, 7, sections through the interganglionic spaces of the nerve cord, stage *B.C*; No. 8, section through the middle of a terminal neuromere, stage *C*.

In embryos just hatched we may obtain good surface views of the lemmatochord by dissecting out the entire nervous system. (Fig. 71.)

In half grown scorpions the lemmatochord is in about the same condition as in the adult.

Merochord.—The lemmatochord tissue extends into the thoracic region, giving rise to the merochord and to two adjacent, parallel cords of dense connective tissue. (Fig. 71.) The first traces of these structures are a few isolated cells, lying beneath the interganglionic spaces of the thoracic and the first two or three abdominal segments. They form lenticular thickenings, which vary in size and appearance in the different segments, the ones between the fifth and sixth neuromeres being the largest. In stage *K*, one of these thickenings forms a disc-like mass of dense tissue, with deeply stained nuclei, lying on the ventral surface of the sternum beneath the sixth interganglionic space of the thorax. (Fig. 229, *m.l.ch.*) This body is the merochord. It appears to be merely an isolated local enlargement of the thoracic portion of the lemmatochord.

C. **Development of the Neural Sinus, Neuroglia and Canalis Centralis.**—The middle cord groove in the scorpion develops in essentially the same way as in Acilius.

From the walls of the intraganglionic portions are formed *a.* ganglion cells; *b.* the epithelium of a central canal; *c.* neuroglia cells. From the interganglionic portions arise *a.* transient nerve fibers of the median nerve connectives; *b.* walls of the neural sinus; *c.* blood corpuscles.

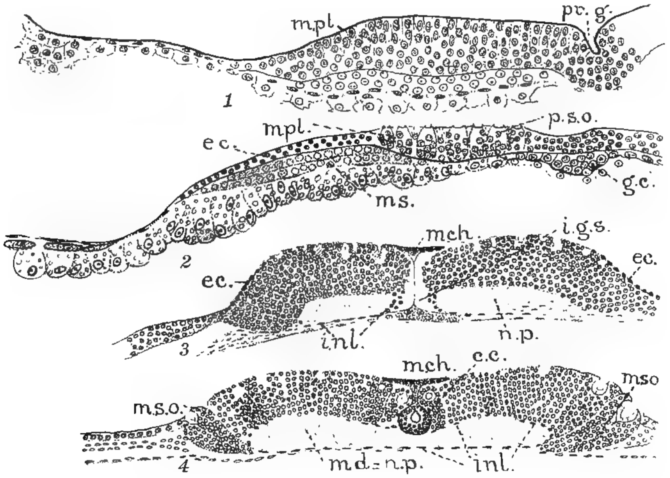

FIG. 227.—Scorpion embryo. No. 1, Section of an abdominal segment in front of the primitive streak, stage *A*; No. 2, abdominal neuromere, showing the breaking up of the medullary plate into primitive sense organs, stage *C*; No. 3, abdominal region, between two neuromeres, stage *E*; No, 4, abdominal region through the middle of a neuromere, stage *E*.

In the adult scorpion, the walls of the neural sinus consist of an endothelial layer of clear cells, often in sharp contrast with the enclosed coagulum. They pass without perceptible break into confused masses of tissue, and these into blood corpuscles, which seems to indicate that the latter are formed from the walls of the sinus during adult life.

It is difficult to define exactly where the sinus terminates anteriorly. In the thoracic region of the adult, the interganglionic spaces may be quite large and filled with the gelatinous substance and free cells, but the spaces do not seem to communicate with each other freely or to be directly connected with the abdominal sinus.

* * * * * * * * *

In surface views of young embryos, the lateral cords are seen to be separated by a continuous shallow groove. (Fig. 15, *A*.) As the cords break up into neuromeres, the median groove narrows and deepens and becomes distinctly divided into a succession of oval pits, one between each half neuromere. (Fig. 15, *B*.) The anterior pits become more distinct for a while; their walls are then incorporated into the body of the neuromere at the points where the transverse commissures are formed. The posterior pits are formed between the future longitudinal connectives; they gradually flatten out and become less distinct in surface views. Sections from this stage show that the ectoderm of the posterior pits thins out and draws away from the underlying basement membrane, forming clear areas, or interganglionic spaces. (Fig. 226^4, *i.g.s.*) They may contain a finely granular substance, a few fibers, and an occasional nucleus, the latter lying just above the basement membrane, or among the fibers extending downward from the roof. In stages *E* and *F*, the abdominal spaces contain a few free cells which are undoubtedly blood corpuscles. As the spaces at this period are completely closed, the blood corpuscles were evidently formed by a modification of the ectodermic cells of the middle cord.

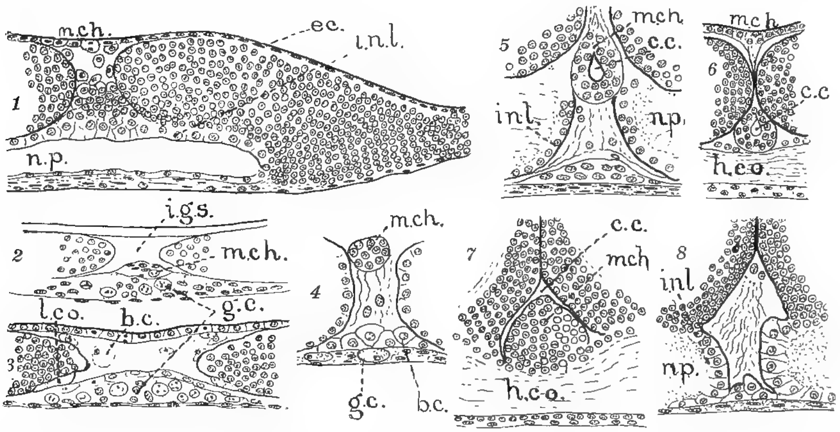

FIG. 228.—Scorpion embryo, stage *G*; cross-sections of the nerve cord, illustrating the development of the middle cord, neuroglia, neural blood-vessel, lemmatochord, etc. No. 1, Section through the posterior margin of the third vagus neuromere (comb segment); No. 2, section through the middle of the third abdominal interganglionic space, or the one next behind the comb neuromere; No. 3, section through the posterior margin of the same space; No. 4, section through the interganglionic space between two thoracic neuromeres, showing the continuity of the outer portion of the middle cord from one neuromere to the other, and also the deeper lying cells derived from the inner portion of the middle cord; No. 5, section between the fifth and sixth thoracic neuromeres; No. 6, section through the middle of the fourth thoracic neuromere; No. 7, section through the middle of the second thoracic neuromere, showing the middle cord as a prominent mass of cells on the bottom of the neural canal. The middle cord is not connected with the ectoderm at this point. No. 8, Section through the space between the second and third thoracic neuromeres.

In stage *F*, a few light colored cells appear on the periphery of the interspaces that mark the beginning of the neuroglia, or the inner neurilemma. (Fig. 227, *i.n.l.*)

In stage *F*, the spaces are small and shut off from the ectoderm by the union of the outer parts of the lateral nerve cords. (Fig. 227^3.) The intraganglionic cord is distinctly tubular. (Fig. 227^{4}.) Owing to the crowding of the thoracic neuromeres, these middle cord tubes almost unite above the interganglionic spaces thus forming a nearly continuous canal.

In the next stage, sections through the middle of each abdominal neuromere show that the invaginated portion of the median furrow is losing its central cavity, and now lies in the heart of the neuromere as a great cluster of cells difficult to distinguish from the surrounding nerve cells. At the anterior and posterior ends of the neuromere, the tissues of the middle cord are continuous with the neuroglia layer separating the medulla from the cortex. (Fig. 228^{1}, *i.n.l.*)

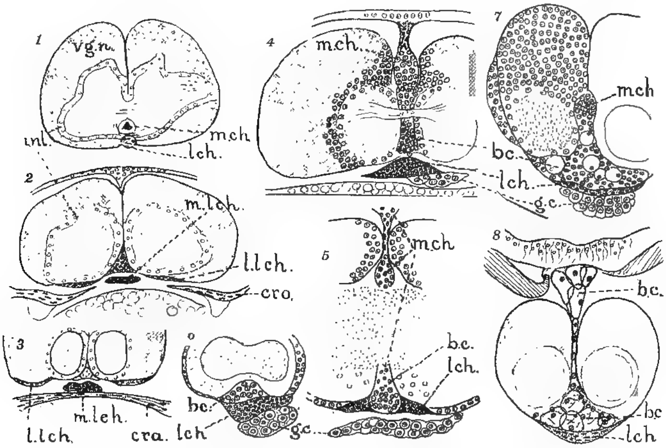

FIG. 229.—Scorpion embryos, stage *K*, showing the later stages in the development of the middle cord, neural canal, neural blood-vessel, genital cells and lemmatochord. No. 1, Section through the posterior vagus neuromere showing the transverse commissural fibers above and below the remnants of the middle cord (neural canal); No. 2 section through the anterior vagus neuromere, showing median and lateral divisions of the lemmatochord; No. 3, section just in front of the sixth thoracic neuromere, showing the local enlargement of the lemmatochord; No. 4, section between the second and third vagus neuromeres, showing the enlarged lemmatochord and the anterior end of the germ-cell cord; No. 5, section through the middle of the third free abdominal neuromere; No. 6, section about midway between the third and fourth vagus neuromeres; No. 7, section through the anterior margin of the fourth vagus neuromere; No. 8, section through the posterior portion of the third free abdominal neuromere.

The interganglionic spaces in the thorax contain, besides a few scattered nuclei, a loose fibrous cord that appears to run from one neuromere to another. It probably represents the remnants of a median nerve.

In stages *H* and *K*, remarkable changes have taken place. All the interganglionic spaces are crowded with rounded cells. They fill the interganglionic spaces and push their way forward and backward under the ganglia till they form a continuous cord. (Fig. 229^{7-8}.) They are everywhere shut off from the surrounding tissues by the inner neurilemma and by the basement membrane. At the anterior and posterior ends of each neuromere they are continuous with the intraganglionic portion of the middle cord. The latter is now reduced to a small but well defined cord of cells in the middle of each neuromere just above the medulla. (Fig. 229^{4-5}.) It is probable that the cells filling the interspaces arose from a rapid proliferation of the ends of the ganglionic portion of the middle cord, as well as from the division of the scattering cells seen in these spaces at an earlier period. The same kind of cells arise in those parts of the middle cord that remain united with the ectoderm, forming there masses of cells continuous with those in the underlying interspaces. (Fig. 229^8, *b.c.*) The wedges are best developed just back of each free abdominal ganglion; their central cells become free blood corpuscles, and the walls form the vertical vessels arising from the neural sinus.

Sections through the vagus neuromeres show that the cells filling the interganglionic spaces are united with those in the spaces in front and behind by two cell cords; one is the intraganglionic portion of the middle cord, and lies in the medulla between the neural and hæmal commissures; the other consists of cells that have pushed their way beneath the medulla. (Fig. 229^1, *m.ch*, *lc.h.*)

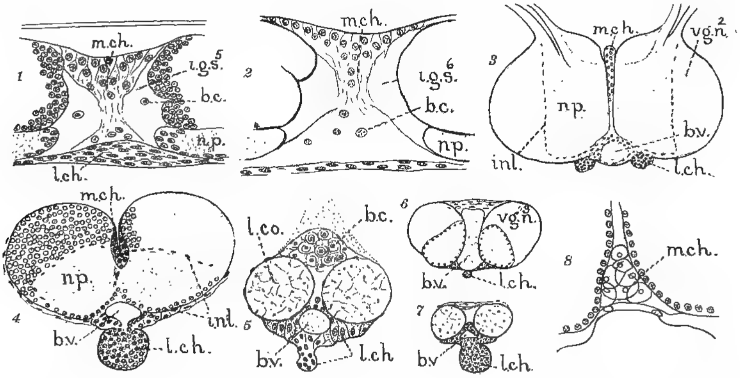

FIG. 230.—Scorpion embryo, about ready to hatch. No. 1, Section through the space between the fifth and sixth thoracic neuromeres; No. 2, section through space between sixth and seventh thoracic neuromeres; No. 3, section through posterior portion of the second vagus neuromere; No. 4, section through the first free abdominal neuromere; No. 5, section between the second and third free abdominal neuromeres; No. 6, section through the posterior margin of the third vagus neuromere; No. 7, section just back of the third free abdominal neuromere; No. 8, section between the second and third thoracic neuromeres, showing the remnants of the anterior end of the middle cord.

Soon after stage *H*, the cell cord that filled the interganglionic spaces, and that extended beneath the medulla of each ganglion, is replaced by a thin-walled tube, the neural sinus.

III. MIDDLE CORD OF LIMULUS.

It is difficult to follow the middle cord in Limulus. In the adult it lies inside the tough outer sheath of the nerve cord, and consists of irregular masses of matted tissues resembling that in the bothroidal cord of the scorpion. (Figs. 55, 67, 68.) It is arranged in two main lateral cords, one on either side of the neuromere, *l.l.ch.* In the vagus region, a conspicuous median mass is present. (Fig. 55, *m.lch.*) The lemmatochord tissue is continuous, by means of fine fibers, with the neuroglia that everywhere permeates the nerve cord and forms an envelop for the ganglion cells and the bundles of nerve fibers.

The condition in Limulus may be compared with the early larval stages in the development of the lemmatochord in Cecropia, where the lemmatochord tissue completely surrounds the cord.

IV. SUMMARY AND COMPARISON.

1. The middle cord of arthropods is of the same fundamental importance in the morphology of segmented animals as the lateral nerve cord.

2. In the arthropods we may recognize two parts in the middle cord, viz. the intra- and interganglionic segments. The intraganglionic segments are located in the central portion of the neuromeres, on the neural side of the hæmal cross commissures. They may give rise in each neuromere to both ganglion cells and neuroglia cells, and they may persist a longer or shorter period as solid cords, or as epithelial canals representing the walls of the original median groove.

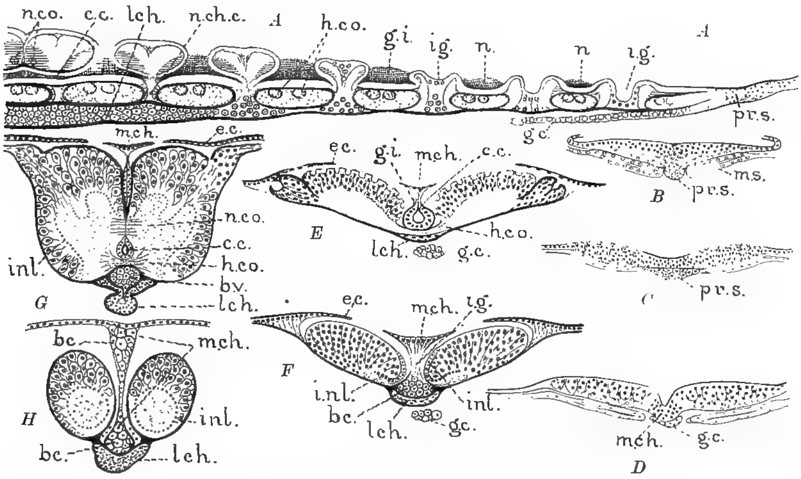

FIG. 231.—Diagrams to illustrate the mode of growth of the axial organs in the arachnids; such as the lateral nerve cords, their infolding, the overgrowth of the ectoderm, and the formation of the cross commissures; the local modifications of the middle chord to form the neuroglia, the lining of the central canal, blood cells, and lemmatochord; and the origin of nerve cords, ectoderm, and germ cells from the primitive streak. *A*, Sagittal section of the axial organs; *B*, *C*, and *D*, cross-sections in front of the apex of the caudal lobe, showing the separation of the nerve cords and germ cells from the tissue of the primitive streak; *E*, section farther forward, through the middle of a neuromere; *F*, between two neuromeres; *G*, still farther forward, through the middle of a neuromere; *H*. same, between two neuromeres.

The interganglionic segments of the middle cord gave rise primarily to the median nerve and its neurilemma. They undergo various local modifications. In the insects (Acilius), the oral segments disappear; those in the leg segments may produce the chiten-lined supports, or furcæ, which are permanently connected with the ectoderm, and which serve for the attachment of muscles; in the abdominal region, the same kind of infoldings are formed, but they separate from the ectoderm at an early period and are converted bodily into the median nerve. In lepidoptera, during the metamorphosis, the neurilemmas of the median and of the lateral nerve cords become enormously enlarged and form a semi-cylindrical, unsegmented cord, lying on the hæmal side of the nervous system, and enclosing the remnants of the median nerve.

3. In the scorpion, the interganglionic pits of the median groove, in the abdominal region, give rise to groups of cells, some of which become free blood corpuscles, others neuroglia cells, and others form the walls of separate sinuses, comparable with the neurilemma of a segment of a median nerve. The interganglionic spaces finally extend forward and backward on the hæmal side of the neuromeres, forming a continuous neural sinus.

4. The bothroidal cord, or lemmatochord, appears to develop from the primitive streak. Later it unites with the wall of the neural sinus. It probably represents the enlarged neurilemma of the lateral and median cords, and together with the neural sinus, corresponds approximately to the lemmatochord of lepidoptera. The merochord represents a local enlargement of the lemmatochord in the sixth thoracic segment.

5. With the crowding together of neuromeres, the interganglionic and intraganglionic segments of the middle cord tend to unite and to form two continuous cords, or canals, which stand on different levels, and which have different functions. One forms an internal cord, or canal, which lies in the central portion of the neuromeres between the neural and hæmal cross commissures; it gives rise to neuroglia cells, nerve cells, and the epithelium of the canal. The other forms an external cord, strengthened by a heavy investment of neurilemma, and serves for the attachment of muscles. Both cords may contain a longitudinal canal, and each canal may open into the other through segmentally arranged openings between the cross commissures of successive neuromeres. These conditions are represented diagrammatically in Fig. 231.

6. These two cords are represented in vertebrates by the epithelium of the canalis centralis, with its adjacent neuroglia tissue, and by the notochord. The embryonic origin of both cords, in vertebrates as in arthropods, may be traced to the growing apex of the embryo, and the method of growth of these organs appears to be essentially the same in both classes.

Whether the median groove is differentiated into its component parts gradually, so that all the intermediate stages are seen at the same time, arranged in superficial linear order from one end of the embryo to the other, as in the scorpion; or whether the differentiation takes place rapidly, at some deep-lying point in the primitive streak, as for example in Amphioxus, is merely an ontogenetic variation due to the amount of detail in the process of recapitulation and to the relative time at which the details appear.

In the vertebrates, the early stages in the differentiation of the middle cord are passed through rapidly, forcing the anterior end of the notochord below the surface as fast as it is formed at the primitive streak. Its primitive relation to the tissues lining the floor of the neural canal is indicated by the temporary communications that obtain between the cavity of the notochord and that of the canalis centralis at the posterior end of vertebrate embryos.

CHAPTER XIX.

THE OSTRACODERMS AND THE MARINE ARACHNIDS.

In the preceding chapters, we have shown that there is essential agreement in the structure and mode of growth of the corresponding systems of organs in the vertebrates and arthropods. This agreement is so intricate and all-pervading that it is intelligible only on the assumption that the arthropods represent the ancient stock from which the vertebrates arose.

But in spite of this underlying agreement in structure, there is a wide difference in outward appearance between any living arthropod and any living vertebrate. To demonstrate a direct genetic relationship between them, we must fill this apparent gap with real animals that are intermediate in character, or account in some other way for the abrupt transition.

In either case, we must determine what are the highest arthropods and what are the lowest vertebrates, and when and how the transition from one to the other took place. Unfortunately there is no *a priori* way of deciding, in a phylogenetic sense, what is "high" and what is "low," until we have found out what are the main lines of progressive evolution, and the directions in which they lead. In an inquiry of this nature there is only one method that can be used, namely the picture-puzzle method, whereby we aim through repeated trials to fit all the facts into a complete and intelligible picture, knowing full well that there is but one way for them to fit, and that when they do, we shall have an accurate picture of the truth.

If on consulting the geological record we find in the remote past some period toward which the genetic lines in question converge, blending there with a group of animals having some characteristics of each, then there will be a very strong presumption that we have correctly identified the upper and lower ends of the break in the series; that that class of animals was the connecting link between them; and that the actual transition took place at, or before, that period.

If on further examination it can be shown that the hypothetical connecting link resembles in several different ways the upper end of the lower series and the lower end of the upper one, and forms with them a continuous graded series, with a tendency on one side of the connecting link to produce special structures, or special methods of growth that are either anticipated or find fuller expression on the other, then our previous assumption of genetic relationship attains thereby the rank of actual demonstration, and it will not be shaken by any amount of negative evidence, or by the threatened collapse of cherished convictions that the picture was going to be something very different from what it actually turns out to be.

Such is the nature of the problem we have before us in the present chapter, and such is the method we have used in seeking an answer to it. Fortunately we are dealing with animals whose size, mode of life, and abundant skeletal structures are highly favorable to their preservation as fossils, and paleontology should, and in my judgment does, give us the materials with which this part of our problem may be solved.

We may state at once that the conclusion we have reached is as follows: The giant sea scorpions, or merostomata, as shown by their living representatives, Limulus and other arachnids, may be regarded in a phylogenetic sense as the highest arthropods, not because they now are the most highly organized, or the most specialized, or the most efficient, because they are not entitled to any of these distinctions, but because of all the invertebrates of their time they had made the greatest progress in the attainment of that particular plan of structure that was later to be so fully elaborated in the vertebrates. They were already in existence in very remote pre-cambrian, or proterozoic times, and had reached a high stage of development in the lower Silurian, when the ostracoderms were making their first appearance, and long before any true vertebrates were known to exist. The newly arrived ostracoderms had all the characteristics of an annectant class, for as all authors admit, they bore a superficial resemblance, at least, in form and mode of life to their arachnid contemporaries and associates, and at the same time they unquestionably resembled the true fishes that were soon to appear on the geological horizon. Paleontology, therefore, points very clearly toward the marine arachnids as the historic predecessors of the ostracoderms, and to the ostracoderms as the probable connecting link between them and the first true vertebrates, such as the early dipnoi and the crossopterygians.

I. The Marine Arachnids and their Origin.

The most primitive arthropods were undoubtedly marine animals of the short-bodied phyllopod type, consisting of a relatively large forehead, or procephalon, and a small body composed of a small number of ill defined metameres.

We have seen that the foundation of segmented animals is the primitive head, and that the primitive head represents the body of their remote cœlenterate ancestors. The cœlenterate, or radiate, stage is probably indicated, more or less clearly, in the embryonic or larval stages of all cœlenterate derivatives. In the annelids and molluscs, it is seen in the trochosphere larvæ. In the arthropods and vertebrates, the corresponding stages are heavily provisioned with yolk, and a free larval form for this stage does not exist; but remnants of it may be recognized in the procephalic lobes, with the included gastrula and stomodæum.

From the trochozoa, the hypothetical, phylogenetic antecedents of these larval stages, evolution proceeds along two, possibly three, main lines. In the molluscan phylum, the main theme consists in variations and specializations arising in the primitive head, and in the incipient, but still unsegmented trunk. In the annelids and arthropods the most important variations and the most significant new characters appear in the growing trunk, while the primitive head from which it arose, gradually dwindles into structural insignificance.

The subdivision of the trunk into a linear series of like parts or metameres was coincident with its elongation and increase in size, and there was probably little difference between annelids and arthropods during the earliest stages of this process. But in the former, the production of new metameres by apical growth frequently persists for an indefinite post-embryonic period, and special groups of metameres may separate from the parent stock by transverse fission, giving rise to a succession of new individuals.

In the primitive arthropods, the increase in the size of the body and in the number of metameres proceeded very slowly. In the primitive arachnids, crustaceans, and insects, the number of metameres produced was small, and precisely limited; in no case was there a persistent production of new metameres, either following normal, fission or otherwise.

The production of new metameres did not take place at a uniform rate, but in a spasmodic, or interrupted, manner. In the arthropods each new generation of metameres consisted of a relatively small number, frequently in threes or sixes, followed, after a recognizable pause, by a new generation, and so on. Thus the primitive arthropod trunk consists of a small number of metameres divided into groups, each group sharply distinguished by the size and the degree of specialization of its organs from the group in front or behind. The general appearance is that of an annelid undergoing transverse fission, and consisting of a chain of incompletely separated individuals.

Various manifestations of this condition are seen in the nauplius, metanauplius, and other larval stages; in the successive addition of metameres in larval trilobites, and in the persistent subdivisions of the body of many other arthropods into tagmata, or groups of like metameres, such as the oral, thoracic, vagal, abdominal and caudal. In these cases each subdivision is produced more or less clearly by a spasmodic generation of metameres, each group arising behind the one previously produced.

This phenomenon is not confined to the arthropods; it is still recognizable in the subdivision of the vertebrate head, and in the successive generations of nephric tubules and other organs in the post-cephalic region. One of the most important events in the evolution of the ostracoderms was the addition, probably during the Ordovician period, of a new generation of caudal metameres to the twenty odd that constituted the sum total of their inheritance from the arachnids.

The main difference between annelids and arthropods, besides the method of apical growth, lies in the extraordinary development of the chitenous mantle or exoskeleton of the latter, the presence of which no doubt exercised profound influence over the whole course of their evolution. Primitive arthropods, on the other hand, appear to resemble the molluscan type in their restricted apical growth and in the presence of the membranous folds arising from the aboral region of the head, and which give rise in a suggestively persistent manner, either to the shell gland, or mantle, or to embryonic membranes, or branchiocephalic folds.

The earlier stages in the evolution of arthropods can only be inferred, as indicated above, from the records of comparative anatomy and embryology. The original phylogenetic records are lost beyond recovery, for in the oldest rocks in which any formal organic remains are found, the eurypterid type appears to be already present. These fragmentary remains, Beltina danai, consisting of tracks, outlines of heads and appendages, were found by Walcott[1] nine thousand feet below the uncomformity between the Proterozoic (Algonkian) and the Cambrian.

During the long subsequent period, including the Cambrian and Ordovician, the familiar types of marine arthropods, such as the short-bodied bivalve ostracodes and the shield-covered phyllopods and phyllocarids, make their appearance in increasing numbers. Trilobites and merostomes are likewise found in great abundance and variety, the former reaching their climax in the Ordovician, the latter in the Silurian and early Devonian.

During this long period, organic evolution proceeded very slowly and there are no indications that any single event took place of exceptional importance morphologically. Nevertheless important progress was made in the arthropods in those complex processes of local suppression, union, and enlargement of multiple organs, that are such essential features of all progressive organizations, and which alone could make a more active, varied, and efficient mode of life in segmental animals a possibility. This kind of reorganization tends to convert the linear succession of like metameres, each complete in itself and independent of the others, into a linear succession of unlike organs, each subordinate to all the others and all together forming a new organism of a much higher order. See Chapters I and II.

While the most important event of the Proterozoic period was no doubt the outgrowth from the radially symmetrical cœlenterate of a new bilaterally symmetrical trunk, and the perfecting in it of a high degree of metamerism, in the Cambrian and Ordovician the important events were the breaking down of this metamerism, especially in the older and more anterior metameres, and the successive merging of its various parts into a more efficient aggregate, the cephalo-thorax, that at a much later period was to become an important part of the complex vertebrate "head."

The trilobites, judging from strategraphical evidence and from their external form, remained what they had been almost from the outset, slow-moving, sea-bottom feeders, like Limulus to-day, making only occasional, apparently aimless excursions, as free swimmers, into the water above.

But most of the merostomes in the manner above indicated had acquired, at a very early period, a superior organization in the head region that enabled them to leave the bottom and swim at large with purpose and effect. So far as

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[1] *Bull. Geol. Soc. Am.*, Vol. X.

we know they were the first arthropods, or for that matter the very first animals of any kind, endowed with the form and mechanical structure, with the sensory and neuro-muscular system, adequate to perceive at a distance, to pursue, and to capture living prey with measurable vigor and skill, and they finally became the most rapacious and effective organisms of their time.

But the very events that were necessary preliminaries to their active life were in the end the cause of their decline. The reduction of the oral appendages, the fusion of thoracic metameres, the enlarged and condensed thoracic neuromeres, gradually led, in the manner fully explained under their appropriate headings, to the closing of the mouth, the inclusion of the lateral eyes in the neural tube, and to other important changes that constitute the most complete metamorphosis in the history of organic evolution.

The ostracoderms, and their allies, were the products of this metamorphosis, and formed the most characteristic animals of the upper Silurian. Not till toward the beginning of the Devonian had they become sufficiently readjusted to their new conditions to again form active and dominant organisms, or to give rise to the true vertebrates.

All the available evidence points to the conclusion that the merostomes gave rise to the ostracoderms in the Ordovician or early Silurian period. The constant association of merostomes and ostracoderms in the Silurian shows that they lived together and were preserved under similar conditions; moreover the similarity in structure and in general appearance between these two types; the sudden appearance of the ostracoderms in the Silurian and their absence in the preceding periods under conditions that are known to be favorable to their preservation, as shown by the well preserved remains of their thinner skinned associates of the Silurian; the culmination of the merostomes at about this period, and their subsequent decline and extinction; and finally the absence of any positive evidence to the contrary, admits of no other conclusion.

II. The Ostracoderms.

The ostracoderms are so unlike any known vertebrates or arthropods that very different opinions have been expressed, and are still held, as to their structure and relations. It is a remarkable fact that in spite of their great antiquity and simple structure, the liveliest discussions concerning them were on the question: Are they vertebrates or arthropods? When the uncompromising verdict of Huxley, and later of Lankester, was delivered in favor of the vertebrates, indeed definitely locating them in a highly specialized group of comparatively modern teleosts, that verdict was generally accepted as final, and the morphological significance that clearly belongs to them was nullified or ignored.

Apparently no one seriously considered the possibility that the ostracoderms might be very primitive vertebrates that would shed a greatly needed light on the character of their remote ancestors, or that they might be annectant forms, standing midway between the arthropods on one side, and the true vertebrates on the other.

No doubt this was due, in part, to the remarkable development of their dermal skeleton, because, for a long time, it had been very generally assumed that an animal with a continuous dermal armor could not be a primitive vertebrate, for in the elasmobranchs, which were supposed to be the most primitive, the body was covered with minute, isolated, dermal ossicles. It was also implicitly believed at that time, as it is to-day, with a conviction born of constant repetition, that the immediate ancestors of the vertebrates were animals like either Amphioxus, Balanoglossus, the tunicates, or the annelids, which had no dermal skeleton whatever.

The author (Patten, 1889) was the first one to claim for the ostracoderms an important place in the phylogeny of the vertebrates, basing this claim in part on the very characters which were regarded by others as evidence of their high degree of specialization.

At that time our knowledge of the ostracoderms was very imperfect and the anatomical foundation for any inference in regard to them was exceedingly insecure. Since then, our knowledge has greatly increased and we now possess in Bothriolepis, one of the higher representatives of the group, an unprecedented wealth of material, which in spite of its great age is in an ideal state of preservation. Indeed, I know of no other extinct animal that has been so abundantly and perfectly preserved in its original form, attitudes, and surroundings.

This new material for the first time enables us to identify with certainty the neural and hæmal surface of an ostracoderm; it furnishes us the first precise information concerning the nature and location of the sense organs, the jaws, mouth, gills, and other viscera, and as to their mode of life; and for the first time it affords a secure basis of fact for the interpretation of other representatives of the group that are not so well preserved. In the light of this evidence, we may now confidently affirm that the ostracoderms belong neither to the arthropods nor to the vertebrates, but constitute a new class standing midway between them, the ancestors of the one and the descendants of the other, the long sought missing link between the vertebrates and the invertebrates.

From the geological record we may conclude that the true vertebrates arose from the ostracoderms not later than the Silurian; the ostracoderms from the marine arachnids not later than the Ordovician; while the marine arachnids had their origin in the immense, unfathomable periods during, or preceding, the Proterozoic.

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Historical Review.

Before proceeding to a fuller description of the ostracoderms, we may to advantage review the earlier literature on their structure and systematic position, for it brings out the most striking features of such important genera as Pterichthys, Pteraspis, and Cephalaspis.

Hugh Miller, the discoverer of Pterichthys, says (*Old Red Sandstone*, p. 50), in comparing a trilobite with Cephalaspis, "The fish and the crustacean are wonderfully alike." "They exhibit the points at which the plated fish is linked to the shelled crustacean." Agassiz was at first in doubt as to whether Pterichthys was a fish or a crustacean.

Sir Roderick Murchison, when first shown specimens of Pterichthys wrote regarding them that, "If not fishes, they more clearly approach to crustaceans than to any other class." Again, "They (Cephalaspis and Pterichthys) form the connecting links between crustaceans and fishes."

In *Siluria* (London, 1854, p. 252), speaking of *Cephalaspis agassizii*, he says: "This fish with its large buckler-shaped head and its thin body, jointed somewhat like a lobster, is perhaps the most remarkable example of a fish of apparently so intermediate a character that the detached portions of its head when first found were supposed to belong to crustacea." In a footnote Murchison adds: "Mr. Miller has requested his readers to compare the head of *Asaphus* (now *Phacops*) *caudatus*, a well-known silurian trilobite, with that of *C. lyellii*, to illustrate how the two orders of crustaceans and fishes seem here to meet—in the view of persons who have not mastered the subject."

Eichwald says (1854, page 105): "It is very remarkable that this colossal crab (Pterygotus) formerly regarded by L. Agassiz as a fish, occurs in the dolomitic chalk of Rootziküll in Oesel, together with another genus, Thyestes, standing between crabs and fishes and resembling Bunodes and Cephalaspis."

The genus Pteraspis was first proposed by Rudolph Kner, in 1847, to include the forms described in 1835 by Agassiz as *Cephalaspis lewisii*, and *C. lloydii*. Their appearance was so unlike the ordinary fish remains that for a long time Kner did not suspect that they had been already described by Agassiz in his *Poissons Fossils*. From a study of their minute structure Kner believed them to be the internal shells of cephalopods allied to Sepia.

In 1856, F. Roemer described a form closely related to *C. lloydii* as Palæoteuthis, and referred it to the sepiidæ, but suggested that the forms described by Kner were crustaceans related to Dithyrocaris or Pterygotus.

In 1855, R. W. Banks in his paper on the Downton Sandstones, after commenting on the association in these beds of Lingula cornea, Pterygotus and Pteraspis (Cyathaspis), made the following observation, page 98, "On the under side of the sharp projections before referred to (on either side of the rounded snout) are protuberances which seem to be projecting horny eyes similar to those of crustaceans."

He remarks further on, that doubtful as it is whether the buckler-like fossil remains above referred to belong to fishes or to crustaceans, it is certain that they are closely allied to *Cephalaspis lloydii* and *C. lewisii*. In a final note, it is announced that Professor Huxley is now minutely examining their structure to determine their true relationship either to the crustaceans or to the fishes. When Huxley's paper appeared, although he gave a very good description of the minute structure of the shell of these animals, and concluded that they were not crustaceans, he entirely ignored the existence of the eye tubercles, although their presence afforded very weighty evidence against his conclusion.

Huxley (1858, page 277) in reply to Agassiz, who had remarked on the singular resemblance between the shell of *C. lloydii* and that of crustaceans, and to Roemer's and Kunth's opinion that Pteraspis was a crustacean, seems to have closed the discussion for the time with his oft-quoted statement that "No one can, I think, hesitate in placing Pteraspis among fishes. So far from its structure having 'no parallel among fishes,' it has absolutely no parallel in any other division of the animal kingdom. I have never seen any molluscan or crustacean structure with which it could be for a moment confounded."

Roemer accepts these statements apparently because they came from Huxley, although he does not make an unconditional surrender of his opinion, for he says "Allerdings manche Analogie der aüsseren Form mit Crustacean-Formen dar bieten wurde."

In 1864, Lankester divided the pteraspidæ into the three genera, Pteraspis, Cyathaspis and Scaphaspis. But in 1872, Kunth described a shield of Cyathaspis, below which he found one belonging to Lankester's genus Scaphaspis, and he rightly concluded that the two shields belonged to the same animal. He maintained that the lower shield bore the same relation to the upper one that the tail plate of a rolled up trilobite does to its head shield, and that between the two were a number of pieces comparable with the segmental trunk plates of a trilobite. Other plates were present which Kunth regarded as locomotor organs, or footjaws. From the above facts Kunth concluded that these remains were not those of a fish, but of an arthropod. In referring to Huxley's statement that there is no molluscan or crustacean structure with which such remains could be for a moment confounded, and to Kner's belief that Scaphaspis was the shell of Sepia officinalis, Kunth adds "so schienen mir diese Ansichten in verein mit unserem vorliegenden Stücks mir zu beweisen dass wir es mit einer Crustacean Abtheilung von ganz eigenthümlicher Schalstructur zu thun haben. Denn jedenfalls giebt es weder einen Fisch noch eine Sepien Schulpe, die eine ähnliche Structur wie die Schilder zeigte; wohl aber ist die Organization des ganzen Stückes beweisend fur Crustaceen Character" (page 6).

Both Schmidt (1873, page 330) and von Alth (page 47) agree with Kunth that Scaphaspis is the ventral shield of Pteraspis, but they deny that any of the remains described as Pteraspis, Cyathaspis or Scaphaspis are crustaceans, although no valid reasons are given for doing so.

Lankester (1868, page 26) admitted the presence in Cyathaspis of tubercles corresponding with similar tubercles in Pteraspis, which are "produced by the supposed orbits;" but how a vertebrate eye, or an "orbit," could be preserved as a beautifully rounded protuberance when all the other soft parts are completely destroyed, is not discussed.

Lankester attached much importance to the presence of scales on the anterior trunk region of Pteraspis, for these scale-like structures were regarded as conclusive proof that the pteraspidæ belong to the vertebrates. He says (1868, page 18) "All that is known as regards the scales of these fishes is from a single specimen found in the cornstones of Herefordshire." This specimen, he says elsewhere (1873, page 191) "Shows seven rows of rhomboidal scales attached (not merely adjacent to) to a portion of the head shield of Pteraspis. That these are true scales, or lozenges of sculptured calcareous matter is absolutely certain. It is also absolutely certain that the shield is pteraspidian and that the scales and shield belong to the same individual organism. The scales are fish-like. I know no arthropod, nor any other organism except a fish which possesses any structure even remotely representing them." "The shields of the chitonidæ and cerripedæ are the only animal structures, except the scales of a ganoid fish (with which they agree exactly) which they could even vaguely suggest." "The form of this shield, and its details as to apertures, processes, etc., agrees with the view that it belongs to a fish most fully. It has not the remotest suggestion of crustacean affinities about it."

After commenting on the fact that the fossil in question was marked with long parallel striæ, and that the middle layer contained the polygonal cavities, he adds (1864, page 195), "This structure, which has no parallel among fishes, or, indeed, any group of the animal kingdom, leaves no possibility of a doubt that the specimen is a fragment of Pteraspis." Lankester further maintains (1868, page 4) that by the discovery of these scales "the piscine nature of these fossils was definitely set at rest."

These positive statements are contradictory and are hardly warranted by the facts, for the crustacean character of the shields had been repeatedly commented on by competent observers, and in his own monograph (page 61) he has described a fragment, possibly connected with Cephalaspis which he names Kallostrakon podura (Tolypaspi ?) "on account of the resemblance to the well-known microscopic markings of the scales of the insect Podura."

But all recent students of the shell of Pteraspis are agreed that it is *not* "exactly" like that of a ganoid fish, in fact its microscopic structure is altogether of a different character, and it is not true that there are no arthropods with structures even remotely resembling the scales of Pteraspis, because in Pterygotus the entire body is covered with an ornamentation astonishingly like fish-scales in outward appearance, so much so as to deceive such a keen observer of fishes as Louis Agassiz. Moreover, in many trilobites, in the ceratiocarina, and in arachnids, (Phrynus), the surface of the shell is ornamented with ridges and grooves not unlike those of Pteraspis in external appearance.

Probably neither Huxley nor Lankester would have made the above statements had they kept Pterygotus in mind, or had they been acquainted with the structure of the shield of Limulus.

In 1889, the author compared the arrangement of plates and sense organs in the cephalic buckler of Cephalaspis and Pterichthys with those on the cephalothorax of certain trilobites, and contended that the ostracoderms were the connecting links between the arachnids and true vertebrates; and in 1894 he pointed out the extraordinary resemblance in the microscopic structure of the shield of Pteraspis and other ostracoderms and that of Limulus. These resemblances in the minute structure of the shields were either ignored by later writers, or regarded as mere coincidences, or as the results of mimicry or of "parallelism."

Lankester, Woodward, Traquair, Rohon and others, agree in denying the existence of arthropod characters to the pteraspids, apparently because of the abundant evidence now available that Pteraspis is related to Cephalaspis, whose ichthyic affinities have rarely been questioned, rather than because the arthropod features of Pteraspis have been dispassionately considered and found wanting.

But within recent years there seems to be a growing tendency to doubt the affinity between Pteraspis and Cephalaspis. Reis protests against their union, and apparently Traquair is in doubt, treating them together largely as a matter of convenience. Lankester in his earlier monograph states that "The heterostraci are associated at present with the osteostraci because they are found in the same beds, because they have, like Cephalaspis a large head shield, and because there is nothing else with which to associate them." More recently he has said (1897) "There is absolutely no reason for regarding Cephalaspis as allied to Pteraspis beyond that the two genera occur in the same rocks, and still less for concluding that either has any connection with Pterichthys." Zittel says, Vol. III, page 147, "Mir scheinen die Beziehungen der Pteraspiden und Cephalaspiden nach Form und Structur so entfernt dass beide besser als besondere Ordnungen betrachtet werden." He remarks further on that while the cephalaspidæ certainly appear to be ganoids, the position of the pteraspidæ is very doubtful.

Muscle Markings.—In 1872, A. Kunth described in *Cyathaspis integer* a series of six "flache Höcher," situated on the under surface of the neural shield, which he regarded as indications of segmentation. Lankester (1873), describes similar impressions on the shield of Cyathapis banksii and believes that in both cases they indicate the position of a series of branchial chambers. In Pteraspis also, Lankester has described five narrow ridges, with four broad shallow depressions between them, which radiate from the center of the inner surface of the neural shield. They are perhaps best marked in Pteraspis crouchii and P. rostratus. These markings I have explained as indications of the original segmentation of the mesocephalon, produced in part by the attachment of strong segmental muscles extending vertically from the inner surface of the neural shield, either to a cartilaginous cranium, or to a series of gill-like, or jaw-like, segmental appendages on the hæmal side. (Fig. 244, *M.*)

The following quotation illustrates the attitude of modern paleontologists toward the ostracoderms. A. S. Woodward, in his text-book of Paleontology (1898, page 5) states that "Nearly all the genera mimic in a curious manner the contemporaneous eurypterids;" and on page 24 of the Introduction, that "The oldest ostracoderms, sometimes claimed as the immediate allies of the crustacean or arachnid merostomata of the same period, are fundamentally different from the latter in every character which admits of detailed comparison; they are to be regarded merely as an interesting example of mimetic resemblance between organisms of two different grades adapted to live in the same way and under precisely similar conditions."

Surely no one knows the precise "way" or the precise conditions under which these forms lived, or any probable advantage to be gained by one mimicing the other. It would certainly be very remarkable if many members of one class should mimic those of another, when the two classes were as fundamentally unlike as the arthropods and vertebrates are supposed to be.

All the ostracoderms are said to "mimic" the eurypterids, because they have a similar shape, similar cephalic appendages, shell covered orbits and mouth parts, and a similar minute structure of the dermal armor. But such a resemblance is too intricate and far-reaching to be accounted for on the ground of mimicry, or functional parallelism, or mere coincidence; it can only be explained on the ground of genetic relationship.

Chamberlin and Salisbury have taken a less conservative position on this question. In their recent text-book of Geology, it is stated, Vol. II, page 482:

No more suggestive combination of ancient life is presented by the geological record than that which is found in these supposed fresh water deposits. The type was foreshadowed by the eurypterids and fishes, of fish-like forms, that appeared in the closing stages of the Silurian, but the record of that time is too imperfect to disclose its deeper significance. Even with the much superior material of the Devonian period, the more profound significance is only just beginning to be realized. The center of interest is a unique group of ostracoderms which were at first interpreted as placoderm fishes, and later classed with the jawless fishes (agnatha, lampreys, etc.), but which seem now to be clearly proven to be an entirely distinct class lying between the arthropods and vertebrates, and having some of the characteristics of each, but not truly belonging to either. Their supreme interest lies in the force they give to the suggestion that the vertebrates sprang from the arthropods.

CHAPTER XX.

THE OSTRACODERMS.

The ostracoderms, as we have seen, constitute a class of animals standing midway between the most primitive vertebrates and the merostome-like arachnids. They are now entirely extinct and only a few representatives have come down to us in the form of fossils that are well enough preserved to afford either full or precise information about them. The recognizable remains usually agree in the minute structure of their exoskeleton, but there is a great diversity in the form and general anatomy of the better known representatives of the class, showing that it must have been a very large one.

The ostracoderms were not a dominant class. Some of them were nearly or quite blind, their powers of locomotion were limited, and their mouth parts were feeble and ill adapted for attack or defense. In all that constitutes active resourceful animals they were less effective, and estimated for that alone, were less highly organized than their immediate predecessors. The reason for this is obvious enough if we accept the conclusions in the preceding chapters, and the fact that they do present this condition is, in itself, important evidence that those conclusions are correct. The ostracoderms, as our theory demands, were transitional forms; they were in a phase of structural readjustment that had a definite course to run before either a condition of organic stability could be attained or a high degree of functional adaptation to external conditions could be acquired. They were in, as it were, the pupal period in the phylogeny of the vertebrates. The period was one of suspended efficiency, because great internal changes were taking place and the functional relations of the whole organism to the outer world were necessarily reduced to a minimum. A new type of exoskeleton was forming; the lateral eyes, but newly transferred to the walls of a hollow brain, had not fully regained their relations to the outer world; paired enteric diverticula opened to the exterior by newly formed visceral clefts; the oral arches for the first time had been transferred to the hæmal surface of the head, a new mouth formed; and the old one closed; and the locomotor functions were about to be shifted from the cephalic appendages to the newly acquired flexible trunk, with its greatly increased number of segments. At no other period of organic evolution were so many important internal readjustments taking place at the same time, and no other great class of animals has so quickly run its gamut of changes and so completely disappeared in the process of giving birth to a new race.

This is as it should be, for it will be seen that the most important events were of the open or shut variety that permit no intermediate stages; when they do occur they at once create totally different conditions, to which the organism must respond by a correspondingly rapid readjustment elsewhere, or go out of existence.

The ostracoderms probably rose from the merostomes during the Ordovician, and reached their highest development in the upper Silurian, after which they rapidly declined, disappearing at the close of the Devonian.

The first recognizable ostracoderm to appear in America is Palæaspis, from the lower Silurian of Perry Co., Penn. (Fig. 244, *B* and *C*.)

Walcott has described fragments of bony plates from the lower Trenton horizon of the Ordovician, Colorado, the primitive character of which is shown by the pronounced lamination of the outer dentinal layers.[1] But evidence based on such fragments, however well preserved, is inconclusive since, as we have seen in Chapter XVI, there is no way to distinguish fragments of the exoskeleton of a primitive ostracoderm from those of the higher marine arachnids.

The ostracoderms, like their arachnid ancestors, are small, usually a few inches long. Two isolated species only attain a length of one and a half or possibly two feet. They inhabited shallow waters, and crawled clumsily, oral side down, over or through soft muddy bottoms, or swam heavily, oral side up, with spasmodic strokes of their oar-like cephalic appendages, aided by the more flexible posterior portions of the slender trunk and tail. They probably fed on minute organisms sifted out of the mud or water, or on the soft parts of plants, or on decomposing organic matter.

Most ostracoderms have large, rounded, or pointed heads, a small trunk, and a tail consisting of a narrow terminal ribbon, or filament, with a ventral lobe some distance in front of the end.

* * * * * * * * *

Subdivisions of the Body.—The body may be divided into a procephalon, mesocephalon, branchiocephalon, trunk and tail.

The *procephalon*, which may form a narrow projecting rostrum, contains on its neural surface the median and lateral eyes and the olfactory organs. It is intimately united with the *mesocephalon*, to which belong the oral arches, or jaws, and the oar-like cephalic appendages.

The *branchiocephalon* may be separated from the mesocephalon by a distinct hinge joint (antiarcha), or by a transverse furrow or scar (cephalaspidæ). It contains six to eight pairs of gills, usually enclosed in a large peribranchial, or atrial chamber, that is covered on all sides, except the posterior, by large dermal plates. The right and left sides of the chamber are continuous on the ventral side, but are separated along the mid dorsal line by the tough tissues that suspend the branchial portion of the head to the inner surface of the branchial shield. The cloaca may open into the posterior part of the peribranchial chamber, its materials being discharged with the water of respiration from the posterior opening. (Bothriolepis.) The viscera, stomach, intestines and reproductive organs lie anterior to the cloacal opening, in that part of the head and trunk enclosed within the atrial chamber. (Bothriolepis). In the cephalaspidæ there is

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[1] Walcott, *Bull. Geol. Soc.*, Vol III

no closed peribranchial chamber, the gills probably lying on the oral surface, beneath the posterior part of the mesocephalon. (Fig. 232.)

The *trunk* is short and slender, generally triangular in cross-section. It may be practically naked, or provided with minute, scattered tubercles only (Bothriolepis); or covered with rounded, overlapping scales (Pterichthys); or with large segmentally arranged oblong plates on the neural surface, and small irregular ones on the hæmal side (Cephalaspis); or with shagreen-like denticles (cœlolepidæ). There are one, or two, unpaired dorsal fins, stiffened by delicate internal rays (Bothriolepis), or by minute oblong dermal plates (Cephalaspis). Pectoral and pelvic fins are absent.

Lateral Fold.—A narrow fold extends along the ventro-lateral margins of the trunk. It may be entirely membranous (Bothriolepis); or supported by minute rays (Pterichthys and one species of Cephalaspis); or it may be formed by the projecting ends of segmental trunk plates (Tremataspis); or it may consist of a series of segmentally arranged, separately movable, appendage-like plates, or fringing processes (Cephalaspis).

The Cephalic Appendages.—Large, oar-like cephalic appendages form one of the most striking features of the ostracoderms. In Bothriolepis they are attached to the posterior hæmal margin of the mesocephalon, in front of the gills, and consist of two joints, or segments, covered with bony plates. They are hollow, triangular in cross-section, and contain indications of a cartilage axis. (Fig. 257.) An opening on the posterior proximal end of the arm, and an adjacent one on the side of the branchiocephalon, serve for the passage of nerves, blood-vessels, and other tissues.

In Cephalaspis the cephalic appendages are covered with minute, semi-isolated dermal plates, and their broad distal ends, of undetermined contour, are horizontally flattened. Parts of armored cephalic appendages similar to those of Bothriolepis have been found in Palæaspis, Cyathaspis, Tremataspis, and Psamosteus. In Pteraspis, Drepanaspis, and Berkenia, there are certain marginal notches, or openings, that have been considered as lateral eye orbits, but which may possibly represent the points of attachment of cephalic appendages. In these genera they were smaller, less heavily armored, if they were armored at all, and were not used as swimming oars.

The cephalic appendages of the ostracoderms are not comparable with the pectoral fins of vertebrates, but with one of the pairs of thoracic swimming legs of the merostomata. They are represented in vertebrates by the so-called "balancers," and the cephalic tentacles of amphibian larvæ, and by similar processes in certain fishes, *i.e.*, Protopterus, Accipenser and Bdellostoma.

Jaws.—The mouth lies in a membranous portion of the hæmal surface, caudad to the projecting rostrum, or to the anterior margin of the procephalon. In Bothriolepis, there are three pairs of bony plates, which represent, in part, the premaxillary, maxillary, and mandibular arches of vertebrates.

The maxillary arch is probably represented by the small movable plates (Figs.

254, 259, *mx.*) The broad premaxillæ, *p.mx.*, have heavy crushing margins on their median ends, and move laterally to and from the mouth, which lies in the median line between them. The mandibles (Fig. 254, *md.*), are narrow, curved, and pointed at their median ends, and form a thick bony covering to a hollow axial portion that probably consisted of cartilages. They move diagonally forward and inward, and backward and outward, pushing or scooping the food forward between the premaxillæ and toward the mouth, *m.* Behind the mandibles, *om.*, the circumoral membrane is stiffened by two thin bands of bone which probably represent the dermal armor of the hyoid arches.

In Tremataspis (Fig. 237), the oral region is occupied by flat polygonal plates, showing little resemblance to jaws. They are arranged in four transverse rows, which possibly represent the premaxillary, maxillary, mandibular, and two rows of hyoid plates seen in Bothriolepis.

In Cephalaspis there are indications of one pair of large crushing jaws. The jaws of other members of the ostracoderms probably resemble those of Bothriolepis or Tremataspis, but no traces of them have as yet been found.

The Skeleton.—The ostracoderms were no doubt provided with cranial cartilages, including an endocranium and a notochord, but they were not voluminous or resistant, for in Bothriolepis no certain traces of them can be seen, although the skin and other soft parts are clearly indicated. In sections of the branchiocephalon small black rings are sometimes seen, mingled with the blackened remnants of the gills and viscera, that may be fragments of the notochord sheath.

The chief interest lies in the bony exoskeleton, which presents a structure intermediate between the chitenous epidermal skeleton of arthropods and the dermal skeleton of vertebrates.

In a primitive ostracoderm, the general character of the external armor is similar to that of a trilobite, or a merostome, in that it may consist of an almost continuous shell, or buckler, for the broad cephalic and branchial regions, and segmentally arranged plates, corresponding with the pleural and tergal plates, on the flanks and dorsal surface of the trunk. The dorsal fin, all but the terminal part of the tail, and the ventral surface of the trunk, may be covered with minute oblong plates similar in structure and surface ornament to the larger ones. (Cephalaspis.)

In its simplest condition, the matrix of the dermal skeleton consisted of parallel, or concentric lamellæ, that apparently have been formed in the same manner as the characteristic lamellæ in chitenous exoskeletons. It is unlike chiten chemically, but resembles it in the varying degree of hardness, color, and other optical properties of the lamellæ, and in the presence of innumerable, parallel, unbranched canals (pore canals, or primitive dentinal tubules) which everywhere penetrate the matrix at right angles to the lamellæ.

The exoskeleton usually consists of three principal layers consisting of a bony or dentine-like substance: *a.* an inner one of horizontal lamellæ; *b.* a middle one of large polygonal spaces, or cancellæ, and *c.* an outer layer consisting mainly of dentine, with an underlying stratum of Haversian, or other, canals. The lamellæ are always parallel to, or concentric with, the walls of the cancellæ, or with those of the larger spaces they enclose. Openings through the inner layer serve for the passage of blood-vessels and other tissues into the cancellæ, and hence to the canals of the outer layer.

The outer surface is denser and harder than the rest, and may be without distinct dentinal tubules or lamellæ, thus forming a thin enamel, or ganoin layer. It is often divided into small polygonal areas, and is variously ornamented with tubercles or ridges.

The most primitive lacunæ are unipolar, or bipolar, and arise as dilatations of the inner ends of primitive pore canals (Pteraspis); or a linear series of lacunæ may be formed from local enlargements of a single canal (Tremataspis). The more highly developed, or typical bone lacunæ, arise from the unipolar lacunæ through the formation of secondary lateral canals, or canaliculi. The primitive lacunæ are located mainly, and primarily, in the deeper lamellæ; that is, in the axial portions of the trabeculæ, and in the partitions separating the cancellæ and larger canals. As the lacunæ develop in size and complexity, they lose their original arrangement and their relation to pore canals, taking up their position between the lamellæ, with their long axes parallel with one another and with the plane of the lamellæ, those in one layer often standing at right angles to those in the adjacent layers. The lacunæ of the same and of the adjacent layers are then united by many branching canaliculi. As the latter increase in numbers, they form an anastomosing network that takes the place of the primitive unbranched and parallel pore canals. The primitive condition of the pore canals is, however, largely retained in the outermost layers of the shell, forming the dentine layers characteristic of the surface ridges, spines, and tubercles.

* * * * * * * * *

The general trend of development in the exoskeleton of the ostracoderms is as follows:

1. The lacunæ become parallel with the lamellæ, instead of with the pore canals.

2. They increase in number, and their numerous canaliculi replace the primitive pore canals.

3. The cancelli break down, owing largely to the increasing number of vascular channels (Haversian canals) and their more uniform distribution throughout the various layers, this process gradually producing a condition similar to that in the typical dermal bones of vertebrates.

4. The armor breaks up into separate plates or "bones" of various sizes, which may or may not be movably articulated, and which may bear some definite relation to the underlying organs, such as the primitive subdivisions of the head, or the arrangement of segmental muscles, appendages, or jaws; or they

may possibly have some relation to the plates that are present in the cephalothorax and branchial regions in their trilobite- or merostome-like ancestors.

5. The armor may also break up into small polygonal platelets, of uniform size, that are quite separate from one another, the lines of fragmentation following the "ornamental" polygonal markings visible on the outer surface of the shield in Limulus, (Fig. 200, *A.C.D.*), in Cephalaspis, or in Ateleaspis. (Fig. 200, *B.*)

6. With this process of fragmentation there is a tendency to accentuate the difference between the inner layers of more highly developed bony tissue, and the outer layers that still retain their primitive stratification and parallel pore canals, and into which neither the bone cells nor the vascular canals have penetrated to any great extent. The isolated ridges, spines, or tubercles of the outer layer, initiate the dermal denticles of the vertebrates, and represent their enamel and dentinal caps; the lower layers initiate the basilar plates composed of true dermal bone. (Fig. 208.)

7. During the phylogenetic process of fragmentation the two layers may undergo unequal development. In such forms as the cœlolepidæ (Thelodus and Lanakia) apparently only the isolated epidermal denticles are retained, while the underlying network of bony plates and trabeculæ has largely, or wholly, disappeared. In Bothriolepis and related forms, the dentinal layer is scanty, or for the most part absent, while the large bony lamellæ of the inner and middle layers are highly developed. In the pteraspidian section all three layers are present, but the underlying ones have no true bone cells, only the spindle-like dilatations of the pore canals.

8. In the antiarcha, as in the vertebrates, the placoid bones were extensively, if not entirely, covered with a layer of epidermal cells. This is indicated not only by their general structure, but is conclusively demonstrated by the faint impressions on their outer surface left there by the nuclei.

9. The dentinal layer of the unfragmented buckler and of the isolated denticles, like the exoskeleton of arthropods and the enamel of vertebrate teeth, was probably the product solely of underlying epidermal cells. Their outer surface was probably never covered with epithelial cells, except by secondary overgrowths resulting from infoldings like those in the developing teeth of vertebrates.

10. A remarkable feature of the cephalaspidæ is the union of the margins of the upper and lower shields by anastomosing bony trabeculæ which, like those in Limulus, form the solid, or cancellous cornua, and the heavy hoop-like margin along the front and sides of the cephalic shield.

In Eukeraspis (Fig. 235, *D*) there are peculiar chambers (marginal cells of Lankester), in the bony tissue on the anterior margin of the shield. They may be merely enlarged cancellæ, or possibly, enclosures formed by a deeply serrated or scalloped margin like that in Thyestes, *A*, or like the enclosures formed by marginal infoldings in the trilobites, *B*.

11. In Cephalaspis (Fig. 232), there are conspicuous oval areas on the lateral margins, and behind the orbits, that are formed by thickened patches of bony

trabeculæ. They correspond roughly with the areas in Limulus where the bony trabeculæ are most highly developed. (Fig. 205.) In Tremataspis, Cephalaspis, and Thyestes, these areas are covered with loose, superficial, polygonal plates which may, and usually do, fall out, leaving sharply defined, shallow openings in the outer layers. (Figs. 235, *A*, 236, *B*.) They have a floor consisting of

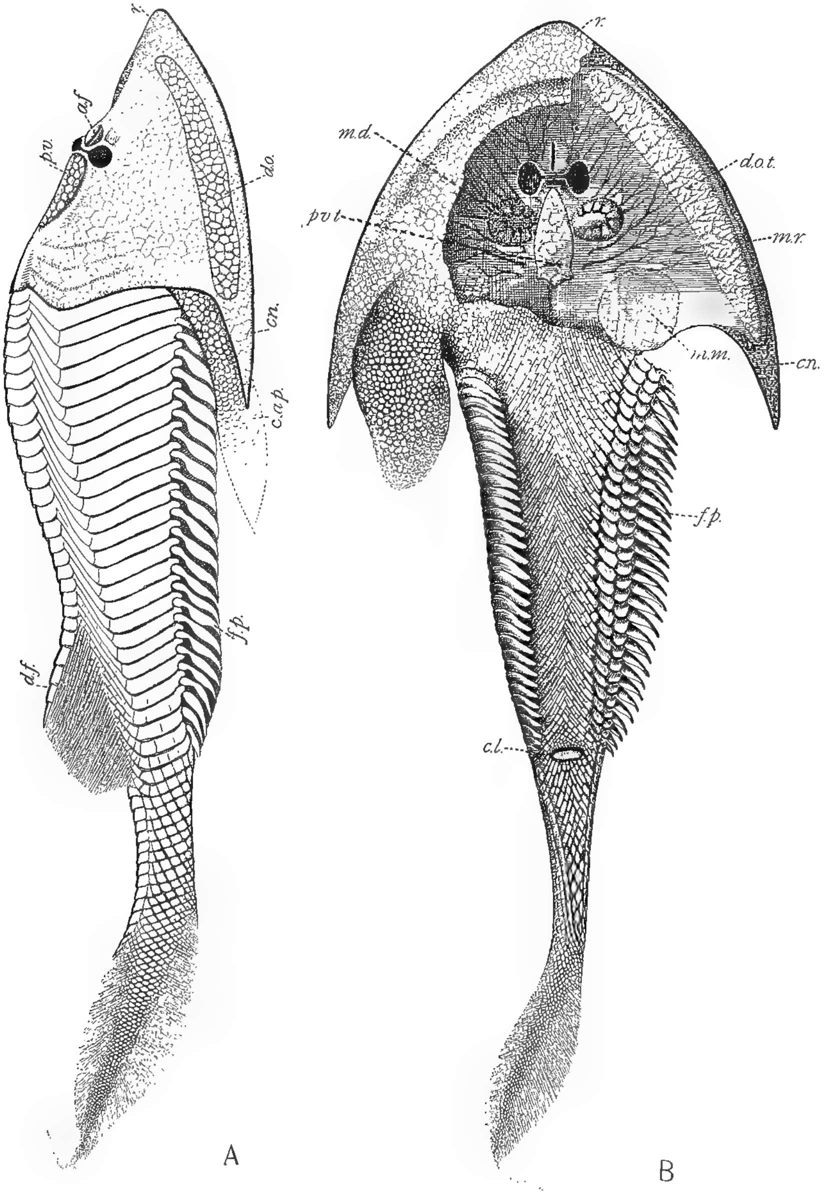


FIG. 232.—Restoration of Cephalaspis. *A*, From the side; *B*, from the hæmal surface. Based mainly on C. murchisoni.

bony trabeculæ belonging to the inner layer. There are no indications that special organs, sensory or otherwise, were located in these openings.

The Eyes.—The parietal and lateral eyes, whenever their position can be certainly determined, are located, with the olfactory organs, on the median dorsal portion of the cephalic buckler, forming in the antiarcha and aspidocephali a very characteristic group.

The lateral eyes in these families are remarkable. They are contained in spherical chambers, the floor and sides of which are formed of a basket work of bony trabeculæ similar to those in Limulus. (Trемataspis, Cephalaspis Figs. 233, *A*, *B*, 239, *A*.) They are situated on short bony stalks that could be lowered into the chamber, or the distal ends of the stalks could be raised, exposing the convex surface of the oval or kidney-shaped cornea. (Fig. 239.) The latter is covered by a thin shell that appears to be an extension of the dermal armor; it is convex and smooth, and in life no doubt it was transparent (Tremataspis and Cephalaspis).

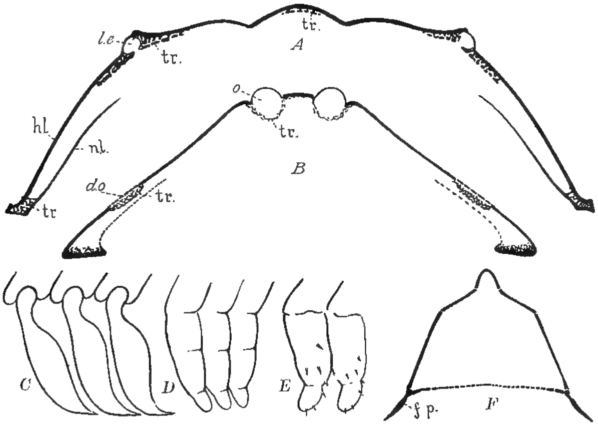


FIG. 233.—*A*, Cross-section through the thoracic shield of Limulus, showing the location of the principal patches of bony trabeculæ; *B*, section through the head of Cephalaspis showing the bony trabeculæ encasing the lateral eyes, the thickened margin, and a part of the hæmal wall of the shield; *C*, fringing processes of C. lyelli; *D*, same of C. pagei; *F*, cross-section of the trunk of C. lyelli.

In the pteraspidian and anaspidian sections, and in Ateleaspis, the lateral eyes are apparently absent, or covered by a thick skeletal layer that, as in young lampreys, effectively conceals their location.

The apparent absence of the lateral eyes in certain ostracoderms is very significant. There is no reason to suppose that the forms without lateral eyes were cave animals, or deep sea animals, or that they belonged to an eyeless stock. The unusually large size of the median eye tubercle, or fossa, and the well developed lateral eyes in their immediate relatives, is sufficient evidence to the contrary. The temporary suppression of such ancient organs as the lateral eyes is best explained on the assumption that they are in a metamorphic, or transitional, condition, midway between the lateral eyes of arthropods, which remain outside the medullary tube, and the cerebral eyes of vertebrates that have been carried into it during the early stages of development. Those ostracoderms in which the lateral eyes appear to be absent are to be regarded as the ones whose newly-formed cerebral eyes (phylogenetically speaking) have not become functionally adjusted to their new environment. The concealed lateral eyes of larval cyclostomes are in a similar condition, and they are to be explained in a similar manner. See Chapter IX.

The *parietal eye* was relatively large, and was lodged in a deep pit on the under side of a projecting tubercle of the cephalic buckler (pteraspidians), or on the under side of a small movable plate, lying between the lateral eyes, (Tremataspis, Cephalaspis, and Bothriolepis). In Bothriolepis there are two additional pits on the inner surface of the postorbital plate, that probably contained another pair of parietal ocelli. (Figs. 252, 253, 255.)

The **olfactory organs** were probably located in a hypophysis-like median sac, situated just in front of the orbits. In Tremataspis, Cephalaspis, and Thyestes, the oval opening to the sac lies at the bottom of a shallow depression, that may be a little deeper on either side. In Bothriolepis there is a small movable, T-shaped plate (Fig. 255, *e*), that stands nearly vertically in the large opening common to the median and lateral eyes. To the outer ends of the plate are attached two concave, lateral wings, *l.e.*, that appear to have partly enclosed the olfactory organs. A narrow canal leads outward from each chamber, opening to the exterior just in front of the top of the plate.

Auditory Organs.—In Tremataspis and Bothriolepis there are two small, sharply defined openings, situated close together in the occipital region, which probably represent the outer ends of endolymphatic ducts.

In Bothriolepis, when seen either in sections or dissections, they lose their sharply defined walls just below the outer surface, and open into irregular chambers that may lead either into the cancellous tissue or into the interior. There are no definite openings corresponding to them on the inner surface of the shell, but in etched heads there may be present a conspicuous spur representing the cast of the inner opening. (Fig. 252.) In Tremataspis, the canals lead into small bony tubes that project some distance from the inner surface of the shield. In Cyathaspis there are two V-shaped ridges in this region, that have been regarded as the surface indications of semi-circular canals.

The ducts are in some way related to the lateral line organs, for in young specimens of Bothriolepis they mark the median termination of the orbital lines.

Cutaneous Sense Organs.—A system of cutaneous sense organs is fully and clearly mapped out in Tremataspis and Bothriolepis. In the former (Fig. 236), each line consists of a series of short, shallow grooves on the smooth outer surface of the shell. A circumorbital line, *a.m*, postorbital, *p.o*, occipital *oc*, a posterior branchial, *p.b*, and a lateral line *p.m*, are represented. The occipital lines lead toward the endolymphatic pores described above. No grooves occur on the ventral side, except for a short line, or dash, on one or two of the oral plates. (Fig. 237, *A*.)

In Bothriolepis the lines form continuous shallow grooves. (Figs. 247, 248.) One line extends from the infra-orbital across the front of the head; there is a V-shaped orbital line connected with the occipital pores, and one on the dorsal surface of the branchial shield; another extends onto the ventral surface, across the maxillary plates, probably connecting with the line on the premaxillary plates; while a lateral line extends along the sides of the branchial shield and appears to be continuous with a furrow extending along the sides of the fleshy trunk.

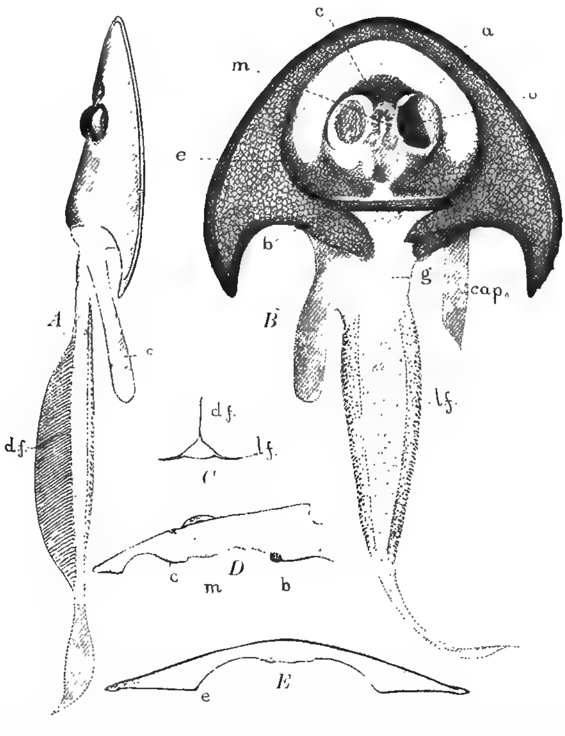


FIG. 234.—A small species of Cephalaspis, *sp.?* associated with Bothriolepis, from Miguasha, Bay Chaleur, P. Q. About natural size. *A*, From side; *B*, hæmal surface; *C*, cross-section of the trunk; *D*, sagittal section of the head *E*, cross-section of the head. In *B*, a heavy bony ridge is seen, *b*, that probably divides the oral from the bronchial chamber. From specimens in the author's collection.

In Pteraspis and Palæaspis there are scattered dash-like markings on the outer surface similar to those of Tremataspis, but less regularly arranged. There is also a special system of canals lying within the shell, the distribution of which is imperfectly known; they may perhaps represent closed lateral line canals (Tremataspis, Pteraspis, and Palæaspis)

In Ateleaspis, *nov.sp*, from Dalhousie, sensory grooves are present similar to those in Tremataspis, but located on a narrow ridge. The infra-orbital, the antorbital, and the anterior end of the lateral line, are indicated. (Fig. 242.)

The prevailing position of the lateral line organs on the neural surface of the head, where they are out of touch with the food or surrounding objects, is only intelligible on the assumption that they represent the remnants of the gustatory and tactile organs that were located on the neural surface of the head, in their arachnid-like ancestors. See Chapter VII, p. 121.

The ostracoderms may be divided into the following orders:

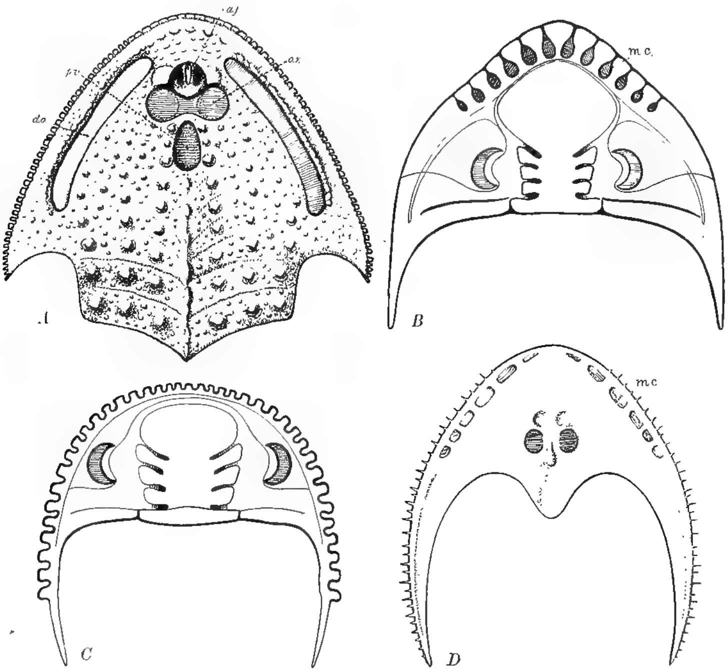


FIG. 235.—Cephalic bucklers of Ostrocoderms and marine arachnids. *A*, Head of Thyestes; *B*, Odontocephalus; *C*, Corycephalus; *D*, Eukeraspis. Silurian.

I. ASPIDOCEPHALI.

Head, thin, broad. Trunk and tail, narrow and small. Exoskeleton forming a continuous cephalic buckler; trunk plates separate, segmentally arranged. Outer surface of dermal armor, smooth, or with low rounded tubercles on polygonal areas, that may separate into small, five- or six-sided plates. Marginal and central openings on the dorsal mesocephalic shield, filled with loose polygonal plates belonging to the outer layer only. Olfactory, or hypophyseal opening, not enclosed in the orbital foramen.

Cephalaspidæ.—The head is shield-shaped, rounded or pointed in front, and with thickened margin; posterior margin expanded, cornuate. Oral region is a small membranous area in the center of the thin, convex, hæmal wall. The branchiocephalic shield, small, indistinctly segmented; hæmal branchial shield absent. Gills not enclosed in an atrial chamber. Large cephalic appendages attached to the under side of mesocephalon, median to the cornua; flexible, with terminal horizontal expansions. Trunk membranous, or covered with segmentally arranged plates, with twenty-five to thirty pairs of separately movable, appendage-like, fringing processes. Lateral eyes, prominent, median. Caudal axis straight, ending in slender filament. Ventral lobe of caudal fin, narrow and subterminal. Upper Silurian to upper Devonian.

Cephalaspis (Figs. 232, 233, 234); Eukeraspis (Fig. 235, *D*); Thyestis (Fig. 235, *A*); fringing plates (Fig. 233, *C*, *D*, *E*).

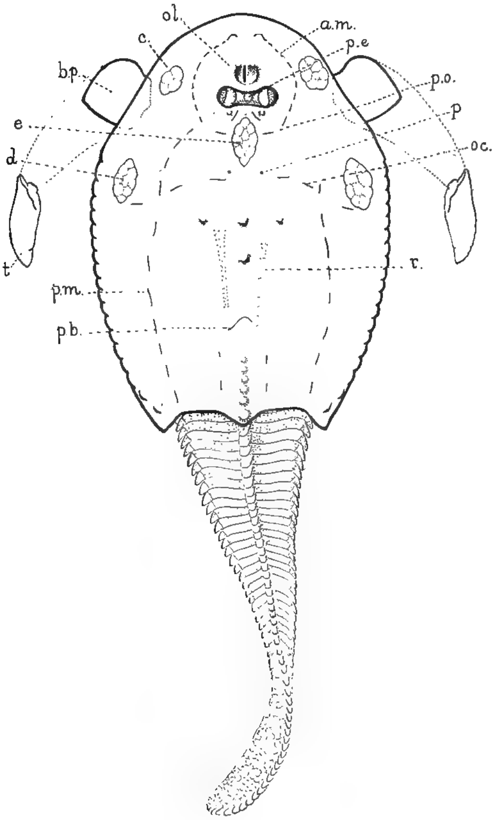


FIG. 236.—Restoration of Tremataspis, seen from the neural surface, and showing the location of the principal sense organs, canal organs, and appendages. × about 1 1/2.

Tremataspidæ.—Dorsal and ventral shields of the mesocephalon and branchiocephalon united to form an oblong, lenticular buckler. Parietal eye plate free. Small, 2–3 in. long. The best known form is Tremataspis Schmidti, whose polished yellow shields are beautifully preserved in fine grained chalky rocks of the upper Silurian in the island of Oesel, Baltic sea.

Exoskeleton.—Divided into the usual three layers; outer surface nearly smooth, polished. Cancellæ, somewhat irregular, small. Two sets of horizontal canals, forming networks just below the outer layer. In one set, the canals are of varying caliber, and terminate in coarse, dentinal canals that dilate at intervals, forming in the outer shell layer vertical rows of multipolar lacunæ; inwardly they lead into the cancellæ, and hence via coarse vertical canals, through the basal layer into the head. The second set are uniform in diameter and open outwardly by clear-cut conical chimneys. (Fig. 205.)

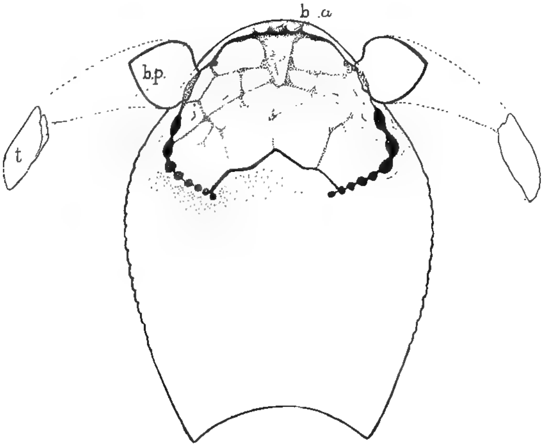


Fig. 237.—Restoration of Tremataspis, seen from the hæmal surface, and showing the arrangement of the circum-oral plates, × about 1 1/2.

Oral Region.—There is a large opening on the anterior hæmal part of the head, near the center of which lies the mouth. (Fig. 237.) It is surrounded by close-fitting plates, seldom preserved in place. The opening in which these plates belong is bounded in front and on the sides by the narrow, overturned rim of the neural shield. On the anterior rim is a triangular, ill defined plate, adhering to the inner surface of the neural shield. It has a median, oval ridge *b*, with a roughened or porous texture. On either side is a polished, conical projection of the narrow rim, *a*. On the lateral and posterior margins of the opening are eight or nine pairs of thick-lipped, semi-circular incisions, whose concave surface is conspicuously porous. There are corresponding incisions on the adjacent

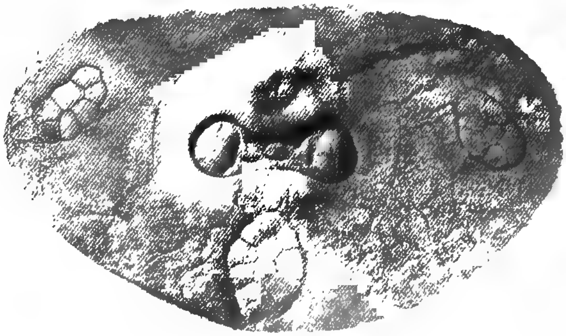


Fig. 238.—Photograph of the orbital region of the shield of Tremataspis. × about 3.

oral plates, thus forming a regular series of openings leading into the interior and increasing in size from behind forward.

The oral plates form four or five transverse rows, the form of the smallest and most anterior ones being imperfectly known. In the only known specimen that has the plates in position, the large anterior pair were crushed and broken. What appears to be one of the same plates has been found isolated and intact. It has a small rounded notch at one end, and appears to represent the premaxillary of Bothriolepis, although its form does not suggest a jaw plate. None of the remaining plates resemble those of Bothriolepis.

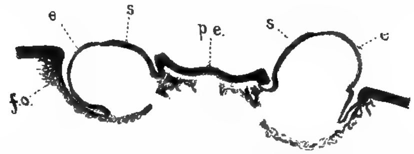


Fig. 239.—Cross-section of the orbits of Tremataspis, showing the movable lateral eye stalks, the parietal eye, the network of bony trabeculæ forming the floor of the median and lateral eye chambers, and the extension of the dermal armor over the corneal surface of the lateral eyes. Semi-diagrammatic. × about 7 1/2.

The exact location of the mouth is uncertain. It was probably in the ill-defined triangular depression between the premaxillary plates. In any case it must have been very small and narrow.

The *lateral eyes* were on short stalks that could be raised above the level of the shell, or lowered into the large spherical orbits, the floor of which consisted of a basket work of bony trabeculæ. The entire outer surface of the eye stalk and the front of the eye itself was covered with a thin layer of the exoskeleton. (Figs. 238–239.)

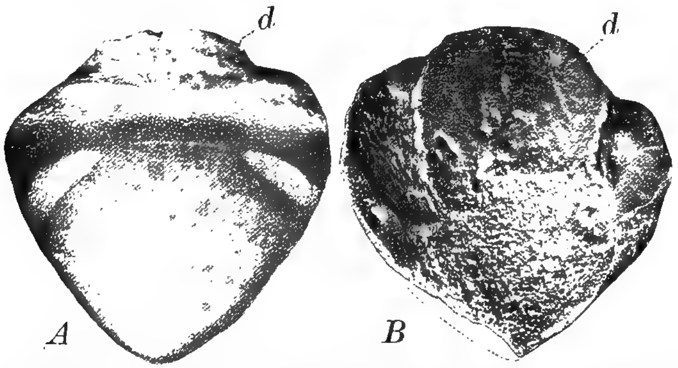


Fig. 240.—Bony plate from the neural surface of the basal joint of a cephalic appendage of Tremataspis. *A*, External surface, showing a circular groove in the polished outer layer, made by striking the edge of the shield in the swimming movements of the appendages; *d*, neck of the plate, attached by flexible membranes to one of the openings on the hæmal margin of the shield; *B*, inner surface of the plate. ×, 10.

The *marginal* and *post-orbital openings* were originally filled with thin polygonal plates; but the latter are usually absent, leaving shallow depressions with scalloped margins, the floor consisting of the modified inner layer of the shell.

Fig. 238 shows a photograph of a head in which the plates are retained in their proper place.

Sections of the whole buckler show that the lateral margins of the upper and lower shields were united by bony trabeculæ, and that two plate-like *entapophyses* projected from the inner surface of the dorsal shield, that probably served for the attachment of muscles. (Fig. 236, *r*.)

The *lateral line organs* consist of short, shallow grooves separate in the younger specimens, but united into longer grooves in the older ones. There is a circumorbital, lateral, occipital, and a posterior dorsal line. Short, sensory grooves occur on some of the isolated oral plates.

Appendages.—Associated with the remains are certain plates that have the same peculiar texture as the shields, and which undoubtedly represent portions of the armored appendages. A complete distal joint has been found. (Fig. 241.)

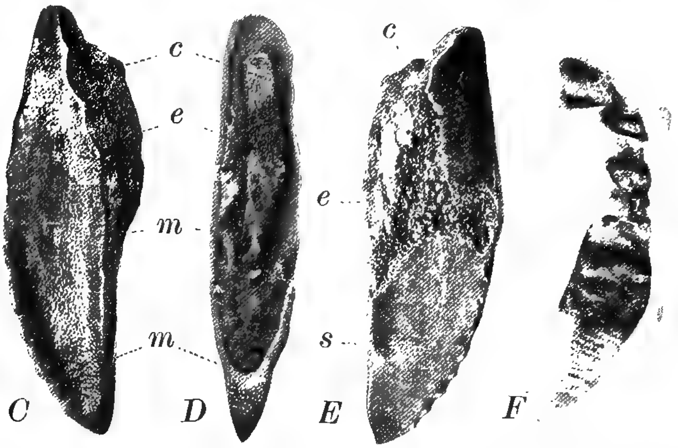


Fig. 241.—*C*, *D*, *E*, Distal joint of a cephalic appendage of Tremataspis; *C*, hæmal; *D*, median; *E*, neural surface; *F*, appendage of some unknown animal associated with the remains of Trematapsis. It consists of five or more joints. A part of the large distal joint has broken off, exposing the impression of the outer surface, that was marked by faint transverse ridges. Superficially, the shell covering the joints resembles that of Tremataspis. Seen from the inside. × 9.

It is oblong, with a broad, partly membranous, posterior surface, a scalloped anterior edge, and an articular process at its proximal end. A convex, heart-shaped plate was also found that represents the dorsal part of the proximal joint. (Fig. 240.) It was attached by a narrow roughened collar probably to the larger anterior marginal incision. In each of the three known specimens of this plate the polished outer surface is cut by a semicircular groove, showing where it struck against the margin of the shield in the forward and backward movement of the arms. (Fig. 240.) There is no place where such plates could be attached to the body or head except in the larger anterior incisions. They fit in this position fairly well and in this position they agree with the corresponding parts of the cephalic appendages of Bothriolepis.

The smaller, more posterior incisions or openings may have served for the attachment, or for the exit of other organs of a similar nature, as for example external gills.

Fragments of what appear to be smaller appendages, covered with a thin calcareous shell, have been found in the same deposits. They have a large, flattened, terminal joint and two or three small segments, or joints, with the surface raised into prominent peaks. (Fig. 241, *F.*) There is no other clue to their origin. They may possibly represent the distal portion of the cephalic arms of Thyestes or of some unknown arthropod.

Ateleaspidæ.—Head rounded, with heavy thickened margin; cornua truncated. Entire body covered with small, five- or six-sided plates, ornamented with bands or radiating lines, or canals, and with low rounded and polished tubercles of varying size. (Fig. 200, *B*, 242, *A.*) No orbits. Sensory canals on trunk and head, consisting of zig-zag, or interrupted grooves on a low narrow ridge. Upper Silurian of England; Devonian of Miguasha, P. Q. Canada.

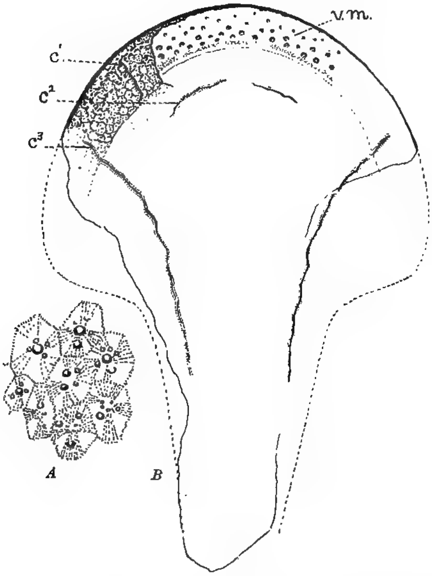


FIG. 242.—Ateleaspis. *A*, Fragment, showing surface ornament, magnified; *B*, neural surface of head and part of the trunk, showing parts of the "lateral line" ridges, marked by a narrow sinuous groove. At *v.m.* the shell is absent, displaying a cast of the broad, flat hæmal margin, ornamented with prominent rounded tubercles. (*From Miguasha, Bay Chaleur, P. Q.* About 2/3 natural size.)

I possess a fairly well preserved example of this very rare family, that was obtained from the gray cliffs of Miguasha, and which probably represents a new species. The greater part of the head is preserved and shows no trace of orbits. (Fig. 242.) The hæmal side of the thickened rim was broad, sharply marginate, and studded with large tubercles. A lateral line groove extends well back onto the flanks, and there are traces of a rostral and an anterior transverse line. The trunk, as far as preserved, was covered with small five- or six-sided plates.

This genus is of special importance, since it shows us an undoubted cephalaspid, probably without orbits, and in which the exoskeleton tends to break up into separate polygonal plates, which correspond to the polygonal areas on the continuous shield of Limulus and Cephalaspis. (Fig. 199.)

II. THE ANASPIDA.

The anaspida include a small number of obscure forms. They were completely covered with small dentinal plates, without multipolar lacunæ, which probably represented the fragmented outer layer of the primitive exoskeleton. Orbits may be covered with bony plates. Small marginal openings indicate the location of gill clefts or the points of attachment of the cephalic appendages.

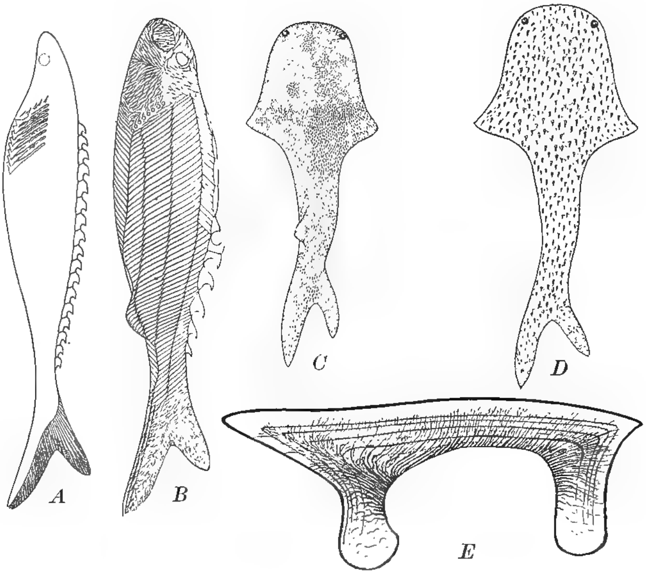


FIG. 243.—*A*, Restored outlines of Lasanius problematicus, Traq; *B*, Birkenia elegans, Traq; *C*, Thelodus scoticus Traq.; *D*, Lanarkia spinosa Traq.; *E*, sagittal section of a primitive dermal denticle (Cœlolepis Schmidti) *A–D*. after Traquair; *E* after Rohon.

Cœlolepidæ.—Resembling somewhat the cephalaspids in form, and covered with separate rounded, or conical, denticles. Upper Silurian, passage beds. Thelodus. (Fig. 243, *C*.) Lanarkia. (Fig. 243, *D*.)

Birkeniidæ.—Fishlike contour, with oblong tuberculate plates. A series of branchial openings, like those in Tremataspis. Birkenia. (Fig. 243, *B*.) Lasanius. (Fig. 243, *A*.)

III. PTERASPIDA.

Head sagittate, or oval, consisting of a small number of large plates. Subdivisions of head united, forming a common cephalic buckler without

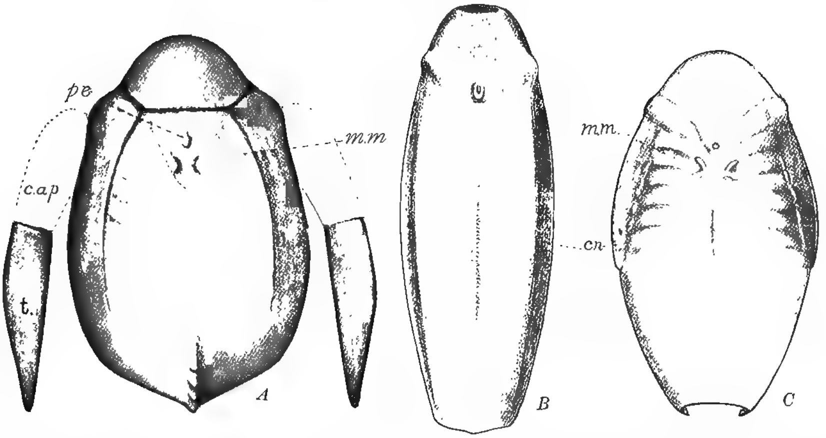


FIG. 244.—*A*, Restored outline of the cephalic shield and cephalic appendages of Cyathaspis, seen from the neural surface, based largely on Lindstrom's specimen from the Silurian rocks of Gothland; *B* and *C*, partly restored outlines of two individuals of Palæaspis (male and female?) from Perry Co., Pa. The shell has been removed, showing a cast of the inner neural surface. About natural sice.

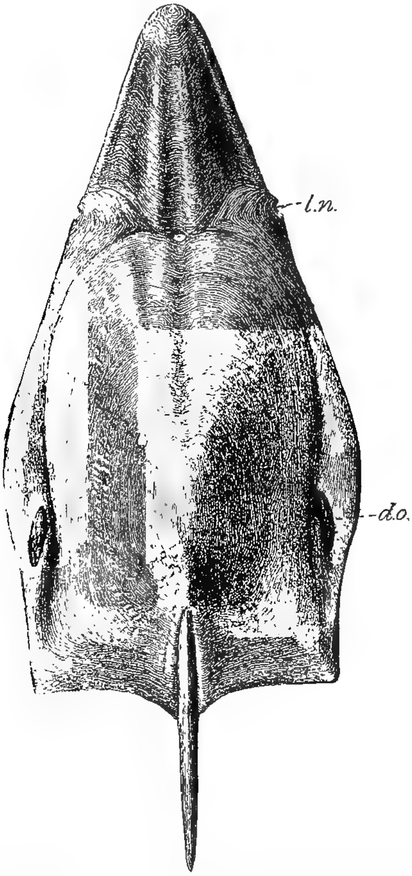


FIG. 245.—Cephalic buckler of Pteraspis, neural surface. (After Lankester, slightly modified) About natural size

lateral eye openings. Gills enclosed in peribranchial, or atrial chamber. Mouth parts unknown. Body plates small, rhomboidal.

Pteraspidæ.—Dermal armor ornamented with minute dentinal ridges and grooves, parallel with the margins of the various plates. Matrix sharply laminate, with numerous unbranched, parallel pore canals, terminating in spindle-shaped unipolar lacunæ. Cancellæ large, rectangular, and in a single layer. Parietal eye lodged in a hollow tubercle, prominent externally, and with the cavity opening inward. Cephalic appendages, where known, large, armored. Oblong marginal openings on dorsal surface of cornual plates leading into the interior of the head. Upper Silurian and lower Devonian. Six to nine inches long. Pteraspis. Kner. (Fig. 245.) Palæaspis, Claypole. Oldest member of the ostracoderms known to occur in America. Onondaga Group, Perry Co., Penn. (Fig. 244, *B* and *C*.) Cyathaspis, Lank. (Fig. 244, *A*.)

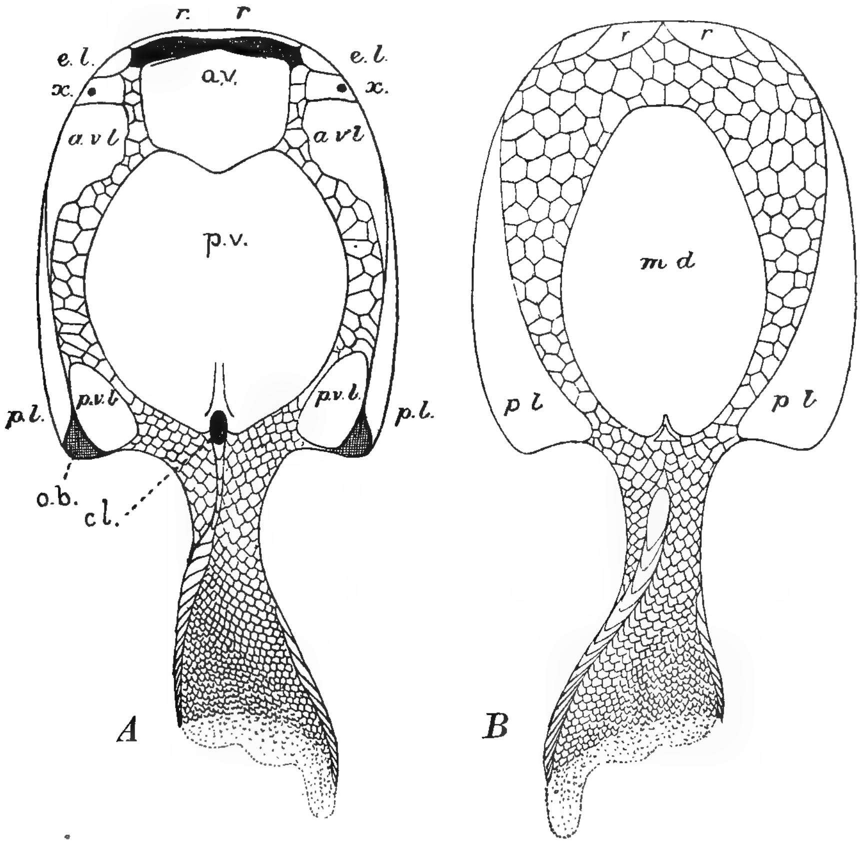


FIG. 246.—Restoration of Drepanaspis gemündenensis, Schl. (After Traquair; slightly modified.) *A*, Hæmal surface; *B*, neural surface.

Psamostædæ.—Head, broad, flattened; trunk, short and thick. Ornament minutely tubercular. Large plates of the head separated by rows of small, five- or six-sided plates. Peribranchial chamber opening on the posterior lateral side of the head, between the posterior lateral and the posterior ventro-lateral plates. Devonian. Drepanaspis, Schlüter. (Fig. 246.)

IV. ANTIARCHA.

Head oval, pentagonal in cross-section. Mesocephalon united with branchiocephalon by a transverse, movable joint. Cephalic armor consisting of large plates; separate, but with little or no movement. Trunk slender, membranous or scaly; triangular in cross-section, with distinct but narrow lateral folds. Two dorsal fins, membranous, with or without supporting rays. Tail long, ending in a narrow ribbon. Cancellæ in one or many layers, often small and irregular. Dermal armor ornamented with tubercles or, with concentric tuberculate ridges. Dentine layer ill defined, thin, or absent. Lacunæ highly developed, multipolar, and extending close to outer surface. Large atrial and pre-oral chambers.

* * * * * * * * *

The best known form is Bothriolepis canadensis, Whiteaves. The author has secured a large number of these fossils, splendidly preserved. Large slabs were obtained showing many entire individuals in their exact attitudes and surroundings at the time of death. With this material at hand, which in abundance and in perfection of preservation has never been equalled, it has been possible to form a very accurate idea of the structure and mode of life of this most interesting animal.

The details of its anatomy have been worked out by means of serial sections and by other methods. They will be reserved for a separate publication; we have space here for only the points of general interest, or those bearing on the subject under discussion.

Exoskeleton.—The outer surface of the dermal armor was ornamented with low rounded tubercles, arranged in concentric rows, often parallel to the margins of the separate plates, or forming wavy, crenulate ridges.

The dorsal *mesocephalic shield* moves up and down, to a limited extent, on the hinge-like joint connecting it with the branchiocephalon. This movement is made possible by the tilting of the *suspensory* or *suborbital* plate, whose thick, ventral edge rests on the anterior lateral margin of the fixed, ventral shield (anterior ventro-laterals). (Figs. 253, *s.o*, 259, *A.*) When the mesocephalon is depressed, the dorsal edge of this plate swings inward, without dislocating the plate, through an angle of almost forty-five degrees. In partly crushed heads it is forced into an abnormal, horizontal position, and lies inside the head with its lateral surface turned dorsally.

As the ventral edge of the suspensory plate fits into a shallow groove, or ridge, its posterior end cannot normally swing bodily outward, after the fashion of an operculum, as one might at first sight suppose. In fact, there is no passageway into the head at this place that could be opened and closed by the movements of this plate, and there is no reason for regarding it, either functionally, or morphologically, as an operculum.

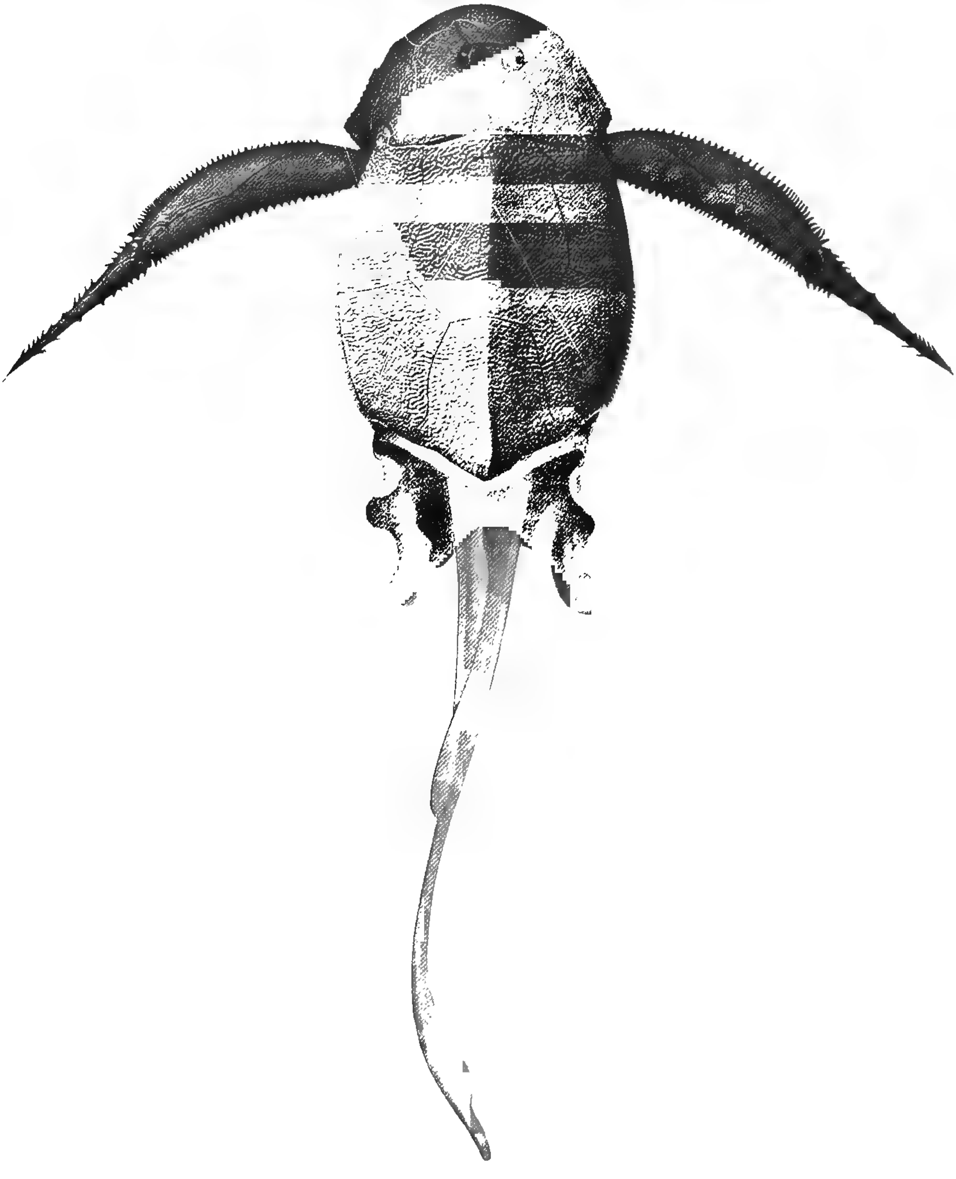


FIG. 247.—Restoration of Bothriolepis canadensis (Whiteaves; from Miguasha, P. Q., Canada.) Neural surface; about 1/2 natural size.

The anterior end of the suspensory plate is narrow and slightly curved, and adjoins a small quadrangular, movable plate that probably represents the *maxillary* plate of the arthrodira. In depressed heads, it is bent over onto the oral surface, and in side views it then appears to be absent. A branch of the suborbital line extends over this plate, apparently connecting with the sensory groove of the premaxilla. (Figs. 254, 262, *mx.*)

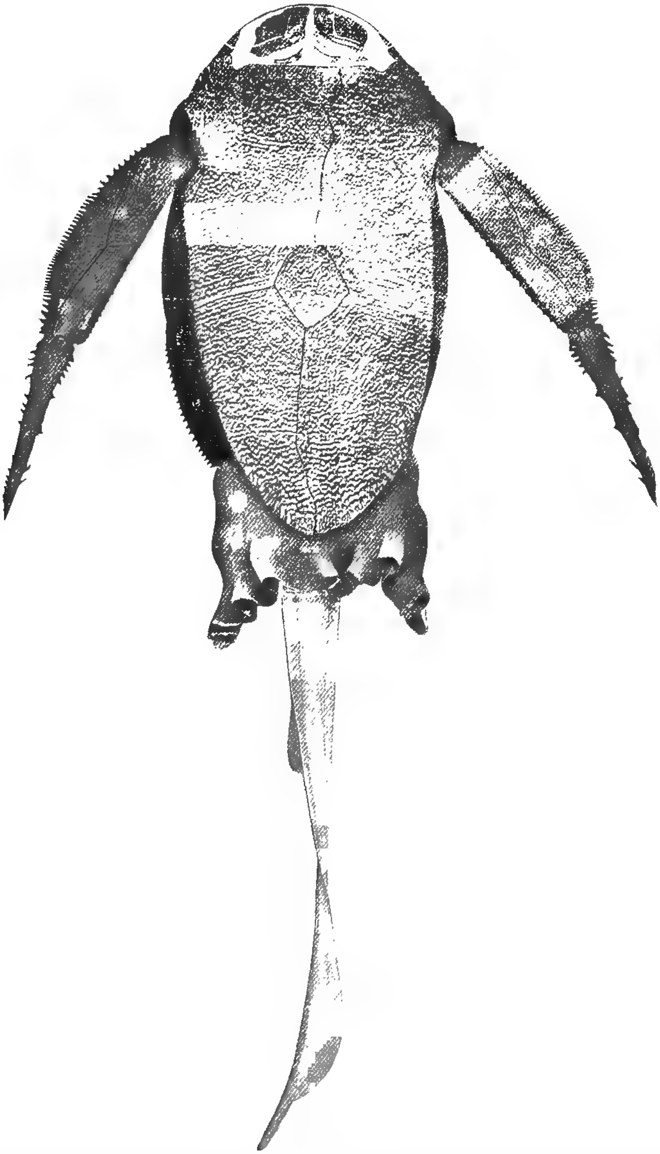


FIG. 248.—Restoration of Bothriolepis canadensis. (Whiteaves.) Hæmal surface. About 1/2 natural size.

The remaining plates of the pro- and meso-cephalic shield, except those in the orbital opening, are practically immovable, and are frequently found as one piece, even when all the other plates have separated through maceration.

The *branchiocephalon* enclosed the gills, atrial chamber, viscera, and repro-

FIG. 249. Photograph of a small group of Bothriolepis. The individual, *a*, after death, came to lie hæmal side up, on what was the bottom at that time; its dorsal fin and tail lie in a horizontal plane. Individuals, *b* and *c*, died in their natural position; that is, buried in the mud, hæmal side down. Their dorsal fins and tail lobes are in a nearly vertical position.

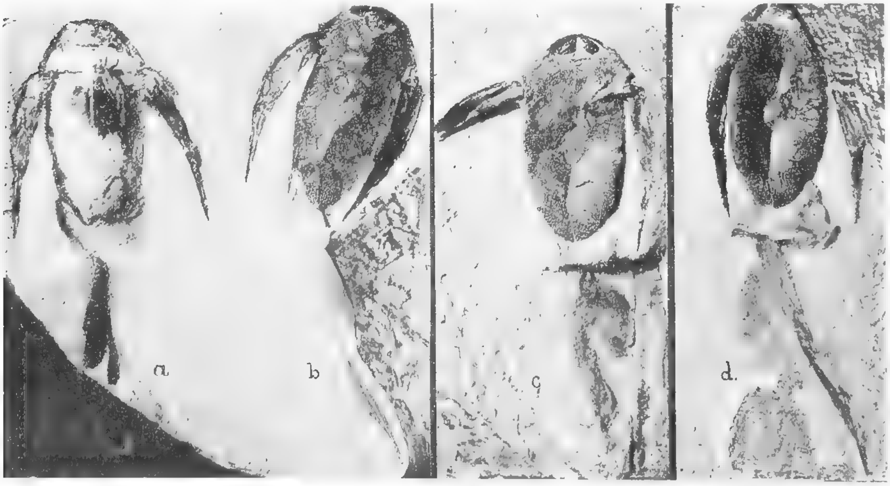


FIG. 250.—Photographs of Bothriolepis, seen from the hæmal surface, showing the conspicuous membranous frills surrounding the exhalent opening of the atrial chamber

ductive organs. The anterior part of the trunk and the branchial portion of the head was suspended from the roof of the branchiocephalic shield by stout fibrous tissue attached to two deep median processes, or ridges of cancellous bone, that projected downward and forward (Fig. 251, *pr.*) The sides and ventral surface, were unattached and were surrounded by a spacious peribranchial, or *atrial chamber*, which opened outward between the sides of the body and the ventrolateral walls of the branchiocephalic buckler.

Atrial Frill.—The lips of the atrial opening were guarded by a membranous frill (Figs. 247, 248). Its ventral portion was broad, often folded or pleated, and sometimes marked by faint, longitudinal lines. It appears to project from the inside of the chamber and to be attached to its ventral wall by a faint transverse ridge. The dorsal portion was much narrower, and appeared to be a membranous extension of the posterior and lateral margin of the shield. The contents of the branchiocephalon are never squeezed out of the posterior end of the buckler. Sections of many different specimens always show the gills and stomach in their proper position, even when the shields are crushed almost flat. If the animal lies ventral side down, the viscera always lie on the ventral wall. If it died ventral side up, they lie on the dorsal shield, and in all cases well in front of the atrial opening.

Gills.—Seven pairs of broad lamellate gills were present on the sides of the head, in about the center of the branchiocephalon. They appear as seven pairs of thin, parallel, black lines, somewhat wavy, with minute black spots. (Fig. 256.) A more conspicuous dark band, or a clear space, separates the gills of one side from those of the other. Altogether they form an oblong nodule about an inch and a half to two inches long, one inch broad, and from an eighth to a quarter of an inch thick. The nodule always consists of a peculiar fine-grained, soft

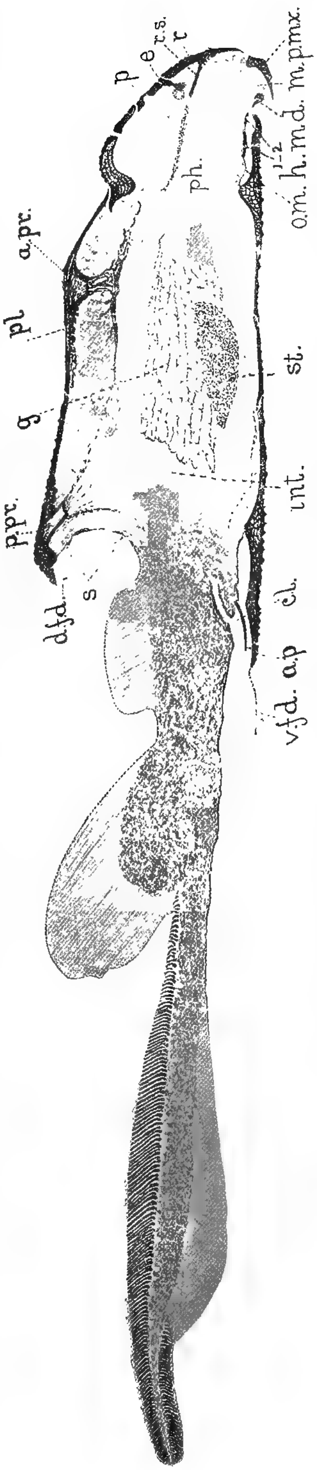


FIG. 251.—Semi-diagrammatic sagittal section of Bothriolepis, showing the location of the cloaca, gills, stomach, mouth, jaws, etc.

matrix not visibly affected by acids. The part of the atrial chamber not occupied by the remnants of the viscera is always filled with a coarse grained sand that evidently worked its way in through the atrial opening after the animal died. When treated with dilute acids, this sandy matrix becomes friable and can often be easily worked away, exposing the contour of the gills and viscera.

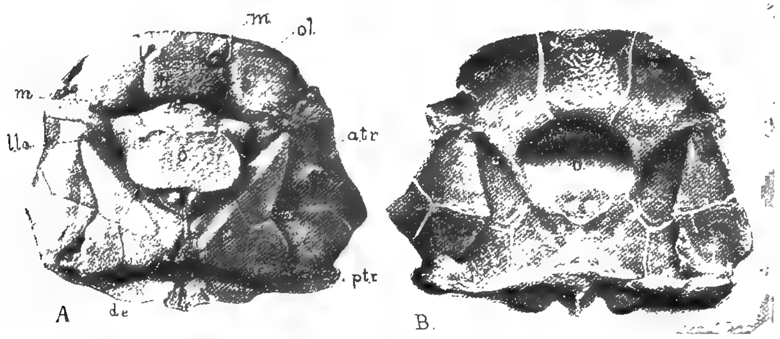


FIG. 252.—Head of Bothriolepis. *A*, The bony cranial plates have been etched away, leaving a natural cast of the inner, neural surface of the head; *B*, bony plates covering the neural surface of the head, seen from the inside. The matrix has been chiseled away. Photographs; slightly restored.

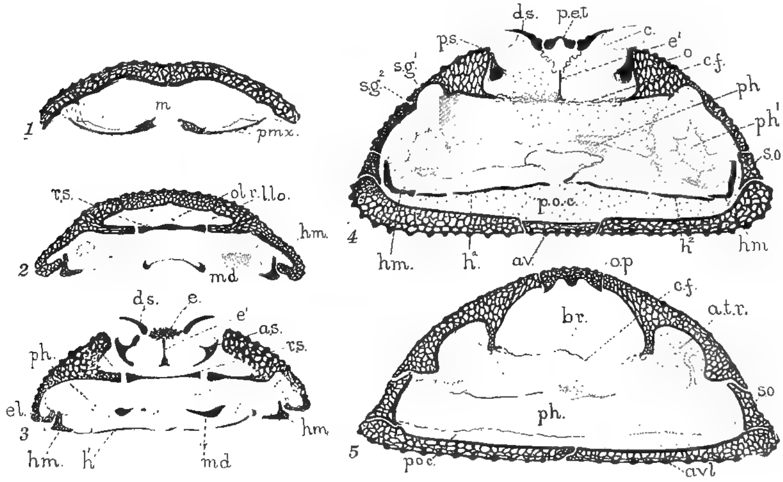


FIG. 253.—Transverse sections of the head of Bothriolepis. The dermal bones black; the coarser, more sandy matrix, dotted; the softer matrix of a chalky consistency, shaded. Slightly diagrammatic.

Viscera.—Above, or to one side of the gills was a large oblong stomach, the contour of which was conspicuous, owing to its carbonized contents. The cloaca was guarded by a thin rounded, *cloacal scale* that is faintly tuberculate on its free or ventral surface and with concentric lines on its dorsal surface. The cloaca opened into the posterior part of the atrial chamber about half an inch in front of the posterior margin of the ventral shield. (Fig 251, *cl.*).

The *pre-oral chamber* lies on the anterior ventral surface; its rim is formed by the anterior margins of the dorsal and ventral shields, which were apparently fringed with short fleshy papillæ. Across the roof of the opening there is a tough *circum-oral membrane* in which are imbedded the large premaxillary plates, the mandibles, and the two narrow bony bands that covered the hyoids. The membrane extends backward, underneath the anterior ventro-laterals, as far as the transverse ridge on their inner surface, to which it appears to be attached (Fig. 251, 254, *om.*)

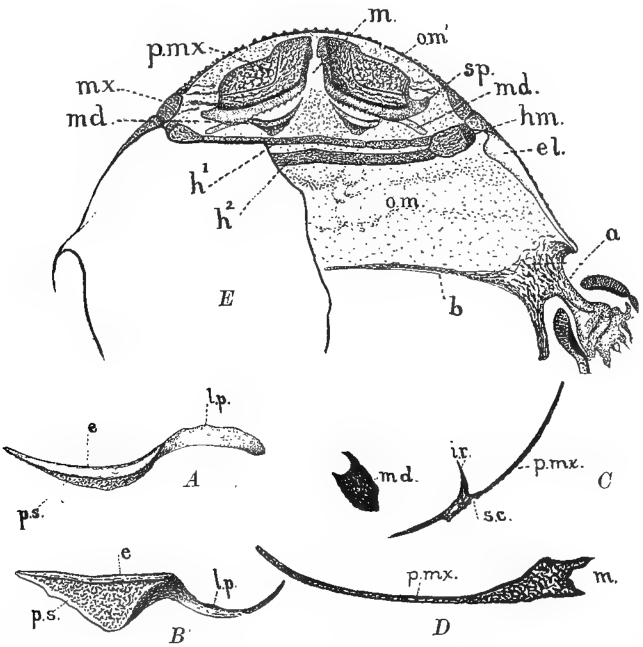


FIG. 254.—*E*, The oral region of Bothriolepis. On the right, the anterior ventro-lateral plates have been removed exposing the dermal armor of the double hyoid arch, imbedded in the circumoral membrane. The latter is continuous with the ridge, *b*, on the inner surface of the anterior ventro-laterals. *A*, The mandibles of Bothriolepis, with the smooth, toothless margin rotated outwards; *B*, same, rotated inwards; *C*, longitudinal, vertical section, a little to one side of the median line, showing the pre-maxillary and mandibular plates in their normal positions; *D*, cross-section of the premaxillæ in the oral region, showing the thickened, crushing, or cutting edges of the premaxillary plates.

The *premaxillæ* are thin, concave plates of dermal bone continuous with the oral membrane on the sides and in front, but with free median and posterior margins. (Fig. 254.) The exposed surface presents the characteristic surface ornament, together with a sharply bent, sensory groove. The rounded posterior margin is smooth and bevelled, ending in an extremely thin edge, nearly the whole length of which is broken into minute irregular tooth-like serrations. The median margin is very thick, with sharpened edges which in the older individuals become rounded or smooth through use. The anterior margin has a prominent shoulder; it is uniformly thin and rounded, and is continuous with the oral membrane. The lateral margin is narrow and slightly concave; a broad spur extends laterally and inward on the visceral side of the oral membrane, serving, no doubt, for the attachment of muscles, *s.p.*

The visceral aspect of the premaxillæ is nearly smooth, except for a very prominent, transverse, sharp-edged ridge, which evidently served for the attachment of muscles that moved them in a median or lateral direction. (Fig. 254, *C.*, *ir.*)

The premaxillæ moved independently to and from the median line, bringing their stout crushing or biting edges together. They are sometimes found in a nearly vertical position, or even thrown forward in front of the head, with their ventral surfaces facing dorsally. Thus it is probable that, like two great lids or covers, they could swing forward and backward on the muscles and the membrane attached to their anterior visceral surface; it is improbable that normally they ever passed beyond the vertical position during life. (Fig. 251.)

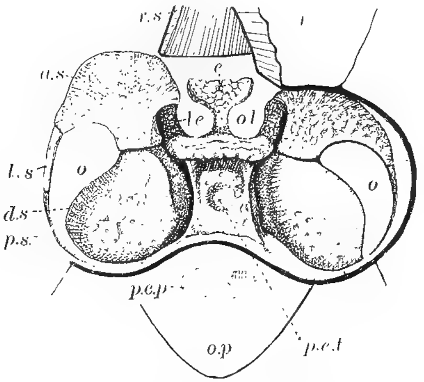


FIG. 255.—The ocular and olfactory plates of Bothriolepis, enlarged. A part of the rostral and lateral plates have been removed on the left, in order to expose the deeper lying sclerotics and the inner end of the ethmoid.

The *mandibles* are peculiar S-shaped plates lying behind, or more frequently underneath, or dorsal to, the premaxillæ. (Figs. 248, 251, 254, *md.*) The median end of each mandible has a smooth, rounded, anterior, or ventral edge, and a finely ornamented, convex outer surface. Its visceral surface is deeply concave. The lateral arm of the mandible is narrow and smooth and lies inside the oral membrane.

The mandibles are usually widely separated in the median line, each being quite independent of the other; they are held in place by the tough skin in which their median ends are imbedded. They appear to have had a free rotary movement, their ventral edges swinging forward and backward; at the same time, their median ends could be drawn together and thrown forward.

The difference in position and structure between the mandibles and premaxillæ makes it improbable that one pair acted directly against the other. The mandibles probably pushed the food forward and inward, where it could be crushed or cut between the stout margins of the premaxillæ, after the manner that prevails among the arthropods.

Hyoid Arches.—Back of the mandibles, the circumoral membrane is strengthened by two bands of dermal armor. They are thin and delicately ornamented, and when the head is in a normal position the posterior band is entirely, and the anterior one partly, overlapped by the anterior ventral plates. The narrow anterior band consists of five or six segments. The posterior one is unsegmented. Both bands are attached to a large lateral plate, the lateral end of which is bent at right angles, and attached to the lateral walls of the head. (Figs. 253, 254, *h.m.*)

The *mouth* was a slit-like opening situated between the premaxillæ and in front of the membrane uniting the two mandibles.

The oral membrane with the attached premaxillæ and mandibles could be protruded a short distance, or withdrawn into the broad but shallow pre-oral chamber.

The Eyes and Olfactory Organs.—The oval opening on the anterior part of the dorsal shield contains the stalked lateral eyes, the parietal eye, and the olfactory organ. These organs were wholly or partly surrounded by small bony plates held in place by tough but flexible membranes. (Fig. 255.)

The *lateral eyes* were enclosed in short, rounded eye stalks that were attached to the margin of the parietal and olfactory plates by hinge-like joints so that the crescent-shaped eye openings on the distal ends of the stalks could be raised or lowered into the orbits. The exoskeleton of each eye stalk consisted of a thick posterior dorsal, *d.s.*, a large anterior ventral, *a.s.*, and two ventro-lateral plates, *l.s.* When the posterior dorsal plate was level with the shield, the corneal opening was concealed within the orbits.

Parietal Eyes.—Between the lateral eyes is a thick quadrangular plate that is nearly perforated by a deep conical pit, opening inward, and covered externally by a thin-walled, lens-like tubercle. This pit contained the anterior parietal eye. There are two similar pits, but not so deep, on the inner surface of the small postorbital. There is no indication of their presence on the external surface.

Olfactory Organs.—The posterior end of the rostral plate divides into an inner and an outer lamella, enclosing a wide triangular chamber between them. (Fig. 251, *r.*) Just above the edge of the inner lamina is a small, T-shaped ethmoid. It stands nearly vertically, with its dorsal transverse bar attached to the anterior edge of the pineal plate. (Fig. 255, *e.*) When the anterior face of the ethmoid is exposed, it is seen that its expanded arms, to which are attached rod-like lateral ethmoids, *l.e.*, and the pedicle form the lateral walls of two rounded depressions in which the paired olfactory sacs were probably located. In the bottom of each pit is a circular opening, leading into the interior of the head, and serving for the passage of the olfactory nerves.

All these plates are held together and attached to the sides of the sensory opening by tough but flexible membranes, leaving a relatively large space for the movements of the organs. It is clear, from the various positions of the plates in different specimens, that the parietal plate could move caudally for several millimeters, drawing the ethmoid backward and upward, thus enlarging the opening to the olfactory chamber. When the outer end of the ethmoid was pushed forward against the posterior wall of the rostral plate, two narrow passages would still remain open, leading from the olfactory pits to the exterior. (Fig. 259, *A*.)

The olfactory pits of Bothriolepis correspond to the antorbital fossæ of the aspidocephali, indicating that the union of the median and lateral eyes and the olfactory organs into a compact median dorsal group of sense organs is very characteristic of the ostracoderms.

Sensory Grooves.—The cutaneous sense organs were located in distinct open grooves. (Figs. 259, *A*, 262.) There is a main suborbital, *r.l.*, united in front in adults, but separate in the young; a V-shaped orbital line usually connecting with the suborbitals in front, and at the posterior end, in immature specimens, leading into the endolymphatic ducts; a V-shaped posterior branchial, *b.l.*, and a lateral line, *l.l.*, extending backward along the sides of the branchiocephalon, onto the sides of the trunk.

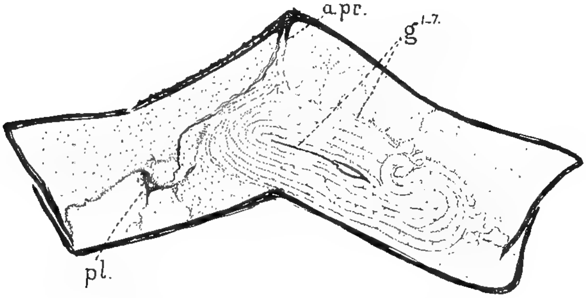


FIG. 256.—Cross-section of Bothriolepis in the branchial region, showing the seven pairs of plate-like gills.

The *cephalic appendages* are large, completely armored, and consist of two movable joints. The proximal one is covered with six plates; it is triangular in cross-section, rounded dorsally, flat ventrally, with a sharp tuberculate anterior margin and a thick, flat, posterior one. (Figs. 247, 248.) An opening at the proximal end of the posterior wall and an adjacent opening in the side of the branchiocephalon served for the passage of blood-vessels and nerves into the interior of the appendage. (Fig. 262.) The dorsal and ventral proximal plates formed a rounded articular head that fitted into a socket in the anterior ventrolaterals. From the center of the socket a fixed bony rod with an expanded head projected into the interior of the appendage, thus holding it in place after many of the softer tissues had completely macerated. (Fig. 254, *a*.) This bony rod is continuous with an axial plate, or bar, of fibrous or cartilaginous tissue that extends into the proximal end of the appendage. The distal joint of the appendage was movable in a horizontal plane only. It was hollow, oval in cross-section, with recurved marginal spines, and covered with numerous polygonal plates.

Habitat. Mode of Life.

Mode of Preservation.—Nodules containing the heads, or other fragments of Bothriolepis may be found on the beach, at the foot of the gray cliffs in Miguasha, near Dalhousie, New Brunswick; but the best specimens, showing the whole body, can only be obtained from the unweathered strata in the cliffs.

The greater part of my material was obtained from a small "table" about twenty or thirty feet in diameter and sixteen to eighteen inches thick. The edge of the table had been exposed by the wearing away of the face of the cliff, showing two or three layers very rich in fossils. The overlying rocks were blasted out, or worked out with pick and bar, as far as, and indeed farther than it was safe to work into the face of the crumbling cliff. We apparently reached the inner limits of the table, and succeeded in removing practically all the specimens contained in it.

Some of the beds were crowded with fossil ferns and Bothriolepis, with here and there a specimen of Scaumenacia, Holoptychius, and other fishes. The animals in the richest beds were badly crushed, and the more delicate parts were obscured by the abundant remains of plants and carbonized organic material. In some of the other beds, where the rock was cleaner and more sandy, there were fewer fossils, but they were not so badly crushed. In these layers there were many specimens of Bothriolepis with the entire body distinctly preserved in the attitude or position they were in at the moment they ceased to live.

The table was no doubt at one time the bottom of a small seashore pool, or inlet, in which shallow-water plants were growing. It was either invaded, at periods of exceptionally high tides, by salt water that carried with it many fishes and ostracoderms, or it was from time to time cut off from the main body of water by shifting sand bars, or by similar causes. In either case, the animals trapped in the enclosures soon died from the effects of the foul or superheated waters, and were shortly afterward covered up and preserved by the shifting beach sands of another invasion.

The great majority of the specimens of Bothriolepis were found in a horizontal position, ventral side down, and headed in the same direction, *i.e.*, a little north of east. These individuals evidently died in this position, oriented by some common external agent.

In nearly all such cases the slender trunk and tail extend in a straight line backward, while the thin membranous dorsal and caudal fins, which were usually perfectly flat and fully expanded, stood in a vertical direction, *i.e.*, at right angles to the plane of stratification. The upright position of such delicate membranes shows beyond question that these particular animals died quietly while still in their natural positions. The fact that these animals were *living partly buried in mud or sand up to the time of their death*, no doubt accounts for their wonderful state of preservation. Side by side with them were other specimens lying either on their back or side, with the dorsal fins and tail expanded in a horizontal plane. They had either fallen to the bottom in this position when exhausted, or turned over in the death struggle, so that the trunk and fins laid flatwise on the upper surface of the muddy bottom. One specimen was found standing on its head, almost vertically. It had evidently been swimming at some speed, when taking a sudden turn, it struck the soft bottom, head first, with sufficient force to stick there in an upright position. This individual was not in the least flattened in a dorso-ventral direction, and when sectioned showed the remains of the viscera settled down in the lower or anterior end of the head. In all other cases the viscera were found lying either on the dorsal or on the ventral wall of the branchiocephalon, according to the side that happened to be uppermost when the animal died.

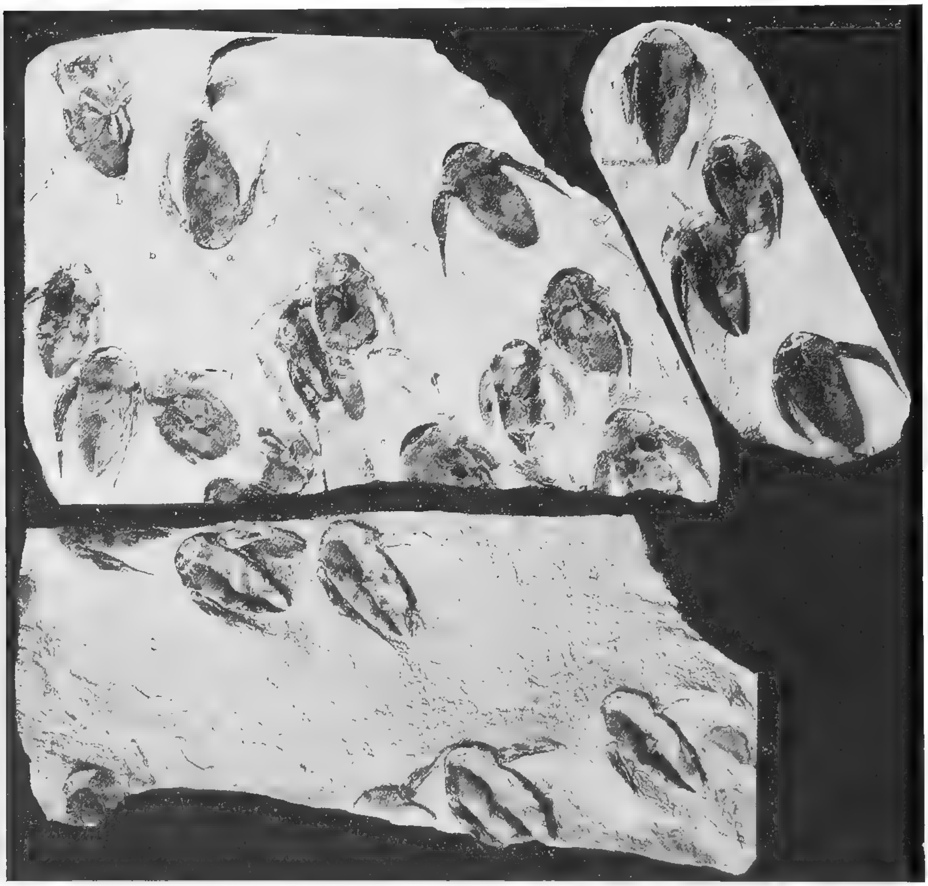


FIG. 257.—Photographs of three contiguous slabs, from approximately the same level, and with the same orientation. The slabs are seen from their under surfaces, and show the uniformity in the orientation of the numerous specimens of Bothriolepis. All are in a natural position, and are headed in the same direction, except four. Of these, two have the ocular, or neural surface exposed (*i.e.*, they lie, haemal side up, when the slab is in its original position); one lies on its side; and one, *a*, lies with its head toward the reader; its tail is gracefully curved toward the upper right-hand corner, apparently by a gentle current of water, that turned the tops of the enclosed water plants in the same direction.

In the large slabs containing many ferns or plant stems, it was clearly shown that the plants were laid down in nearly parallel lines with the tops turned in the same direction, as though at the time they were deposited they had been bent over by a slow current of water.

One of the larger slabs, containing ferns and Bothriolepis in great numbers, is specially instructive. (Fig. 257.) It shows most of the fern tops turned in one direction, with most of the Bothriolepis heads turned in nearly the opposite one, their thin, soft bodies extending in straight lines backward. But one specimen, *A*, is lying on its back in a direction diagonal to the fern tops, thus showing that when this individual died it fell on the bottom oral side up; that the current then turned it partly around, bending its tail in a gentle curve in the same direction as the fern tops.

In some cases several individuals of Bothriolepis were found close together, and at different levels, but nevertheless all turned in the same direction, showing that they were probably oriented by the same agents and died at the same time. From these facts we may infer that they were moving along the soft bottom, some completely covered with mud or sand, others on the surface, just as the adult Limuli do when in great swarms they come up the sandy beaches at high tide to lay their eggs; or as the young Limuli, when feeding, plough about through the soft mud, from three to six inches below the surface.

Locomotion.—It is evident, therefore, that Bothriolepis was a bottom feeder, moving about on its flat oral side, either covered by soft sand or mud, or leaving only its projecting eyes and dorsal surface exposed. But it is evident that it was also a free swimming form, using both its flexible tail and trunk and its large cephalic appendages for that purpose. They probably swam, with their flat oral side uppermost, by powerful backward strokes of their cephalic appendages, just as the eurypterids and possibly many trilobites did in the palæozoic seas, and as many phyllopods, entomostrica, or indeed as adult Limuli continue to do to-day.

It will be observed that the appendages are attached well forward on the margin of the flat and narrow ventral surface; that the head is quite thick, and the dorsal surface wide and strongly arched. A body shaped like this would naturally move through the water like a boat right side up. It is evident that Bothriolepis could not be driven through the water, dorsal side up, without a strong tendency to pitch downward head first, or to roll over. As the cephalic appendages were very narrow and had little dorso-ventral movement, they could hardly succeed in counteracting, or preventing, that tendency. Hence it is clear that the animal had to swim with its dorsal side down, and with its center of gravity below the level of the supporting appendages. In this position equilibrium could easily be maintained either by the arms or by the tail, and the curved anterior surface of the head, according to the rate of its forward movement, would greatly aid in uplifting the cumbersome head in the water.

Food.—Well preserved specimens always contain, in addition to the remnants of other soft parts, a thick oval disc of carbonaceous material, that undoubtedly represents the contents of the stomach. A microscopic examination failed to reveal any definite structures in it, such as diatomes or fragments of bones or shells. It has the same appearance as the remnants of plants seen outside the body, and like them readily burns when heated, leaving a whitish ash. We may therefore infer that Bothriolepis fed on the ferns or other water plants that were so abundant in the places where they have been found. Such a diet was apparently better suited to the peculiar structure of their jaws than any other.

We therefore again come to the same conclusion that was reached in another way, namely that there is a close resemblance between the ostracoderms and the amphibia, for Bothriolepis, with its big head and small tail, its vegetable diet, the peculiar action of its lower jaws while feeding, and in its general mode of life, greatly resembles the tadpole larva of the common frog. The most striking difference between them is the apparent absence in the tadpole of the large cephalic appendages, but these organs are probably represented by the sucking discs, which in turn are comparable with the "balancers" of Amblystoma and other urodeles (Fig. 169), and with the long filamentous cephalic appendages of Dactylethra or Zenopus. (Fig. 170.)

CHAPTER XXI.

THE VERTEBRATES.

We are now in a position to see more clearly the relation that the true vertebrates bear to the ostracoderms. The full recognition of the ostracoderms as the common ancestors of all vertebrates will prove to be a fruitful idea and will go far toward laying at rest the obscession of the last thirty years or more, that the foundations of vertebrate morphology rest on Amphioxus and the elasmobranchs; that in them is the beginning and the end, beyond which lies a fathomless abyss.

It will be a great step forward if it can be demonstrated beyond a reasonable doubt, as I believe it can be demonstrated, that the heavily armored ostracoderms, with cephalic appendages and a large atrial or peribranchial chamber, form the starting point for all animals entitled to be called vertebrates; not the dermal-denticled shark, nor the naked-skinned cyclostomes, nor the impotent remnants of animals that constitute the acraniates.

If we attempt precisely to define the natural limits of the ostracoderms and their immediate descendants, we at once meet with great difficulties and after all we must for the present resort to arbitrary definitions. It is doubtful, for example, whether we should, or should not, exclude the cœlolepidæ and the anaspidæ from the ostracoderms, or whether we should, or should not, include with them the arthrodira, or even the antiarcha. The dipnoi might be excluded from the "fishes" on the ground that they are really primitive amphibians. If so, we should then have remaining, as representative fishes, the elasmobranchii, holocephali, teleostomi and cyclostomes, forms very unlike in structure and origin. However, while recognizing the inadequacy of the current terminology, we shall nevertheless adopt it, as indicated in the tabular scheme of relationships, without attempting to build up a new one that might express more clearly the views herein set forth.

The ostracoderms may be briefly characterized as follows: They consist of a comparatively small number of metameres, and are provided with a highly developed dermal armor, cephalic locomotor appendages, paired jaws, a large atrial or peribranchial, chamber, and with eyes and olfactory organs located near the middle of the aboral surface of the forehead. The form and general appearance suggest that of a trilobite or merostome, or an amphibian tadpole, rather than that of a true fish. Their negative characters, compared with those of the vertebrates, consist in the presence of a diminutive notochord, without definite constrictions or thickenings of the sheath to form centra, and without recognizable neural or hæmal arches, pectoral or pelvic appendages, or teeth.

It is a remarkable fact that the descendants of the ostracoderms, in their several respective phyla, have independently acquired the same kind of organs, or they pass through similar phases of development. In other words, there appear to be present in the ostracoderms certain latent conditions that produce, sooner or later, the same results in their various descendants, long after the stock is broken up into separate phyla. For example, in all descendants of the ostracoderms the dermal skeleton tends to break up into smaller plates which ultimately disappear, leaving the skin naked. In the cyclostomes and in Amphioxus, the dermal skeleton probably disappeared at a very early period in their history. The same thing took place, but at a later period, in the holocephali; still later in the elasmobranchs, teleostomi, and amphibia. Teeth, pectoral and pelvic fins, neural

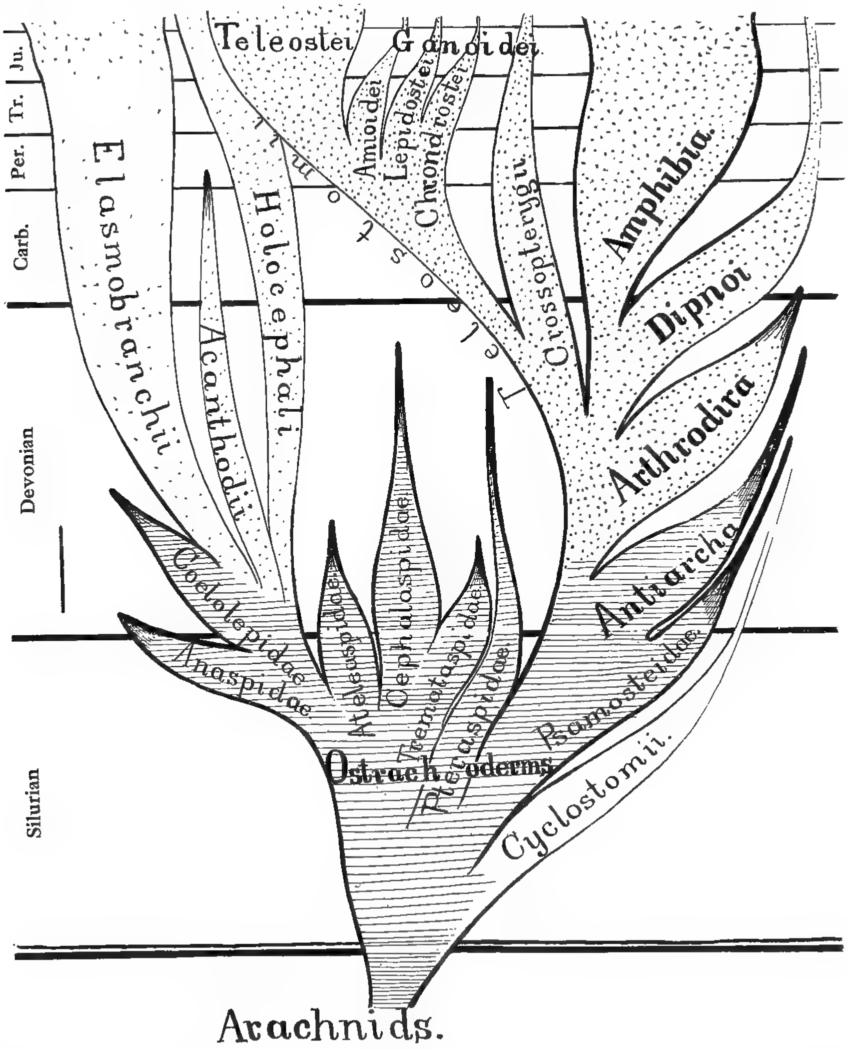


FIG. 258.—Diagram to illustrate the probable phylogeny of the arachnid, ostracoderm, vertebrate stock.

and hæmal arches, and vertebral centra are not recognizable in the ostracoderms, yet they make their appearance in the elasmobranchs, holocephali and teleostomi, in each case apparently arising independently of the other. There is also a well-marked tendency in all these three groups, or in their more remote descendants, for the lateral eyes, olfactory, and auditory organs, to become greatly enlarged; for the eyes and olfactory organs to take up a more lateral position; for the paired jaws to unite; the trunk and caudal segments to increase in number; the viscera and anus to take up a more caudal position, and for the dental plates and branchial chamber to disappear.

At some time, probably not later than the Silurian period, at least three or four well defined phyla grew out of the ostracoderms, as indicated in the accompanying table. (Fig. 258.) The main line of ascent probably leads from the typical ostracoderms, through the antiarcha and arthrodires, to the crossopterygians, dipnoi and amphibia. Evolution along this line is steady, comparatively rapid, and in every respect leads consistently upward to the first air-breathing land vertebrates, the culminating metamorphosis depending on remote antecedent changes in the dermal skeleton, appendages, air bladder, and heart.

The remaining phyla stand quite apart from this main stem. They are characterized by the breaking up of the dermal armor into minute plates (elasmobranchs) or by their absence altogether (the later holocephali); by the absence of an air bladder, branchial chamber, and leg-like fins. At no time in their history, so far as it is known, do they show any indications whatever of developing into air-breathing vertebrates. They do not possess the necessary anatomical structures, and their evolution takes them into quite other directions. The cyclostomes end in lampreys; the holocephali in chimæras, and the elasmobranchs in sharks and rays. We may characterize the several phyla arising from the ostracoderms as follows:

I. CYCLOSTOMATA.

The cyclostomes may be regarded as one of the earliest off-shoots of the ostracoderms. We may consider their chief characteristics under three heads, namely those derived from the ostracoderms, those gained, and those lost since their separation from them.

1. The cyclostomes retain the following organs derived from the ostracoderms: A median, practically unpaired, olfactory organ, merged with a persistent hypophysis that opens on the dorsal surface of the head. An uncommonly large and well developed parietal eye. The lateral eyes, on the contrary, are relatively small, and are very late in acquiring a functional union with the superficial ectoderm. Hence, except for the insignificant visual power possessed by the parietal eye, there is a long post-embryonic blind period corresponding to the permanent blind period in some of the earlier ostracoderms. It is explained on the assumption that the lateral eyes, during the ostracoderm stage in the phylogeny of the

vertebrates, had for the first time been forced into the brain chamber by the infolding of the medullary plate, and had not completely regained their functional relations with the outside world.

There are, in the adults of some genera, three pairs of oral arches provided with rudimentary appendages. The arches are comparable with the three pairs in amphibian embryos, *i.e.*, premaxillæ, maxillæ, and mandibles, and with the three dental-plate arches of adult ostracoderms and arthrodires. (Fig. 175.) The true mouth is not always circular, but may be a narrow, longitudinal slit. The oral region may be surrounded by a wide papillate fold of ectoderm that forms a shallow, circumoral antechamber, or pre-oral hood, comparable with the membranous folds on the free anterior edges of the dorsal and ventral shields of Bothriolepis.

The thyroid gland, which represents a liver-like diverticulum comparable with that on the hæmal surface of the thoracic gut in arachnids (Figs. 43, 44, 181, 182, 308), is very large, reaching here its maximum development in primitive vertebrates. The peribranchial chamber may be in part retained.

2. The cyclostomes have lost, probably at a very early period, their ancestral dermal armor, including the jaw plates; also the cephalic swimming appendages and lateral folds; and the tadpole-like form does not appear in any phase of their development.

3. The cyclostomes have failed to develop many important organs that have appeared in the other descendants of the ostracoderms. There are no paired pectoral or pelvic appendages; the notochord persists in a practically unmodified condition; no traces of ring-like calcifications of its sheath appear, and only the most diminutive neural and hæmal spines are developed. The air bladder and teeth of the vertebrate type are absent.

The actual progress made by the cyclostomes since their separation from the ostracoderms is therefore insignificant, the only noteworthy gain being in the increased number of body segments, giving additional freedom and facility of locomotion, and an imperfect adaptation to a parasitic mode of life. The cyclostomes may therefore be regarded as very ancient animals, deriving their underlying primitive characters from the ostracoderms, and owing the present simplicity of their organization to a precocious senility that was never preceded by a vigorous, creative youth.

II. The Elasmobranchii and Holocephali.

The Elasmobranchii.—The advent of the elasmobranchs is clearly foreshadowed in the Silurian period by the appearance of the cœlolepidæ with their fish-like form and shagreen-like armor. The successive steps in the fragmentation and final disappearance of the dermal armor are well shown in this branch of the ostracoderms. The process begins in the cephalaspidæ with the formation of well-marked, but immovable polygonal areas, followed by the appearance of the small free plates of Ateleaspis and Lasanius, and by the isolated dermal denticles of Thelodus and the elasmobranchs, which finally disappear altogether in their naked-skinned, modern representatives. The primitive elasmobranchs quickly acquired a fish-like form, losing the extensive ancestral peribranchial chamber, and at no phase of their development showing, so far as known, any trace of a tadpole stage.

The notochord, at an early period, is invested and largely replaced by well-developed cartilaginous centra, and an elaborate system of more or less calcified cartilaginous gill bars, and neural and hæmal arches is developed.

The lateral fold is generally retained for a longer or shorter period, giving rise by local enlargement to well defined pectoral and pelvic fins. The parietal eye is not conspicuously developed; neither are the three pairs of embryonic oral arches, nor the corresponding appendages. True teeth appear on the upper and lower margins of the mouth, but they are not preceded by any recognizable dental plates. An air bladder is absent.

The ova are very large, fertilized within the body, and the males are provided with highly specialized intromittent organs or claspers.

The elasmobranchs, owing largely to their well developed sensory and locomotor organs, and to their formidable jaws and teeth, developed rapidly in efficiency during the late palæozoic period, but they pass the climax of their evolution without producing a noticeably higher type of organization. While the internal skeleton may be highly developed and more or less calcified, it never develops into true bone.

The elasmobranchs are pelagic or deep water fishes rather than frequenters of the shallow brackish waters of the shore.

The absence of an air-bladder excluded the possibility of their becoming air breathers, and the pectoral and pelvic fins show no signs of developing into elongated, digitate appendages suitable for locomotion on land.

The Holocephali probably arose from the cœlolepid branch of the ostracoderms, developing along somewhat similar lines as the elasmobranchs, but retaining certain features of the parent stock not seen in the latter. The notochord is persistent, but enveloped by ring-like calcifications of its sheath more numerous than the cartilagenous neural and hæmal arches. They retain the large head and small trunk, or tadpole form, of the ostracoderms; a peribranchial chamber, and a short body cavity, with the viscera and anus placed well forward. Three pairs of dental plates are present, consisting of vascular dentine and growing from persistent pulps. They probably represent the premaxillary, maxillary, and mandibular plates of the ostracoderms and arthrodires, and belong to the three pairs of primitive oral arches seen in amphibian embryos. The general shape of the mouth and the form of the jaws resemble those of the ostracoderms and amphibian tadpoles rather than those of an elasmobranch. No true vertebrate teeth are developed.

The primitive characters above mentioned are those of the ostracoderms and are sufficient to distinguish the chimæras from all other adult vertebrates. But the cartilaginous internal skeleton, the large-sized ova, the internal fertilization, the anal claspers of the males, and the absence of an air bladder, indicate an affinity, although probably a remote one, with the elasmobranchs.

III. The Arthrodira, Teleostomii, Dipnoi, and Amphibia.

The antiarcha, at some time probably not later than the early Devonian. gave rise to the arthrodira. From the latter sprang the teleostomii and dipnoi, and from them, near the beginning of the carboniferous, the first air-breathing vertebrates, or amphibians from which, at some subsequent period, all the higher vertebrates had their origin, directly or indirectly. (Fig. 309.)

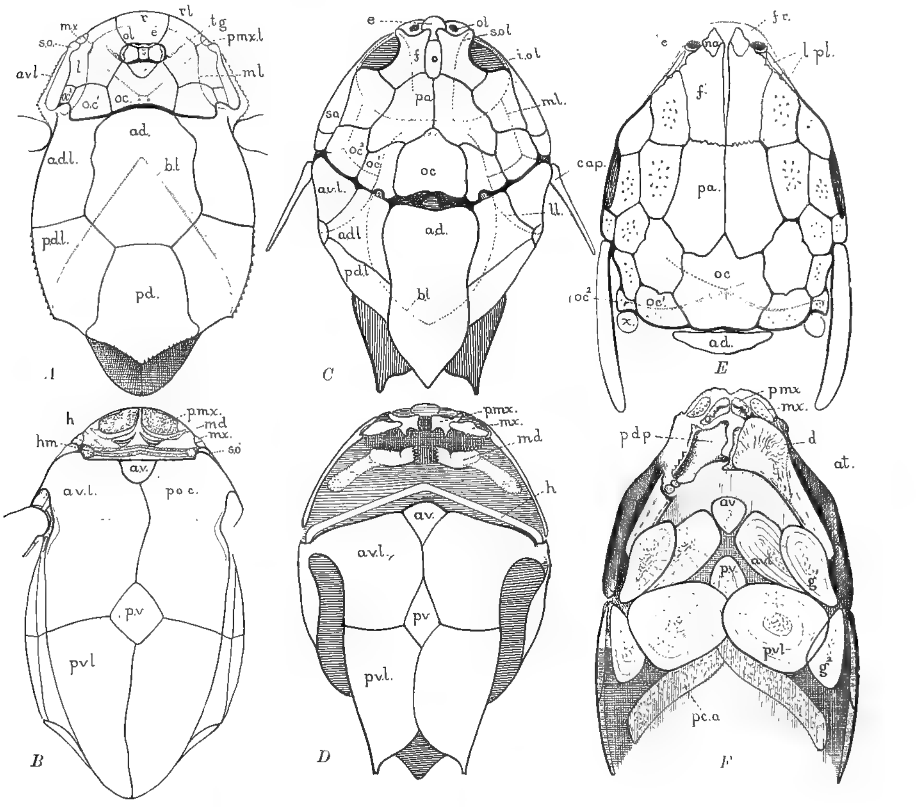


FIG. 259. FIG. 260. FIG. 261.

FIGS. 259, 260, 261. Figures illustrating three important stages in the evolution of the head and oral arches of vertebrates, as shown by an ostracoderm (Bothriolepis), an arthrodire (Coccosteus) and a primitive dipnoan (Scaumenacia). The important steps are: (1) the union of the three pairs of oral arches to form an unpaired upper and lower jaw, with denticulate jaw plates; (2) the separation of the olfactory organs and lateral eyes, and their migration to their typical position in vertebrates; (3) the breaking up, the reduction, and the more intimate union with the head, of the dermal armor to the visceral and respiratory organs, and their transformation into the opercular plates that cover only the respiratory organs.

C and *D* are semi-diagrammatic restorations, based on the descriptions of Dean, Traquair, Hussakof, and Jaeckel; *E* and *F* are restorations of Scaumenacia curta (Whiteaves), made from a large number of well preserved specimens in the author's collection. In *F*, the mandibular plate, *d*, is removed on the left, exposing the under surface of the large dental plate of the lower jaw, and the pre-maxillary and maxillary plates of the upper jaw.

These animals, the most vigorous and varied offspring of the ostracoderms, form a homogeneous stock that stands distinctly apart from all other primitive vertebrates. In practically all of them the ancestral dermal armor has a prolonged and flourishing existence, and is rarely, or never, entirely suppressed. In the more primitive groups it survives in the form of large superficial plates ornamented with low rounded tubercles, or with sinuous, beaded ridges. On the trunk and tail they are usually smaller, forming irregular, polygonal, or rounded scales which tend to sink deeper into the skin and eventually to disappear, leaving even in such primitive forms as Bothriolepis and some coccosteans a practically naked skin behind. But in the adults of all branches of the phylum a considerable number of the ancient, large-sized cranial plates are retained in the head region, forming a characteristic covering for the roof and sides of the head, jaws, gill chamber, and pectoral arches. With this prolonged survival of the primitive dermal armor, there is an early and vigorous development of an endoskeleton, consisting of true bone, which here makes its appearance for the first time in the history of the animal kingdom.

A bony floor and sides to the endocranium are formed, as well as complete bony vertebræ consisting of centra intimately united with neural and hæmal arches and transverse processes.

A large peribranchial chamber is always present, but the rigid, armored walls of this chamber, so characteristic of the ostracoderms, are greatly shortened in the arthrodires, and in the teleostomes, dipnoi, and amphibia, give place to membranous folds that may or may not be strengthened by movable opercular plates.

Three pairs of oral arches are usually conspicuous in the embryonic stages, and the branchial arches may retain remnants of arachnid appendages, in the form of external gills, hyoidian "balancers," oral arch papillæ, tentacles, or adhesive discs.

The parietal eye is generally well-developed, and so far as known, a large, lung-like air bladder occurs in all the main subdivisions of the phylum. The primitive pectoral and pelvic appendages may be narrow and elongated, with a bony internal skeleton that in the earliest fish-like descendants of the arthrodires shows, for the first time in the evolution of the vertebrates, distinct traces of the radiate terminal digits, and the jointed axis characteristic of all primitive land vertebrates (Eusthanopteron. Fig. 265.)

The ova are of moderate size, frequently covered with an adhesive, gelatinous substance, and are generally fertilized externally. The antiarcha, coccosteans, dipnoi, and primitive teleostomes were preeminently shallow water, shore-loving forms, as are their survivors to-day. Their highly developed air bladder, leg-like fins, specialized breeding habits, and the general structure and mode of life characteristic of the higher members of this phyla, afford an easy anatomical and physiological transition to the amphibia, and hence to the higher air-breathing land vertebrates.

On the other hand, the young of many amphibia, dipnoi and, teleostomes pass through a larval, or tadpole, stage generally characterized by a large head, by the presence of rudimentary appendages on the oral and branchial arches, by a small mouth with a feeble lower jaw, short body cavity and slender tail, and by the absence of postbranchial paired appendages. This tadpole larva is clearly the recurrence of the ostracoderm stage in their phylogeny. (Fig. 167.)

The Arthrodira.—The arthrodires closely resemble the ostracoderms in the structure of their jaws and in the arrangement of their cranial plates, and without doubt are directly descended from them. While it is not possible to identify in detail all the various structures involved in the general resemblance that runs through them all, we can trace a progressive series of structures and events that lead steadily upward from the ostracoderms, through the arthrodires, to the vertebrates.

Without entering into a detailed discussion of the arthrodires, an examination of Coccosteus, a fairly well-known and typical representative, will show us the more important respects in which they approach the vertebrates.

In Coccosteus (Figs. 260, 263), the central aggregate of procephalic sense organs seen in the ostracoderms has separated. The lateral eyes have increased greatly in size and have taken up an antero-lateral position, losing apparently some of their dermal armor and their power to rise and fall in the orbits; the parietal eye is lodged in a small median plate, located in about the same position as before, while the olfactory organs have moved forward and laterally, occupying a more nearly terminal position.

Jaws.—Three pairs of jaws are present. The premaxillæ are relatively smaller than in the ostracoderms, and although still distinctly paired, are less freely movable in a transverse direction. The rudiments of toothed maxillæ are present, for the first time, as small free plates that probably represent the small ventrolateral plate of Bothriolepis. The mandibles have increased greatly in size and may be provided with prominent tooth-like spikes on their anterior and median borders, being in this respect more like arthropod jaws than those of Bothriolepis, the only ostracoderm whose mandibles are known. Like the ostracoderm mandibles, they were capable of very complex movements. Both ends were free; that is, they were not firmly articulated to any cartilage or bone, and could be either rotated, or moved in a transverse and longitudinal direction. Their exposed median ends were probably held in place by the integument, while their lateral ends were buried in the tissues of the head, and served for the attachment of the sinews and powerful muscles that controlled their movements.

A single hyoid arch (Fig. 260, *h*), covered with dermal bone, extended across the throat behind the mandibles, in place of the two arches of similar structure seen in Bothriolepis.

The cranial bones are more numerous than in the antiarcha, owing probably to the breaking up of the large orbital plate by the lateral migration of the eyes. The same movement has probably opened the way for the formation, for the first time, of a supra-orbital line of cutaneous sense organs.

The branchial shield retains nearly the same number and arrangement of plates as in the ostracoderms, but it is greatly reduced in size, and deeply incised on the flanks, thus opening up the peribranchial chamber. It thereby takes on more distinctly the character of a true operculum, and apparently serves solely for the protection of the gills and heart, the digestive and urogenital organs taking up a position farther back, wholly posterior to the respiratory region, as indicated by the large size of the postbranchial section of the trunk, and by the probable location of the cloacal opening.

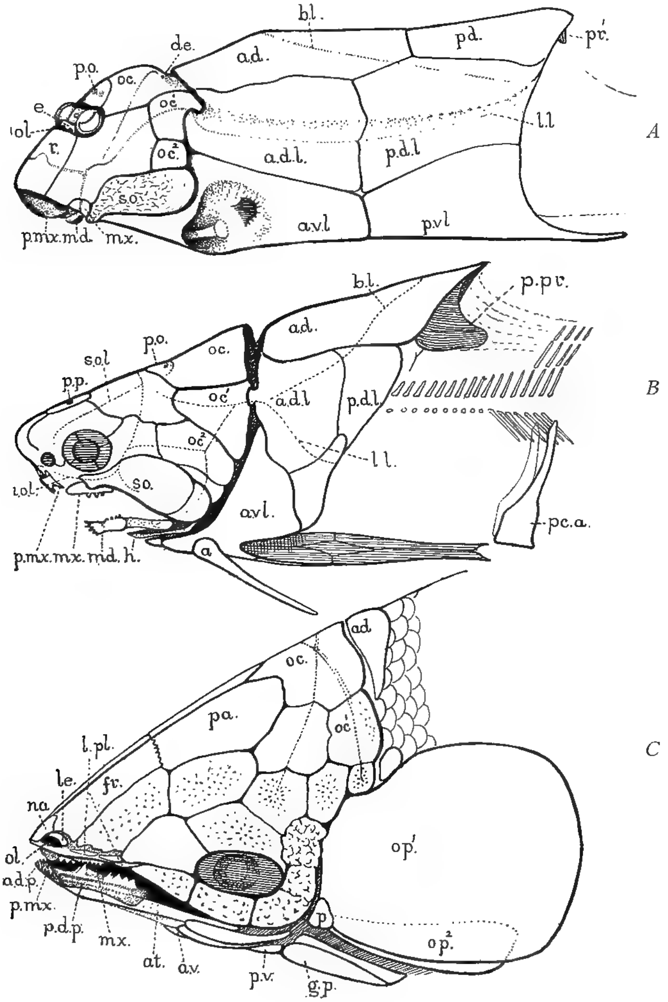


FIG. 262, 263, 264.—Side views of the heads of: *A*, Bothriolepis; *B*, Coccosteus; and *C*, Scaumenacia curta, Whiteaves. In the latter, the outer part of the left mandible has been omitted, exposing the large mandibular dental plate and the row of minute teeth on the anterior margin of the mandibles.

In probably all arthrodires, the notochord persisted throughout life with little or no change. Although there are no indications of vertebral centra, we see for the first time a well-developed series of neural and hæmal arches, the forerunners of a true vertebral column.

The cephalic appendages, *a*, that were so characteristic of the ostracoderms, are here rudimentary and probably functionless. With the relative decrease in the size of the head and the increase in the size of the trunk, the whole body is better balanced and more suitable for an active, free swimming existence. Locomotion was probably effected largely by the flexible trunk and tail, although immediately behind the branchial region there are traces of supports for small pectoral fins, the first appearance in this phylum of paired appendages of the vertebrate type. Pelvic fins were apparently absent.

The arthrodires clearly represent a higher type of animals than the ostracoderms. They have successfully emerged from the precarious period of profound metamorphosis in which the ostracoderms were engaged. While it lasted, an active life was inhibited by the changes going on in the old organs, and by the imperfect adjustment of the new.

With the arthrodires that period is past. They have increased notably in size; the eyes are fully adjusted to their new location within the neural tube; the mouth has become capacious, and the jaws large and powerful, with formidable cutting, or toothed margins, well suited for capturing and devouring animal food; the respiratory region is set apart from the digestive and urogenital regions, and the body is better balanced and better adapted for an active, free swimming life. The arthrodires, therefore, quickly developed from the sluggish, plant-eating stage of the ostracoderms, into the most active, rapacious, and formidable animals of their time. But as a class they were short-lived, for the structural conditions within had as yet attained only a temporary equilibrium, and the new mode of life was rapidly producing new creative forces. Out of these conditions arose the first true vertebrates of this phylum, the dipnoi and the teleostomes.

The anatomical changes involved in the creation of the new types of animals were comparatively insignificant. The head became relatively smaller and more compact, the trunk larger, and the whole body assumed a more fish-like appearance. (Figs. 261–264.) The lateral eyes grew still larger and took up a position on the sides of the head, well behind the olfactory pits, which have also greatly increased in size. The premaxillæ fused, forming the fronto-nasal process, and together with the maxillæ became permanently fixed to the floor of the cranium. The distal ends of the mandibles united in the median line, and their proximal ends articulated with a cranial cartilage, to which the hyoid arch was also attached; they then lose their rotary and transverse movements, and swing forward and backward against the maxillary arch in typical vertebrate fashion.

With the fusion in the median line of the three pairs of oral arches, their dermal armor becomes the three pairs of fixed dental plates characteristic of the dipnoi (Fig. 261, *p.mx,mx.d.p.*), and from which the isolated socketed teeth of the higher vertebrates arose.

The plates in the dorso-lateral walls of the primitive branchial shield now form movable opercula, and those in the ventral wall become attached to the mandibular and hyoid arches to form the gular plates.

The dermal plates on the dorsal surface of the head (mesocephalon) increase in number, and approach the typical arrangement seen in the primitive air-breathing vertebrates. The base of the endocranium becomes ossified; bony centra appear in the sheath of the notochord and, uniting with the neural and hæmal arches, form true vertebræ.

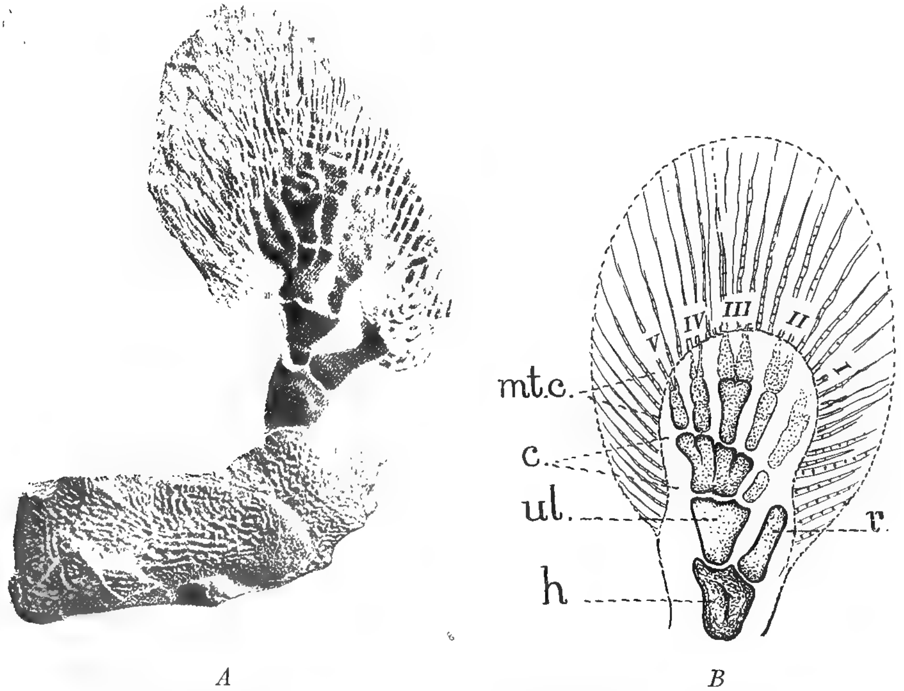


Fig. 265.—Photograph of the left pectoral appendage of Eusthanopteron fordi (Whiteaves). The skeleton of the basal portion of the appendage was exposed; that of the terminal portion was apparently covered by skin which has shrunken sufficiently to show the arrangement of the internal skeleton. The skeleton of this appendage resembles that of the land vertebrates, and indicates the way, as shown in *B*, in which the typical skeleton of the pectoral appendage of the tetrapoda has been derived from the biserial pectoral fin of fishes. (From specimen in the authors collection from Scaumenac Bay. P. Q., Canada.)

The pectoral fins enlarge and the girdle extends dorsally, uniting with the occipital portion of the cranium.

Within the pectoral fins, for the first time in the phylogeny of the vertebrates, appears an axial skeleton that approaches, in the arrangement of its elements, the characteristic structure of the appendages of the land vertebrates, *i.e.*, Eusthenopteron. (Fig. 265.) Pelvic fins appear in the anal region.

* * * * * * * * *

Thus the broad foundations for the evolution of the first air-breathing land vertebrates is laid in the dipnoi and ganoids, the armored fishes of the upper

Devonian; reaching down through them to the arthrodires and to the ostracoderms of the Silurian, and then again beyond them to the merostomes, trilobites, and primitive phyllopods of the Ordovician, Cambrian, and Proterozoic.

In this vigorous phylum, evolution follows a logical and consistent course, each important event being the direct, or indirect result of the preceding ones, and they themselves creating the conditions that bring about those that follow. The various independent sets of organs, such as the brain, sense organs, appendages, jaws, internal and external skeleton, in their own peculiar ways move steadily onward toward the same end, in a manner that could hardly be possible except in a real, not an imaginary, line of evolution. The perfection with which these immensely varied and complicated facts and details fit together to form a definite, intelligible picture, carries with it the overwhelming conviction that that picture is an image of the truth. The precision with which each event creates again and yet again, new conditions, new organs, and new readjustments, shows that the primary forces that sustain and direct the main lines of evolution are self-creative, and lie within, not without, the organism.

PART II. THE ACRANIATA.

CHAPTER XXII.

THE CRANIATES AND THE ACRANIATES.

The Statement of the Problem.—One of the chief difficulties in the study of the origin of vertebrates is to correctly estimate the value of contradictory evidence and to assign due weight to opinions based on a particular point of view, or on a particular source of information. Thus Amphioxus, Balanoglossus, Cephalodiscus, the tunicates, echinoderms, and annelids have been variously exploited as the ancestral stock from which the vertebrates arose, and each view has had its followers that from time to time have openly confessed their faith and duly readjusted their estimates of morphological values.

From the very outset the analysis of the vertebrate head and trunk by means of comparative anatomy and embryology seemed to demonstrate that the ancestral vertebrate was an elongated animal composed of many like metameres, each one consisting of sharply defined members of the more important system of organs, *i.e.*, nephridia, neuromeres, myotomes, sense organs, gut pouches, and gill clefts, thus suggesting the condition so clearly presented by many annelids. For many years, therefore, Amphioxus was regarded as the most primitive existing vertebrate, because its simple structure and the sharply defined segmentation of its mesoderm, gill clefts, and other organs, appeared to represent the actual embodiment of the ideal vertebrate. But the organs that are the first to show a metameric arrangement in the invertebrates, and the ones to maintain it most persistently, such as the appendages, sense organs, and nerve cords, were in Amphioxus either absent or without any indication of segmentation.

The fact that in typically segmented invertebrates, such as the arthropods and annelids, the nerve cord nearly always consists of sharply defined and widely separated ganglia, or neuromeres, while in Amphioxus little or no indication of such a condition is visible, occasioned little comment, while much was made of the segmental arrangement of the myotomes, gill clefts, and later of the nephridia.

When it was shown that the development of the tunicates was very similar to that of Amphioxus, and that the tunicate larva had a well defined notochord, which later disappeared during a process of degenerative metamorphosis, the problem was greatly complicated, for the tunicates clearly belonged to a lower type structurally than Amphioxus, yet they were farther removed from the hypothetical, ideally segmented ancestor of the vertebrates than either Amphioxus or any of the true fishes.

The clue was apparently leading in the wrong direction, into the darkness rather than into the light, and the problem was by no means simplified when it appeared, more and more clearly, that Balanoglossus resembled Amphioxus and the tunicates in certain important particulars, especially in the structure and development of the cœlom and gill clefts, while its larva resembled that of the echinoderms.

Again the problem was still further complicated by the discovery of Cephalodiscus and Rhabdopleura, at first supposed to be related to the polyzoa, and consequently suspiciously close to the brachiopods, but later very generally recognized as also related to Balanoglossus, and hence in some way involved with the tunicates and amphioxus, which outwardly they did not in the least resemble. An amphioxus-balanoglossus-like animal with six pairs of legs, such as those of Cephalodiscus, was perforce accepted without a grimace, although it was not very readily assimilated.

The trail was leading well down toward the roots of the animal kingdom, but certainly not toward anything like a worm-like ancestral form composed of many well defined, similar metameres. The evidence that was accumulating, while in some cases more concrete than that produced in the earlier history of the problem, became less convincing. It led in too many directions, and was forcing morphologists at large to accept conclusions against which their better judgment rebelled, but from which there was apparently no escape. While many preferred to doubt the evidence rather than accept the conclusions, or even began to lose faith in the efficacy of comparative embryology as a means of solving large problems in phylogeny, others, with commendable loyalty, adhered to the particular faith in which they had been educated, and advocated it with sufficient ardor, at least until the next hypothesis appeared. But as the number of attractive theories increased, the older morphologists apparently concluded that it was wiser to accept neither one nor the other, and to beware of them all. It was perhaps realized that one might live very happily wedded to one view, if it was not for the others; for it was increasingly evident that embracing any one theory created more difficulties than were overcome, since each rejected one was then sure to look more formidable than ever.

However, our new hypothesis is not open to these objections, for in accepting the arachnid theory we shall have the privilege of adopting into our household, as her children, many of the other attractive theories that have from time to time won our affection. The arachnid theory opens the way to a reconciliation of the conflicting views above indicated. It offers a solution that is logical, consistent with the facts, so far as we know them, and in harmony with the basic principles of morphology.

In brief, we recognize two great groups of animals that have independently acquired some of those characters commonly associated with the chordata. Both groups are descended exclusively from primitive arthropod stock, that is, from small bodied animals of a small number of ill defined metameres (resembling a nauplius or an ostracode) and which in turn were derived from rotifer-like trochozoans. Neither the annelids nor any other worm-like forms were included in this stock. (Fig. 309.) The first group, the syncephalata, includes together with other arthropods, the phyllopod-arachnid-ostracoderm-vertebrate phylum, or the craniata; the second group, or the acraniata, includes the cirripeds, tunicates, Amphioxus, echinoderms, enteropneusta, pterobranchia, phoronida, polyzoa, chætognatha, and brachiopods.

Our problem is in a measure clarified, and at once assumes an entirely new aspect, as soon as we recognize that the chordata consist of several phyla derived from the arthropods via as many separate lines, and that some of the striking features in which they resemble one another were independently acquired. We associate, for example, Amphioxus, Balanoglossus, and the tunicates with the vertebrates because of their notochord, perforated gill slits, hæmostoma, and atrial chamber. But, as we have already seen, these basic characters, in one form or another, are actually, or potentially present in all primitive arthropods, and presumably, they may be expressed in all their descendants, although, perhaps at different times, and in varying ways, in different phyla.

The assumption that several independent caudate phyla have arisen from the arthropods is of two-fold value, for it enables us to explain why the tunicate-balanoglossus group resembles at the same time both the arthropods and the vertebrates, without being in the direct line of vertebrate descent; and it enables us to attach these heretofore isolated and obscure phyla to the great trunk line of organic evolution, and to thereby obtain a new basis for the interpretation of their morphology.

Let us first consider in a summary way the more important features of these two great groups.

The Craniates.

We have shown in the preceding chapters that the trunk line of vertebrate descent runs through the dipnoi-arthrodire-ostracoderm-arachnid-phyllopod stock, which almost from the very outset consisted of highly specialized segmented animals. Primarily they were neither sessile nor parasitic, but large, vigorous free swimming forms with highly developed nervous system, sense organs, cephalic appendages, and paired jaws. They were often, at times predominantly, frequenters of the warm littoral, of fresh or brackish waters, and of the land. At every stage of evolution, with a few notable exceptions, the animals that constituted the advancing crest of this stock have been on the whole the largest, and the most active, the greatest consumers and spenders of energy, the most highly organized, the most progressive and innovating, and the most widely distributed animals of their day and generation.

They had a chitenous, dentine-like exoskeleton, a cartilaginous endocranium, gill cartilages, middle chord, gill sacs, voluminous enteric diverticula, a trioccellate parietal eye, frontal, or olfactory sense organs, and compacted cephalic neuromeres. The vast majority of them were free moving forms during their early post embryonic, and adult stages. Their highly specialized appendages, well developed sense organs, and neuro-muscular systems enable them to execute varied movements with great precision in response to exceedingly complex surroundings; they were the first animals to acquire an effective response to stimuli of distant origin, to perceive the intangible, to pursue, and to capture. Their eggs contained a large quantity of yolk, and the embryos did not leave the egg till they had attained an advanced stage of development.

In this phylum the theme was metamerism. Progress was first attained by perfecting metamerism, later by its suppression or elimination. The larger possibilities of this type of structure were practically exhausted in the arthropods, and it had already entered another phase before the critical period arrived that was to give rise to the vertebrates. During the early history of the phylum, progressive evolution was effected by a gradual increase in the number of metameres, and by gradually increasing the perfection, or the fullness and precision with which metamerism was expressed. Metamerism then began to decline, owing to the local exaggeration, suppression, and fusion of organs. This process was most strongly marked at the anterior, or older end of the lengthening series of metameres, thus leading to the formation of an extensive and extremely complex head region, to a new linear arrangement of unlike organs and functions, and to the production of a higher and more unified type of organization than has been attained in any other phylum of the animal kingdom.

The formation of new metameres at the caudal end, and the specialization of the older ones at the cephalic end, on the whole proceeded simultaneously, so that at no stage in the evolution of the phylum did the body consist of a long series of like metameres. Only a few metameres, if any, ever approached a condition of ideal perfection, that is, one containing all the so-called segmental organs. Serial homology in the craniate phylum is, therefore, necessarily imperfect, and the organs at one end of a series are never fully comparable with those at the other.

II. The Acraniata.

The second great group of animals with arthropod affinities constitutes the acraniata. It may be called the cirriped division of the arthropod stock, for the cirripeds appear to form its central figure, and because many of the more striking features of the various sub-phyla are most clearly expressed in the cirripeds. We include in the acraniata, the cirripeds, tunicates, Amphioxus, echinoderms, enteropneusta, chætognotha, pterobranchia, phoronida, polyzoa, and brachiopoda, all of which, with the exception of the polyzoa, are exclusively marine. They are all derived from cirriped-like forms, or with them, from ostracoda, or small nauplius-like arthropods that consisted of a small number of imperfectly developed metameres. They form more or less independent subphyla, in no way directly united with the vertebrate stock, and in no sense to be regarded as the ancestors of the vertebrates.

From every point of view, and from every point of departure, the evidence leads more and more decisively to this conclusion. The vertebrates, however far back we may go, do not lead to the acraniates, and the acraniates do not take us back to the same stock as that from which the vertebrates arose. Indeed all the acraniates are chiefly notable for the absence of those very structures and modes of growth so characteristic of the craniates. In the acraniates a different set of organs are emphasized, and the general direction of evolution is different.

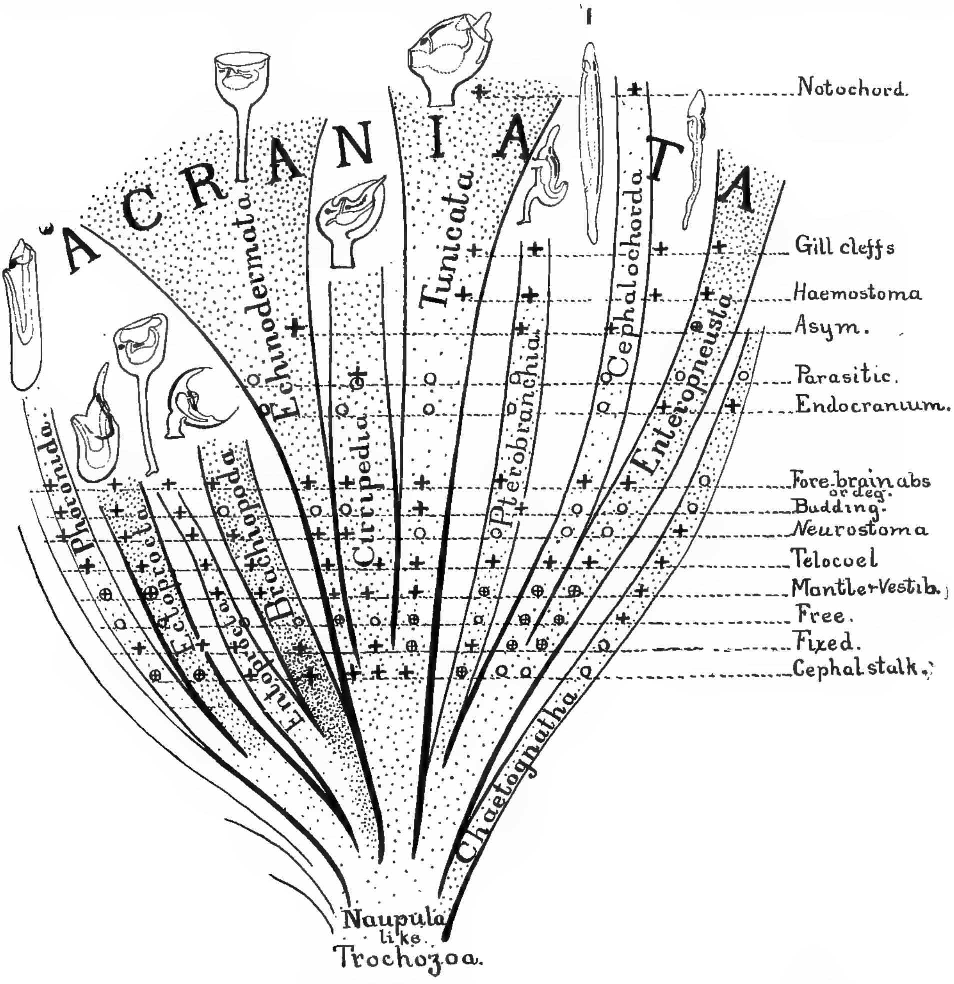


FIG. 266.—Diagram to illustrate the probable interrelations of the acraniata, and their origin from a small nauplius-like arthropod ancestor. The characteristic shape of each division and its normal orientation to its point of attachment is indicated. The neural surface may be identified by the brain and nerve cord, in black. The principal characters of each division are indicated by the presence of a + or o sign opposite the descriptive term on the right. When a character may be either present or absent, or doubtful, the plus sign is enclosed in a circle. The more specialized characters stand, as far as practical in such a diagram, at the top of the list.

In every subphylum metamerism is suppressed, the structure simplified, and evolution has of necessity led toward a less active, less complicated mode of life; in fact, farther and farther away from the characteristic condition in the craniate stock, rather than nearer to it.

* * * * * * * * *

The chief characteristics common to the exceedingly heterogeneous group of sub-phyla constituting the acraniates may be defined as follows:

Metamerism.—The metameres are few in number, except in Amphioxus, and are rarely if ever sharply, or fully defined. Even when the metamerism is fairly well expressed in the younger stages, it degenerates or becomes greatly obscured, or it may disappear altogether in the adult (cirripeds, tunicates). Whether this is a true degeneration, or merely a special form of development, is a matter of definition. It is certain, however, that the possibilities of the metameric type of structure, so fully realized in the arachnid division, are never realized here.

There is no organic union of specialized metameres to form a compound head, although in the cirripeds we may recognize one or two pairs of temporary antennæ, three pairs of jaws, and five or six pairs of abdominal appendages, indicating the division of the body into tagmas, corresponding approximately to the procephalon, mesocephalon or thorax, and metacephalon or branchial region of the arachnids. (Fig. 275.) In the cirripeds, the primitive head and thorax are the first to lose their metameric structure, the only indication of it left in the adult being the jaws, and even these may disappear.

The main divisions of the body, but with little or no indication of their further subdivision into metameres, are recognizable in the other sub-phyla as the proboscis, the collar, and branchial regions (Amphioxus, enteropneusta, pterobranchia); or they are probably represented merely by the principal subdivisions of the cœlom seen in the ectoprocta, phoronida, chætognatha, and echinodermata.

The appendages are always simple in structure, stub-like, tentacular, or altogether absent. Their serial identity is only vaguely indicated, but we may recognize the rudiments of procephalic appendages, probably corresponding to the antennæ of cirripeds, copepods, and other crustacea, in the adhesive papillæ of the tunicate and echinoderm larvæ, and possibly in the tentaculate arms of ectoproctous polyzoa, brachiopods, rhabdopleura, and phoronis.

The five primordial tentacles of the echinoderms probably represent a group of thoracic, or abdominal appendages (Figs. 291–295); those of Cephalodiscus and the entoproctous polyzoa represent the thoracic, or both circumoral and abdominal groups. (Figs. 299–301.) The appendages may be absent from the outset, or if present they may disappear completely in the adult. After the larval period, they are never used as locomotor organs in any member of the group. In the chætognaths, the cephalic appendages have the appearance of typical arthropod oral appendages.

The nervous system is always small, exceedingly simple and primitive in structure. Sense organs, such as visual and auditory organs, are absent, or very rudimentary. Even in the cirripeds, the lateral and parietal eyes of the larva quickly disappear, or become functionless. Only in a few tunicates does the parietal eye function to any extent in the adult. A neuro-muscular apparatus, capable of elaborate or varying responses to external stimuli, is never present.

The mode of life is rigidly prescribed by these conditions. The absence of armored grasping appendages, of well developed sense organs, and of a complex neuro-muscular apparatus, excludes the possibility of elaborate reflexes, of perception at a distance, of pursuit and capture. The inevitable result has been the practically universal adoption of either a sessile, a subterranean, or a parasitic mode of life, depending for food on micro-organisms, or on other finely divided matter sifted from water or soil, or on fluids absorbed from other animals.

Degeneration.—There is a strong tendency in the entire group toward a retrograde or degenerative development, that appears to be due to some prevalent lack of adequate internal conditions or of materials. It makes its appearance during, or shortly after the larval stages, cutting down the first promises of a clear cut, vigorous organogeny to one that is feeble, blurred, or defective in definition; or one in which important parts are absent. It may manifest itself in the absence of structural detail, in diminished local outgrowths, or in the absence of appendages (Amphioxus, enteropneusta, tunicates, chætognaths). It is seen in the degenerative metamorphosis of tunicate larvæ; in the reduction in size, or absence of organs, so common in male cirripeds; and in the progressive disappearance in many parasitic cirripeds of both sexes, of mouth, anus, appendages, nervous system, and alimentary canal; in fact, of practically everything except the integument and reproductive organs.

In some cirripeds (rhizocephala), this process is carried so far that if it were not for the presence of the characteristic appendages in the larvæ, their identity would be exceedingly difficult, perhaps impossible, to determine. We have merely to assume that the suppression of appendages has been carried a step further back in the ontogeny, to account for their total absence in Amphioxus and the enteropneusta.

In the rhizocephala, the parts of the body left after the extensive degeneration of organs, and the casting off of the abdomen, acquire a new, almost unlimited power of growth, forming extensive, root-like processes that penetrate in every direction the tissues of its host. In the ectoprocta, there is also an extensive degeneration of organs, similar to that in parasitic cirripeds. That is, the nervous system, appendages, and alimentary canal disappear, or fail to develop, and from the apparently formless remnants, strangely enough, buds are formed, destined to give rise to new and more perfect zoids. It may be that there is some relation between the degenerative, or retrograde development of the tunicates, pterobranchia, and polyzoa, and this retention and renewal of the power of budding.

Attachment.—We have seen that many phyllopods are temporarily attached to foreign objects by means of a sort of sucking or adhesive disc on the hæmal side of the head. Many parasitic copepods and cirripeds are permanently attached in this manner, aided by a pair of modified appendages that have moved round onto the hæmal side of the head. In cirripeds the larva attaches itself, head first, neural side down; it then turns a forward handspring on its rudimentary adhesive antennæ, bringing the neural side up; meantime an enormous outgrowth develops from the hæmal surface of the head, forming the peduncle by which the animal is permanently attached. (Fig. 274.) This extraordinary mode of attachment, accompanied by the same peculiar rotation and cephalic outgrowth, occurs with but slight variation in the tunicates, echinoderms, pterobranchia, phoronida, polyzoa, and brachiopods, in fact in every subdivision of the acraniates except Amphioxus, the enteropneusta and chætognatha.

Mantle.—Before the young cirriped becomes attached, the valves of the thoracic shield make their appearance as a longitudinal circular fold. The free edge of the fold gradually extends toward the neural surface, enclosing the body and appendages in a large vestibular, atrial, or branchial chamber. (Figs. 289, 281.) A similar mantle forms a familiar and conspicuous feature in the larval and adult stages of the tunicates (Figs. 284–286), echinoderms (Figs. 291, 295), polyzoa (Fig. 301), phoronida (Fig. 305), and brachiopods (Fig. 304). In the polyzoa and echinoderms, the vestibule may develop very early as a closed chamber; but it is soon ruptured by the growing appendages within, which then protrude through the opening in the same manner as those of a cirriped. In the enteropneusta the mantle consists of two longitudinal pleural folds that form an imperfect branchial chamber. (Fig. 298.)

The rudimentary mantle fold is a conspicuous feature of the larvæ of cirripeds, echinoderms, enteropneusta, polyzoa, phoronida, and brachiopods. Its free margin may be drawn out into characteristic projections or lobes, that, heavily ciliated, form the primary longitudinal ciliated band characteristic of the naupula. It should not be confused with the transverse ciliated band characteristic of the trochophore larva. (Figs. 267–296.)

Skeleton.—An endocranium occurs only in the enteropneusta and chætognatha. In the enteropneusta it consists of a low grade fibro-cartilage, probably of mesodermic origin, and comparable with the primitive endocranium of the phyllopods. See page 312. No neural or branchial cartilages appear, but in Amphioxus and the enteropneusta, a complicated framework of chitenoid gill bars supports the margins of the gill clefts and the tongue bars.

The exoskeleton may consist of a voluminous chitenoid, celluloid, or gelatinoid secretion of the ectoderm; it is not shed at regular intervals, as in the arthropods, but is retained throughout life. The only exception appears to be the appendicularia, which often shed their enormous "gelatinous house" soon after its formation. It may be heavily calcified, forming characteristic polygonal plates, and greatly complicated by epidermal folds and channels containing vascular or other tissues (cirripeds, tunicates, brachiopods).

The Heart and Circulation.—In the acraniates the heart and the vascular channels are feebly developed and may be altogether absent or unrecognizable. There is no definite vascular system in the polyzoa and chætognatha; and a distinct heart is absent in cirripeds, Amphioxus, the phoronida, and the echinoderms; it exists, if at all, in a highly modified condition in the enteropneusta and pterobranchia. In the tunicates and brachiopods a small, oval heart is present. In the ascidians it is a small fusiform tube, unsegmented and valveless, and composed of epithelio-muscular cells. Its cavity is derived from the so-called blastocœle and it is enclosed in a pericardium derived from the cœlom. In these respects, and in respect to its location, the distribution of the principal blood channels, and in its mode of development, it resembles the "heart" of phyllopods. The tunicate heart is notable for its "reversing circulation," that has been regarded as something unique in the animal kingdom; but a similar phenomenon has been observed by Scott, in the parasitic copepod Lepeophtheirus. See page 418.

The Sexual Organs.—Both ovaries and testis may be present in the same individual. In the cirripeds, the testis usually occupies the posterior part of the trunk, opening to the exterior at the apex of the caudal lobe. The ovaries are lodged in the cephalic region, extending also into the peduncle and mantle folds, and even into the recesses of the exoskeleton. The oviducts open outward near the middle of the body, at the base of the first pair of abdominal cirri. (Fig. 275.) In the tunicates a similar condition may prevail, *e.g.*, in Polycarpa, where "there are many complete sets of both male and female systems attached to the inner surface of the mantle, on both sides of the body." Moreover embryonic "kalymmocytes," or egg follicle cells, frequently pass through the ectoderm into the cellulose test, suggesting a former connection with the mantle, like that in cirripeds.

In the brachiopoda there are two pairs of genital glands, both pairs located in the mantle, one in the anterior fold, the other in the posterior. The genital cells are usually discharged by a pair of nephridia-like ducts that open on the neural surface near the middle of the body, or just behind what appears to represent the thoracic region; chætognatha, pterobranchia, polyzoa, brachiopods, phoronida.

The germ cells of arthropods may make their appearance as the so-called pole cells at a very early period, before any germ layers are recognizable. In parasitic copepods, they arise from the undifferentiated blastoderm, and later form a small but conspicuous cluster of cells on the neural surface, between the abdominal and thoracic neuromeres. (Fig. 242.) In the chætognatha and polyzoa, the germ cells are conspicuous at an early period in a corresponding position. (Figs. 301, 306.)

Development.

It will be necessary to abandon, or greatly modify some deep-rooted conceptions as to the significance of the germ layers and early embryonic processes in segmented animals, for they are based either on errors of observation, or upon a too literal interpretation of the phenomenon of embryonic growth in terms of adult cœlenterates. There is little or no foundation for the prevalent assumption that the blastopore elongates, closes in the middle, leaving a mouth at one end and an anus at the other. On the contrary, segmented animals elongate primarily by a localized apical growth, never by stretching a gastrula lengthwise. Neither the mesoderm nor the notochord ever helped form the walls of a primitive, functional, alimentary canal, with the mesocœle opening into the enterocœle.

The principal source of confusion in the interpretation of these fundamental processes has been the failure to recognize the difference between a true gastrula and a mesentocœle, between a trochosphere and a naupula, neurostoma and hæmostoma, or the hæmal and neural surfaces; and in assigning a fictitious and artificial significance to the so-called "archenteron" and "cœlomic pouches." We base our conclusions on the following assumptions, that we regard as axiomatic.

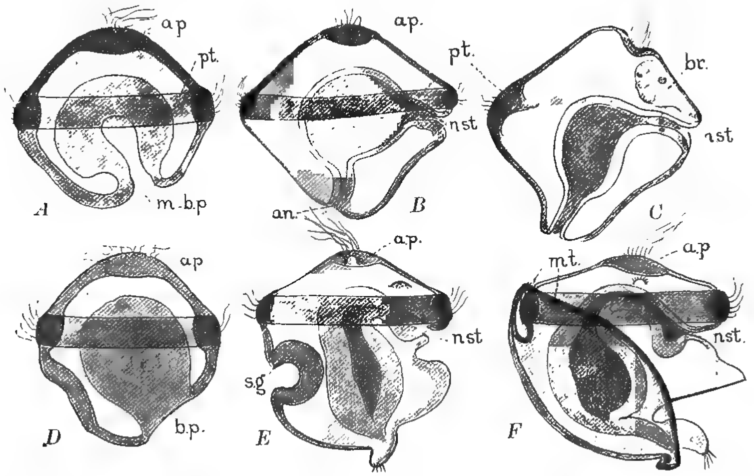


FIG. 267.—*A*, *B*, *C*, Diagrams of an annelid larva in the trochosphere, or coelentreate stages, showing the relations of the gastrula, blastopore, mouth, and anus to each other; also the origin of the trunk, as an outgrowth from the primitive head; *D*, *E*, *F*, same of a molluscan larva.

1. The fixed point in all morphological problems is the central nervous system. When it is located, and its direction of prolongation determined, we may identify the six sides of any bilaterally symmetrical, acrogenous animal, and approximately locate the characteristic organs of each side. 2. In all bilaterally symmetrical animals, the primitive mouth, or neurostoma, and the neuron, or axial cords of the central nervous system, are always laid down on the same side of the body, or egg, *i.e.*, the neural surface. 3. The neural surface increases in length primarily by apical growth at the anal or posterior end of the principal axis. 4. The right and left sides of the body are formed as lateral outgrowths from the principal axis, the growth and differentiation being in a neuro-hæmal direction. 5. The primitive mouth, or neurostoma, always lies between the anterior ends of the lateral cords. 6. The anal or caudal end of the body is always the youngest,

the cephalic or oral end the oldest. 7. The neural surface of the embryo is laid down and differentiated earlier than the hæmal surface, the difference between the time of formation and the amount of specialization in the two surfaces being governed largely by the volume and distribution of the yolk mass. See Chapter XIII, p. 219.

There is a well marked difference between the embryonic processes in the craniates and acraniates on the one side, and the molluscs and the annelids on the other, due to a prevailing difference in the volume of yolk in the four groups, the period at which the embryo is liberated, and in the unequal emphasis placed on growth at the cephalic and caudal ends of the body.

The principal features of these groups may be summarized as follows:

A. Molluscs and Annelids.—In these animals we have a true gastrulation in its original meaning, for the blastular infolding gives rise to endoderm only, and the blastopore, without noticeable elongation persists as the mouth. The mesoderm arises from cells lodged in or near the posterior lip of the blastopore. The young usually escape from the egg as so-called trochospheres, a larval form representing the cœlenterate phase of their development. Its characteristic feature is a transverse, or equatorial ciliated band encircling the principal axes between the mouth and the apical plate. (Fig. 267.)

In the annelids the trochosphere forms only the head, the body always arising as a new local outgrowth, not by the elongation of the trochosphere as a whole. When there is a considerable amount of yolk present, the trochosphere stage may be passed within the egg membranes; in these cases the trunk is formed by the rapid proliferation of a special group of large terminal cells, or teloblasts, of which there may be several kinds, each giving rise to a linear series of some particular kind of organ, as nerve cords, nephridia, entoderm, etc.

In the molluscs the trochosphere is transformed into the adult with little or no axial elongation.

The molluscs and annelids, therefore, are characterized by small or medium sized eggs that pass through a true gastrulation; the blastopore persists as the mouth, and the larva is a cœlenterate-like trochosphere. The germ layers of the trunk arise simultaneously with the progress of apical growth, no one layer arises from another, the mesoderm never forms a part of the functional enteron, and the mesocœle never opens into the enterocœle.

B. Craniates.—In the arachnid-vertebrate stock, the embryo grows film-like over the surface of a large body of yolk. It passes rapidly through the gastrula and trochosphere stages, and is retained within the egg membrane till the trunk is well developed, rarely being liberated with less than fifteen or twenty highly specialized metameres. (Figs. 25 to 32.)

The only recognizable remnants of the gastrula are found in the primitive cumulus, or circular germ disc, at the point where the primitive mouth and procephalic lobes are formed. (Figs. 25, 269.) The body, or trunk, is a new formation that has no real homologue in a cœlenterate, and it is formed solely by the multiplication of cells that lie beyond the limits of the true blastopore, that is on the posterior margin of what represents the body of the gastrula. The bands of new tissues, or organs, formed by the teloblasts, such as the nerve cords, mesoderm, and entoderm, are usually quite distinct and preserve their normal position and relation to one another from the outset. But as a result of diverse conditions created by growth, the entire mass of proliferating cells may be bodily invaginated (insects, crustacea, amphibia) forming extensive axial, or terminal, infoldings from which the products of apical growth are gradually separated. (Fig. 269, *t.p.*) These infoldings, so often confused with gastrulation, are of a purely secondary nature and of no special phylogenetic significance. The process has nothing in common with gastrulation, and the invaginated cells do not represent a primitive enteron. The cavity of the infolded teloblasts may be called a telocœle, and its external opening the telopore.

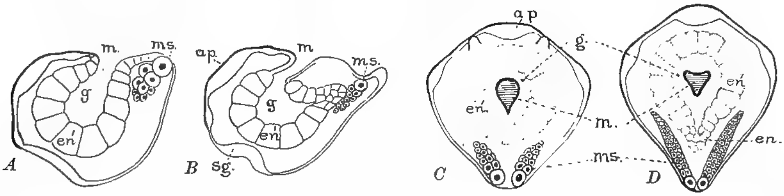


FIG. 268.—Diagrams of a molluscan trochosphere; *A*, *B*, in sagittal section; *C*, *D*, seen from the neural or oral surface. The diagrams indicate the relation between the gastrula, blastopore, mouth, and anus; and the site of apical growth.

The concrescence that occurs in the craniates is the concrescence of the peripheral margins of an expanding embryonic area, not that of an elongated blastopore. (Fig. 157.)

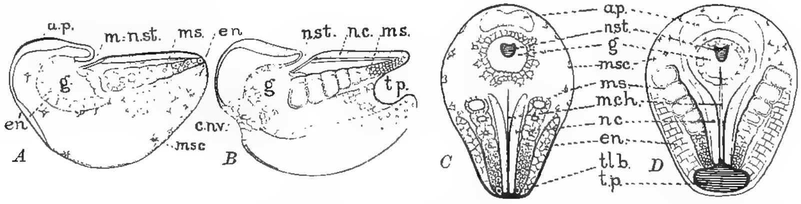


FIG. 269.—Diagrams of an arthropod embryo. *A*. *B*, Sagittal sections; *C*, *D*, the embryo seen from the neural surface. The figures indicate the relations between the gastrula, cephalic navel, neurostoma, telopore, and teloblasts; and the axial structures formed from the latter. Here the gastrula gives rise only to those structures belonging to the primitive head, or that part of the embryo derived from a coelenterate ancestor. The teloblasts, with or without the formation of a terminal infolding, or telopore, give rise to the axial cords, out of which, like an appendage to the old radially symmetrical head, the new, bilaterally symmetrical, segmented trunk is formed.

In the craniates, therefore, the gastrula and trochosphere stages and the blastopore are omitted, or are but faintly repeated at the head end of the medullary plate, while a conspicuous false gastrulation is produced by the infolding of the teloblastic areas at the end of a rapidly growing trunk. The organs of the trunk, produced by apical growth become recognizable, or separate from each other from before backward, at varying periods in different members of the group, and there is a general tendency to carry the development within the egg up to later and later stages, so that the young, when liberated, usually develop into the adult without a marked metamorphosis.

C. The Acraniates.—In the acraniates the embryonic development takes place under a new set of conditions and is expressed in a new set of forms. The eggs as a rule are very small, practically devoid of yolk, and develop rapidly, with continuous epithelial layers and folds. The gastrula stages are passed within the egg membranes, and the embryo escapes at an early period as a small unsegmented larva, or naupula, representing under various disguises the nauplius stage of their crustacean ancestors. For such a large and diversified group of animals, the early embryonic and larval stages are remarkably uniform. The small, more or less transparent eggs undergo a total and nearly equal cleavage, forming a small, hollow blastula (cirripeds excepted). No true gastrulation, such as that in the annelids, occurs in the group, but there is a large infolding, or mesentocœle, at the posterior end of the blastula, in which the teloblasts and their earlier products are involved. (Fig. 271, *A*.) It opens outward by a telopore that marks the caudal end of the body, and closes near the point where the anus is formed. It never remains open as the primitive mouth, and is never formed in the oral or cephalic region.

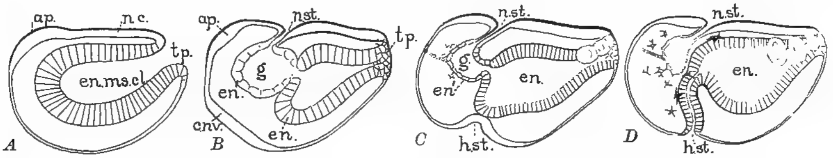


FIG. 270.—Semi-diagrammatic sagittal sections through the embryo and young larva of Balanoglossus, to illustrate the relation of the neostoma and hæmostoma to the gastrula, telocœle and telopore.

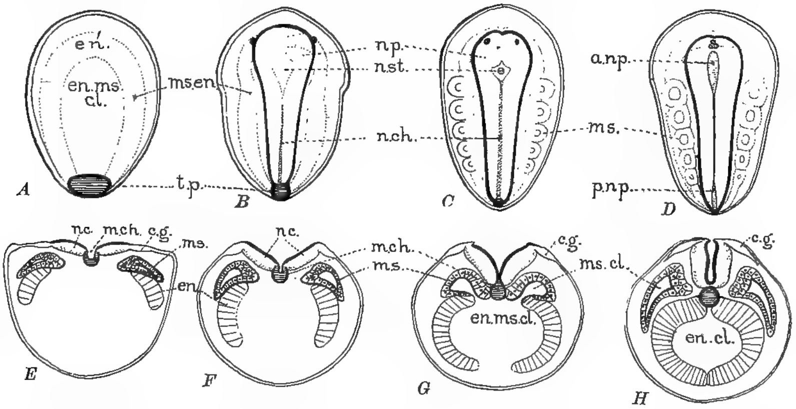


FIG. 271.—Diagrams of the development of a vertebrate and acraniate seen as a semi-transparent object from the neural surface. The primitive gastrula is indicated only by the remnants of the neurostoma, now a shallow pit lying on the floor of the procephalic lobes, and later, after the closure of the medullary plate, giving rise to the infundibulum and the saccus vasculosus. The teloblasts have increased greatly in importance, and, like those in the arthropods, give rise to a large terminal infolding, or false gastrula, from the walls of which the axial cords, such as the notochord, mesoderm and endoderm are formed. These structures separate at various periods, and in various manners, as shown by the cross-sections *E–H*, but in all cases the end-result is the same, and the real sources of the axial cords are special groups of proliferating cells lying at the caudal apex of the trunk.

The component parts of the infolded layer begin to separate, or first become recognizable, at the head end, the process extending backward with the growth of the body. When viewed in cross-section, the mesoderm and notochord appear, at first sight, to be in the act of arising from the endoderm. (Fig. 271, *G.*) As a matter of fact, what is really taking place is the belated separation of the mesoderm bands, notochord, and endoderm from one another, while all of them owe their origin to terminal groups of proliferating cells, just as in the typical craniate embryos.

An enteron, or primitive gut, does not exist till after the products of teloblastic growth have separated, and the lateral bands of the endoderm have united to form a closed tube. The mesoderm may separate from the lateral walls of the mesentocœle as hollow vesicles, either during (Amphioxus), or before its division into somites, or cœlomic chambers (echinoderms). In either case the process is not a primitive, but a secondary one. It is merely another way of attaining the same conditions seen in the annelids and arachnids, and is probably the result of a rapid development of yolkless eggs. Owing to the almost universal absence of a considerable volume of yolk in the acraniates, there is no terminal concrescence like that in the craniates.

Mouth.—A functional neurostoma and primitive stomodæum are formed between the anterior ends of the nerve cords in the cirripeds, chætognatha, echinoderms, brachiopods, and polyzoa. In all the other sub-phyla, a vestigial, or transitory neurostoma is formed as a median depression in the anterior end of the medullary plate. It opens outward, in those forms in which the anterior end of the medullary plate is not infolded to form a closed forebrain vesicle (enteropneusta, pterobranchia, phoronida, polyzoa, chætognatha. Where the medullary plate is infolded and closed, the neurostoma lies in the floor of the forebrain vesicle (tunicates, Amphioxus). The infolding for the primitive mouth may be of considerable depth, forming a true primitive stomodæum, opening permanently into the mesenteron as in the case of the dorsal tubercle and subneural gland of the tunicates; or a blind pocket may arise from the midgut, that grows toward the primitive mouth, representing either the cut off remnant of the primitive stomodæum, or that part of the midgut that formerly communicated with it. (enteropneusta, pterobranchia, (and phoronida ?)).

The hæmostoma is a new formation arising independently of the old mouth, from the anterior hæmal surface of the body.

The Naupula.—The larva of the acraniates, or the naupula, is a small, usually free swimming, pelagic form resembling a cirriped nauplius. It may undergo a part of its development in the brood pouches, or recesses, of the atrial chamber (cirripeds, tunicates, echinoderms, brachiopods, and polyzoa). The naupula differs from a trochosphere in that it represents a distinctly older phylogenetic stage, and undergoes a special kind of metamorphosis. It possesses a longitudinal, circular fold, representing a larval mantle fold or carapace, that usually has a ciliated margin. The larva comes to rest, neural side down, and becomes permanently attached, usually by an adhesive disc, aided by rudimentary cephalic appendages. Subsequently the larva rotates, bringing its neural side up (cirripeds, tunicates, echinoderms, polyzoa, brachiopods (?)), and the hæmal surface of the head rapidly grows into the characteristic voluminous stalk, or peduncle, by which the animal is permanently attached.

The Cœlom.—The primitive body cavity is the space enclosed between the somatic and splanchnic mesoderm. It was probably primarily segmented, forming two completely closed chambers for each metamere. On the sides and hæmal surface, the walls separating adjacent chambers tend to break down, forming extensive sinuses containing loosely united or isolated cells (blood cells). On the neural surface the original segmentation is usually more strongly marked and more permanent, and certain portions may be retained, or set apart, as thin walled chambers, lined with epithelium, and devoid of free amœboid cells or blood corpuscles.

They may consist of a small part of a single mesoblast segment, the part that is directly connected with the excretory or nephridial duct, or that developed mainly as a tubular outgrowth from it (Figs. 279, 294); or several such portions may unite to form more extensive chambers. They are lined in part by flat, indifferent endothelium, and in part by more specialized excretory cells, and they may open to the exterior by glandular ducts, or nephridia, of which only the terminal portion is of ectodermic origin. These so-called cœlomic chambers are often referred to as the true cœlom, and have been regarded as the primitive body cavity, but they are in reality either special portions of more primitive and more extensive spaces, or the parts that remain hollow, after the other portions have been shut off as vascular spaces or canals, or have been completely filled by the growth of fibrous, muscular, or other tissues.

CHAPTER XXIII.

THE CIRRIPEDS, TUNICATES AND ECHINODERMS.

I. The Cirripeds.

The cirripeds are the only members of the acraniates in which the more typical arthropod characters are retained. They present an extraordinary diversity of form and structure, but many of their peculiarities, such as the enormous cephalic stalk, the mantle, pigmyism, the absence or disappearance of appendages, of sensory and alimentary organs, and of external segmentation, we shall see expressed in a more stable and permanent form in other members of the group.

The Nauplius and the Naupula.—The young leave the egg like many other primitive arthropods, in the nauplius stage, as a small, free swimming larva with three pairs of appendages. (Fig. 289.) Its minute structure is doubtless very similar to that of a parasitic copepod. The larva of the latter being better known, it may be taken to illustrate the structure of the nauplius, the basic larval form of the entire group of acraniates.

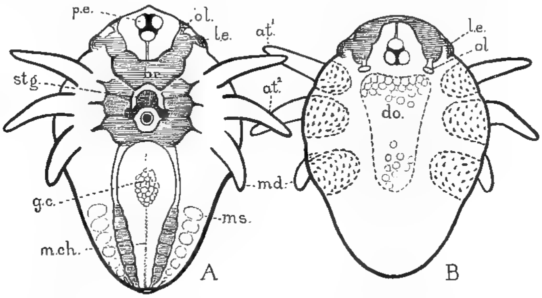


Fig. 272.—Diagrams of a nauplius, based in part on Pedeschenko's figures of Lernæa; *A*, neural surface; *B*, hæmal.

In Lernæa branchiata, which has been carefully studied by Pedaschenko, the nauplius (Fig. 272), is provided with a well developed brain, *br.*, frontal organs, *ol.*, rudimentary lateral eyes, *l.e.*, a trioculate median eye, *p.e.*, and stomodæal ganglia, *st.g.*, very similar to those we have already seen in Branchipus, in other phyllopods, and in Limulus. There is also a large cephalic navel, *do.* (dorsal organ) that undergoes a characteristic degeneration and absorption by the yolk cells.

Behind the mandibular ganglion the nerve cords are widely separated, but they unite again at the caudal end, forming the rudiments of the abdominal neuromeres, or ventral cord. The latter increases in length by the multiplication of prominent telo-neuroblasts. A middle cord, *m.ch.*, is clearly indicated.

The germ cells appear in the undifferentiated blastoderm at a very early period, and later form a conspicuous cluster of cells in the middle of the neural surface of the nauplius, between the separated nerve cords, *g.c.*, in the same position, therefore, that they have in the polyzoa and pterobranchia.

In the cirripeds two prominent longitudinal pleural folds are formed that represent the beginning of a two-lobed thoracic shield comparable with that of the ostracodes and other primitive crustacea, and from which the mantle will develop later. (Fig. 289, *mt.*)

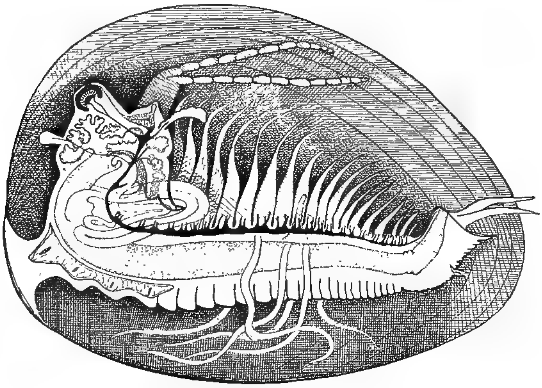


FIG. 273.—Limnadia lenticularis. (After Nowikoff.) × 7 1/2.

In the later stages of the nauplius there is usually developed an enormous labrum (Figs. 7, *ro.* 289, *l.*), that overhangs and conceals the mouth, and a prominent caudal lobe, *a.l.*, with the anus on its hæmal side. An adhesive disc forms near the apex, or the hæmal surface of the head, by which the larva, for a longer or shorter period, is attached to foreign objects.

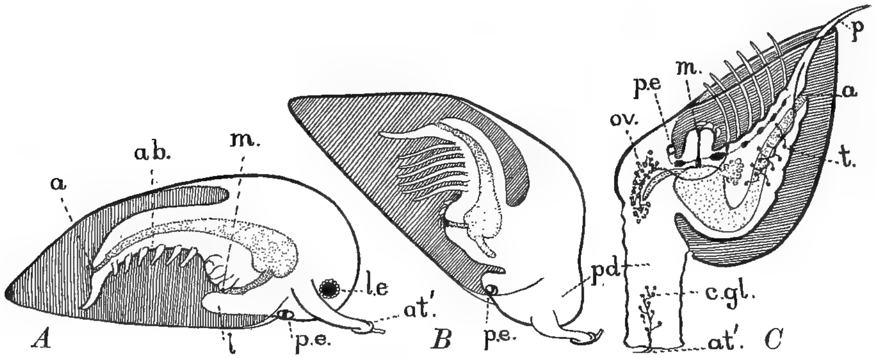


Fig. 274.—Diagrams of a cirriped larva, illustrating its mode of attachment, revolution, and metamorphosis.

A nauplius-like larva, with most of the characters indicated above, occurs under various disguises and modifications in all the subphyla of the acraniates. In its modified form we shall refer to it as the *naupula*.

The Metamorphosis.—In the cirripeds the larval cephalic shield is usually very large and the body lies on its concave neural surface. Its margin is sensitized and drawn out into very prominent horns or lobes, of which there are usually two especially long ones in front, two behind, and minor ones between. (Fig. 289.) After a time the caudal lobe elongates, the antennæ migrate forward and hæmally, and the thoracic appendages and the rudimentary lateral eyes make their appearance.

The larva, having taken on the shape and general appearance of an ostracode (cypress stage) which it will be recalled is one of the first forms to make its appearance in the geological record, attaches itself to some foreign object, hæmal side down, by glandular, disc-like expansions of its first pair of appendages. (Fig. 274.) Cement glands appear and the greatly enlarged cephalic outgrowth becomes firmly attached. The body next turns completely over; the stalk elongates, carying with it the remnants of the first pair of appendages, and the animal gradually takes on the adult form. (Figs. 274, 275.)

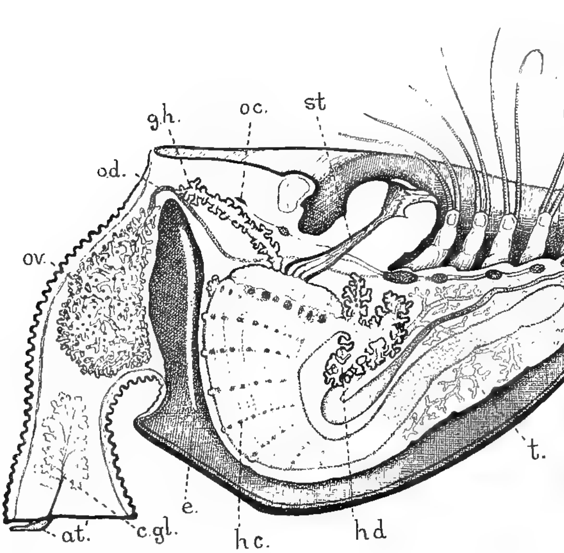


FIG. 275.—Semi-diagrammatic sagittal section of a cirriped. Lepas.

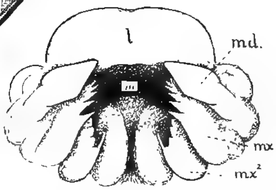


FIG. 276.—Mouth parts of Lepas.

Appendages.—Eleven pairs of appendages may be represented; two pairs of antennæ, three pairs of jaws, including the mandibles, and the first and second pairs of màxillæ, and six pairs of abdominal appendages. With the metamorphosis there is a strongly marked tendency toward the reduction, or atrophy of many important larval organs. All of the eleven pairs of appendages present in the larvæ are never fully developed in the later stages. Even in the least modified forms, the two pairs of antennæ are either greatly reduced or absent; the three pairs of jaws or oral appendages are very small, and two or three pairs of the six pairs of abdominal appendages may be absent. Only nine pairs are present in the alcippidæ and eight in the cryptophialidæ. In apodous forms only the jaws and one pair of antennæ are retained, while in the rhyzocephalidæ all traces of the appendages disappear.

Alimentary Canal.—The stomodæum is generally small, and leads into a large pear-shaped enteron provided with prominent gastro-hepatic glands. (Fig. 275.) The larger ones form a circle of racemose diverticula, or pouches, said to be provided with two kinds of cells, hepatic and pancreatic, *h.d.* and *g.h.* Circular bands of smaller pouches, or patches of cells having a special structure, are arranged at regular intervals over the remainder of the stomach, diminishing in distinctness toward the caudal end, *h.c.* The anus, *a*, is located on the hæmal side of the elongated caudal lobe.

Cœlom.—True cœlomic chambers are well developed in the cirripeds and copepods. In Lernæa ten pairs, one apparently for every metamere except the first, have been described by Pedaschenko. (Fig. 279, *A.*) They form large segmentally arranged chambers enclosed in thin but well defined epithelial walls. They are completely shut off from the remaining parts of the primitive cœlom, or hæmocœle, which consists of irregular, extensive, unsegmented spaces that are surrounded by mesoderm and contain free mesodermic cells.

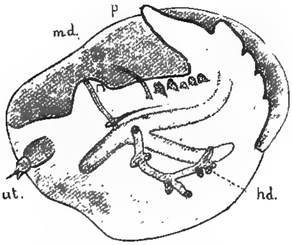


FIG. 277.—Petrarca mira (after Fowler); commensinal in the mesenteric chamber of the coral Bathyactis. Ramifications of testis, ovary, and liver in the mantle folds.

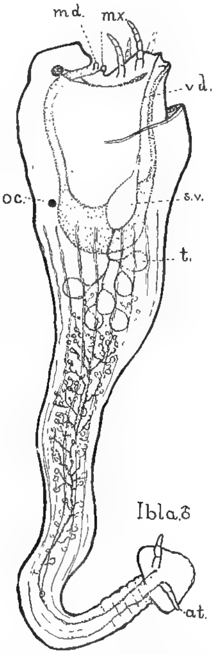


FIG. 278.—Ibla quadrivalis, male; parasitic on the female, within the palial chamber. (From Gruvel, slightly modified 3–4 mm. long.)

In the adult cirripeds three pairs of cœlomic chambers have been recognized, although their early history and identity are not known. (Fig. 279, *B.*) There is a small pair of completely closed sacs in the head region, lined with excretory cells that probably represent the remnants of the antennary cœlom and the antennary gland, c^1. The second pair lie in the thoracic or circumoral region, on either side of, and close to, the stomach, c^2. They are extensive chambers that communicate with each other across the median line, in front of and behind the mouth (Gruvel). They are completely separated from the hæmocœle, but open to the exterior through the nephridia-like ducts of the shell gland, *mx.d.* They probably represent the combined thoracic cœloms together with the excretory portion of the "shell gland" or "coxal gland" of the second pair of maxillæ. The third pair, c^3, lie external to and somewhat behind the second. They are completely closed, and probably represent the remnants of several pairs of united abdominal cœlomic chambers.

Excretory Organs.—Two pairs of nephridia-like excretory organs are conspicuous in the arthropods and remarkably constant in their location. The so-called green gland of the second antennæ, and the shell gland of the second maxillæ of crustacea (coxal gland of the fifth pair of thoracic appendages in arachnids). The characteristic thin-walled end sac of these organs is derived from a portion of the cœlom, but a variable one. It may represent a single somite (Limulus) or a small part of one (Lernæa), or the whole, or a part of several combined somites (cirripeds and other acraniates).

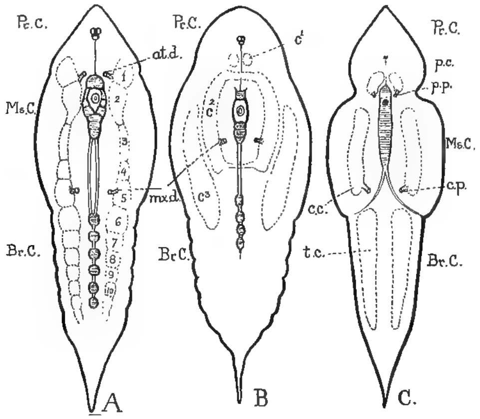


FIG. 279.—Diagrams to illustrate the relations of the cœlomic chambers, and their excretory ducts, to the main subdivisions of the body (tagmata) and to the central nervous system. *A*, Larval copepod (Lernæa); *B*, an adult cirriped; *C*, Balanoglossus.

In the cirripeds the excretory organs of the fifth metamere have very voluminous end sacs, c^2, and the nephridia-like tubes that lead off from them open at the base of the second pair of maxillæ. A small pair of excretory sacs lie in the head region in front of the mouth that probably represent the remnants of the antennary glands of other crustacea.

The sexual organs are of exceptional volume in the cirripeds, the racemose testis ramifying through the whole trunk and opening at the apex of the modified tail lobe. (Fig. 275.) The location of the ovaries is noteworthy in that they lie mainly in the cephalic stalk and anterior portion of the mantle, the ovarian lobules, in some cases, extending into the recesses of the exoskeleton. The oviduct opens outward near the middle of the body, at the base of the anterior pair of abdominal appendages, *o.d.*

In the more degenerate cirripeds, the sexes are separate, and the males are reduced to minute forms parasitic on the females. (Figs. 278–281.)

Degeneration.—The wide range of variation in the cirripeds is largely due to the varying amount of degeneration following the metamorphosis. The mantle, integument, and sexual organs are often the only parts that retain the normal powers of growth. The degeneration may be manifest in the diminished size of the whole body, and by the absence, or dwindling of appendages, muscles, alimentary canal, sense organs, and nervous system. The anal opening may close (Petrarca, Fig. 277, females of Alcippe, Fig. 280), or the proctodæum, stomodæum, and the entire mesenteron may disappear, as in the dwarf males of Scalpellum (Fig. 281), of Alcippe (Fig. 280), and many copepods (Figs. 282 and 283).

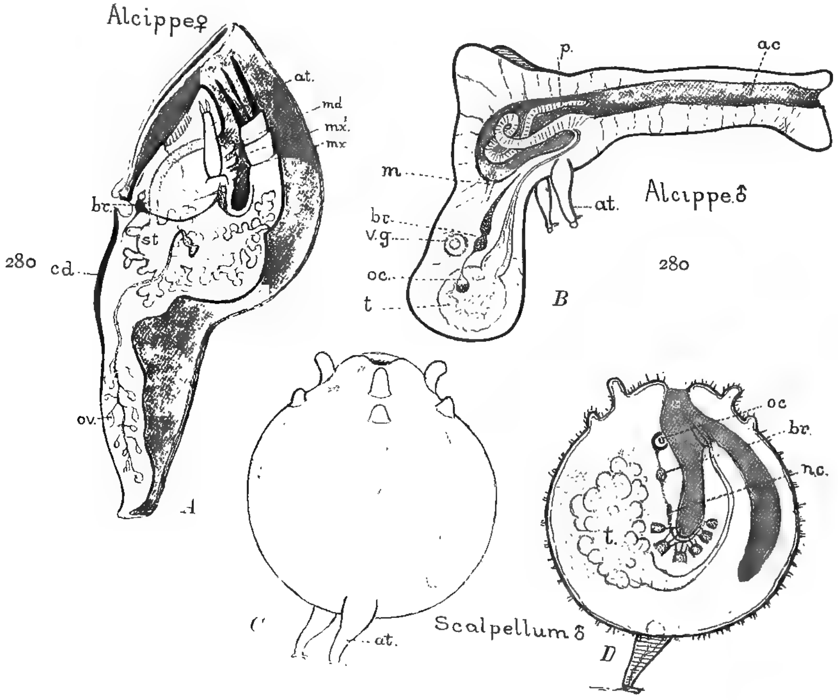


FIG. 281.

FIG. 280.—*A*, Alcippe lampas, female; about 8 mm. long; *B*, male, parasitic on disc of female; about 1 mm. long. Probable position of the remnants of the mouth, indicated at *m*; cement glands and alimentary canal, absent; excretory organs closed (?). (After Berndt, slightly modified.)

FIG. 281.—*C*, Scalpellum vulgare, dwarf male; surface view; *D*, in optical section. Fixed to the hermaphroditic individuals; mouth and ailmentary canal absent. (After Scott, slightly modified.)

It is doubtful whether these dwarf males survive long after the maturation of the spermatozoa, but there is a certain vegetative vigor in the surviving organs of the larger individuals, *i.e.*, females and hermaphrodites, that is not so seriously affected by degeneration.

The Old Mouth and the New.—A highly significant aspect of degeneration in cirripeds is the closing of the mouth (neurostoma), and the dwindling or disappearance of the stomodæum. We have already witnessed a tendency in this direction, in the arachnid-vertebrate stock, and the origin of a new mouth, or hæmostoma, from the dorsal organ, or cephalic navel, p. 253. Similar conditions are latent in the cirripeds. A typical embryonic dorsal organ is a conspicuous feature in the young nauplius of Lernæa and of many other primitive crustacea. Its invagination, or ingrowth into the yolk, followed by disintegration and absorption, probably played an important part in establishing a permanent opening into the enteron at this point, from which, in the other sub-phyla of the acraniates, the new mouth arose. The exact way in which the new opening was established, and its relation to the adjacent gut pouches, to the adhesive glands, and to the cephalic stalk are not clear because very little is known about the details of these important structures. But it is certainly significant that in the rhizocephala, where the old mouth closes, the animals manage to survive by the absorption of nutrition through the root-like outgrowth of the cephalic stalk that is formed at the place where the dorsal organ closes. The condition in Tubicinella is likewise suggestive, for Gruvel states, p. 279, that according to Marloth, the tubicinellæ secrete a peptonizing ferment that diffuses through the membranous base, transforming into peptones the albuminoid substances of the skin of the whale, to which these forms are attached. Without doubt we have here a glimpse of the way in which the old mouth disappeared, and the way in which the new one was

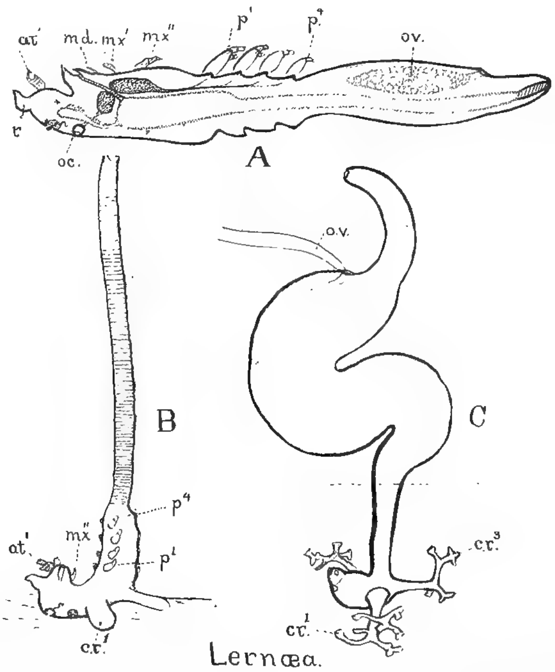


FIG. 282.—Lernæa branchialis. *A*, Young fertilized female; *B*, penella stage; fertilized female in gill of Whiting; *C*, adult female, attached. (After Scott, slightly modified.)

formed that became the hæmostoma of the tunicates, enteropneusta, and other acraniates.

It is often assumed that a sessile or parasitic mode of life is the initial cause of degeneration. The various anatomical peculiarities common to the copepods, cirripeds, and acraniates do not bear out this conclusion. The fact that in these diverse sub-phyla we see the same shifting of cephalic appendages to the hæmal side, the same cephalic outgrowths, and the same degeneration of the neuro-muscular organs, indicates that there are certain initial defects, or peculiarities of germinal material, common to the whole group, that is the underlying cause of a defective organization, and the defective organization is in every case of such a nature that a sessile, or parasitic, or vegetative mode of life is the only one possible.

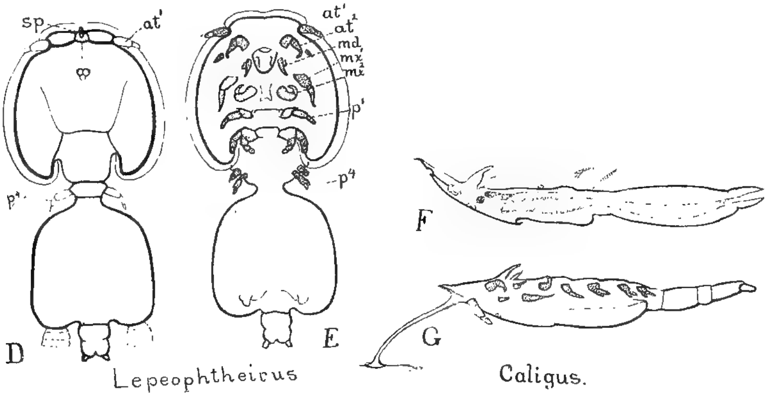


FIG. 283.—Lepeoptheirus. *D*, Hæmal, *E*, neural surface. *F*, *G*, Caligus. (From Scott, slightly modified.)

II. THE TUNICATES.

It was from a stock similar to that of the copepods and cirripeds, and one dominated by the same fundamental defects in germinal material, that the tunicates arose. They are built on the same general plan, pass through a similar larval existence, and undergo a similar retrograde metamorphosis. But all this is at first sight effectively disguised by the permanent closing of the old mouth, and the opening of a new one on the hæmal surface; by the absence of both the chitenous and calcareous exoskeleton and appendages; and by the conspicuous development of perforated gill sacs, and of the middle cord, or notochord. Like the cirripeds they begin life with the same brave display of animal vigor, of well developed brain, eyes, and locomotor organs that bespeak an efficient past and a hopeful future, only to have them dwindle almost to extinction in a peaceful, sedentary existence.

The early stages of the tunicate embryo are essentially like those of a primitive crustacean (Moina, Cetochiles, Balanus, or Palæmon). In both types there is the same kind of cleavage; the same terminal proliferation or infolding to form a telocœle; the same slipper-shaped medullary plate; the same middle cord or notochord arising from the ectoderm and projecting forward from the anterior lip of the telocœl; the same lateral bands of mesoderm; the same kind of trioculate median eye; the same infolding of the medullary plate on the neural side of the head to form the primitive stomodæum, or subneural gland, and a similar organ on the opposite side of the head representing an actual or a potential hæmostoma; and a similar larval metamorphosis.

When the tunicate larva escapes from the egg, three glandular tubercles appear on the anterior hæmal surface of the head, representing the remnants of arthropod cephalic appendages. After a short, free swimming existence, it attaches itself by these appendages to some foreign object, head down, and in a nearly vertical position, and then begins its metamorphosis. (Fig. 284, *A*.) It undergoes a partial rotation, turning neural side up; the cephalic tubercles are gradually merged in the larger cephalic stalk; the body contracts, taking on a pronounced curvature that draws the head end upward toward the root of the tail; the latter atrophies, and with the growth of the mantle, the remnants of the body are completely enclosed in the large atrial chamber.

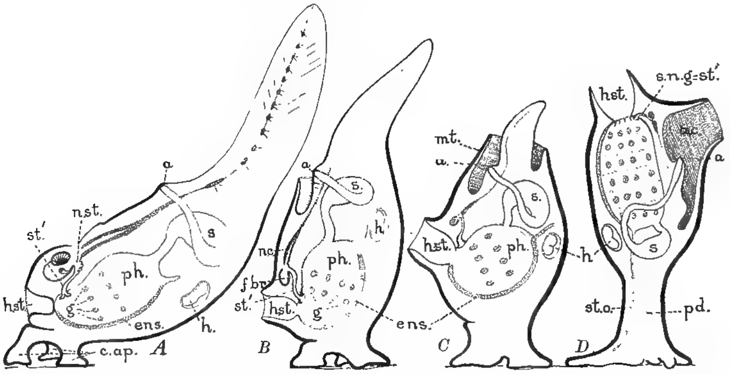


FIG. 284.—Diagrams illustrating the mode of fixation and the metamorphosis of an ascidian.

In Figs. 285 and 286 I have attempted to show, in a purely diagrammatic way, the manner in which a cirriped-like animal could be metamorphosed into a tunicate. These figures should be compared with what actually takes place in a tunicate (Fig. 284), and with the conditions that actually occur in the metamorphosis of a typical cirriped, such as Lepas (Fig. 274), or with that which prevails in the adult condition of more degenerate cirripeds, such as Ibla and Alcippe, Scalpellum, Petrarca, and Sacculina. (Figs. 278 and 280.)

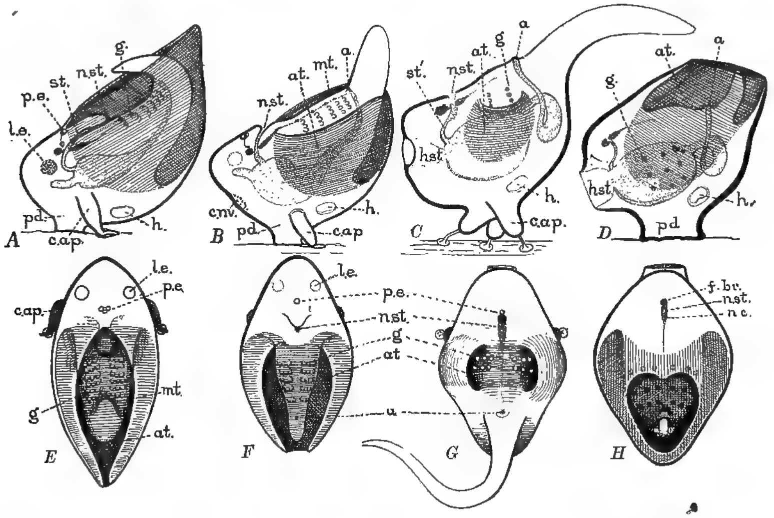
With the atrophy of the body, the notochord disappears and the elongated nerve cord is reduced to a small, compact cerebral ganglion which, like that in many parasitic cirripeds, still surrounds the proximal end of the old stomodæum, *i.e.*, the subneural gland, *s.g.*

In the cirripeds (Lepas), the anterior end of the enteron forms an immense chamber with numerous enteric pouches arranged in transverse bands. (Fig.

275.) In the tunicates similarly arranged enteric pouches are formed, which unite with the lateral walls of the body, or with infolded rudimentary appendages, forming gill clefts that lead from the enteron into the atrial or peribranchial chamber, and thence to the exterior.

* * * * * * * * *

The Heart and Vascular System.—In both tunicates and cirripeds the vascular system is imperfectly developed; nevertheless there are some interesting points for comparison. In the tunicates there is a short, oval heart on the posterior hæmal surface of the thoracic region. It is similar in form and location to that in primitive crustacea, and the general arrangement of the associated blood channels is also similar.



FIGS. 285, 286.—Diagrams illustrating the manner in which a sessile, cirriped-like arthropod is supposed to give rise to a tunicate. *A–D*, Seen from the side; *E–H*, same, seen from the neural surface.

In the cirripeds the heart is absent. But in many of the primitive, short-bodied crustacea, a heart is present, and consists of a short oval sac containing but one pair of openings (cladocera, Fig. 9, *h.*), or a small number of them. It no doubt arises in typical arthropod fashion from the fusion of the lateral mesoderm plates of the posterior thoracic metameres. The circulation in the tunicates is chiefly remarkable for the periodic reversal of the direction in which the blood is made to flow, a condition generally assumed to occur nowhere else in the animal kingdom.

In the copepods a slowly pulsating heart, similar in appearance to that of cladocera, may be present, but in parasitic forms it is said to be absent, although there are certain channels through which the blood flows in a definite direction. In Lepeophtheirus, for example, according to Scott,[1] the circulation, while wholly

Liverpool Marine Biol. Com. Memoirs. VI, 1901.

lacunal, follows well marked channels. The remarkable part of it is that the blood currents, as he states, "Do not continue to flow for any length of time in the one direction. At one period they may be flowing as indicated. . . . . They then suddenly slacken and reverse and stream for a time in exactly the opposite course." (p. 21.) In this particular, therefore, the circulation is astonishingly like the well known reversing circulation of the tunicates.

The Eyes.—In the tunicates the lateral eyes are absent, as they are in the adult stages of cirripeds and all other acraniates. The parietal eye, however, may be retained, and in some forms, as Salpa, it may be present and even well developed in the adult stages, resembling in a very striking manner the nauplius eye, or trioculate median ocellus of primitive crustaceans.

The details of its early development are obscure, especially the manner in which the several retinas are infolded and become lodged on the roof of the neural tube. Judging from the structure of the eye, and from what is known of the development of the medullary tube, the tunicate parietal eye appears to develop in essentially the same manner as the median eye of Branchipus. In other words, it is to be regarded as a true parietal eye, consisting of two pairs of ocelli, the retinas of which have become loosely united to form the walls of a common unpaired vesicle, opening into the cavity of the forebrain, and forming a part of its roof. (Fig. 287.) The eye is innervated by two principal nerves, *n*, that arise from a dorsal ganglionic mass, probably representing the forebrain plus the optic ganglia.

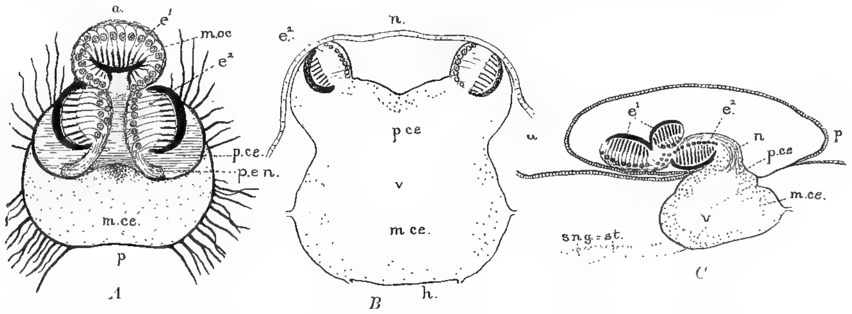


FIG. 287.—The forebrain, ventral cord, and ocelli of Cyclosalpa, chain form, adult. *A*, Seen from the neural surface; *B*, in cross-section; *C*, in longitudinal section. (After Metcalf, slightly modified.)

The Old Mouth and the New.—When the medullary plate, which represents the entire brain and nerve cord of the ancestral arthropod, was infolded, the parietal eye and primitive stomodæum were carried in with it, and when the medullary tube finally closed, the primitive mouth and the stomodæum were permanently shut off from the exterior; but they retained their original structure and relations essentially unchanged, for the stomodæum persisting as the subneural gland and its duct, opens at its outer end, through the floor of the embryonic brain into the rudimentary cerebral vesicle; while the inner end still opens into the enteron as the so-called dorsal tubercle. (Figs. 284–286.)

In the adult Salpa the oval ventral portion of the brain (Fig. 287, *m.ce*), from which arise numerous pairs of peripheral nerves, and which formed the floor of the anterior part of the medullary plate, probably represents the condensed remnants of several thoracic neuromeres. The dorsal portion, *p.ce.*, represents the primitive forebrain, or supraœsophageal ganglion. The cavity, or space between them, represents the rudiments of a cerebral ventricle. Before the neural tube is completely closed, the subneural gland, or primitive stomodæum, opens into this space and thence to the exterior (Fig. 287, *C.*)

The new mouth, or hæmostoma, arises from the opposite side of the head, in the region of the cephalic naval, or dorsal organ.

The Mantle.—A characteristic feature of the tunicates is the thick, fibroid, translucent secretion of the ectoderm that forms a flexible covering for them, and that takes the place of the ectodermal skeleton of arthropods. In its general appearance and consistency it is not unlike the softer forms of chiten; but it differs from it chemically, consisting of a special substance, tunecine, said to be identical with cellulose, although it is doubtful whether a more careful analysis will bear out this conclusion. It may be regarded, provisionally as some modification of chiten, or of a closely related substance.

At an early stage of development, it is invaded by numerous spindle- or star-shaped cells, differing in character and in origin; some arise from the ectoderm, others from the mesoderm, others from the ovary. It is also broken up by the presence of canals and spaces that permit the invasion of blood-vessels and other tissues, and there are occasional deposits in it of calcareous and silicious specules. In one form, Chelyosoma, it consists of "horny plates" that recall those of cirripeds.

The mantle of tunicates may be regarded as a special modification of the exoskeleton of arthropods, resembling most nearly that of the cirripeds. The cirripeds have a type of exoskeleton not known to occur elsewhere in the arthropods; it, therefore, has a special interest and significance for us. Unfortunately, I have not had an opportunity to examine at first hand into the details of its minute structure and development. It develops, according to Gruvel, underneath, or inside, the hypodermis of the mantle, by the secretion of concentric or parallel layers of chiten which then become heavily calcified. It is never cast off, and continues to increase in volume during life.

In the early stages, the chitenous matrix is crowded with regular spaces, each containing a live cell, which however dies with the progress of mineralization. (Gruvel, p. 362.) In Pachylasma (Fig. 288, *A*), the shell consists of two principal layers, an outer one of small chambers with thick laminated walls secreted by infoldings of the hypodermis, *h*, and a basal layer derived from the inner surface of the mantle, *m.l.* In Balanus (Fig. 288, *B*), the outer layer contains large spaces or parietal canals, *cn.*, and the hypodermis, *h*, extends inward in the form of spreading or branching plates. The peripheral spaces or parietal canals, *cn.*, were formed by ingrowths from the inner layer of the mantle and contain, for a time, living tissue. In Corunula, the shell contains large spaces which stand in direct communication with the central cavity of the test, and in which is imbedded that part of the ovary that gives rise to the eggs. (Gruvel, p. 368.)

The remarkable structure of the shell in the cirripeds recalls that of Limulus and Pteraspis (Figs. 196–204.) At the same time the invasion of its matrix by isolated hypodermal cells, by pyramidal ingrowths of the mantle, and by ovarian tubules, is comparable respectively with the presence of the test cells, vascular ingrowths, and the so-called "kalymmocytes," or egg follicle cells, in the mantle of the tunicates. The principal difference, therefore, between the exoskeleton of the tunicates and the complicated ectodermal skeleton of Limulus, the pteraspids, and the cirripeds apparently lies in the different chemical composition of the non-cellular matrix.

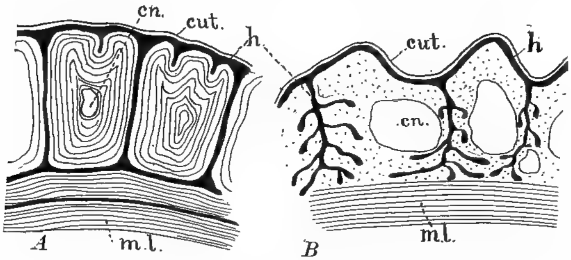


FIG. 288.—Sections of the shell of cirripeds. *A*, Pachylasma; *B*, Balanus. (After Gruvel.)

Tunicates and Cirripeds. Summary.

It is unnecessary to carry our comparison into further detail. The structure and mode of growth of the tunicates justify the conclusion that they are descended from animals in which the salient characteristics of primitive arthropods were fully established; in fact, from that particular subdivision of the arthropods to which the cirripeds and copepods belong. Here some inherent defects in the germinal material impose on both ancestors and descendants those peculiarities of structure and mode of life that are common to both.

The tunicates resemble the cirripeds: 1. In the structure of their larvæ, in their mode of attachment, and in their subsequent revolution, degeneration, and metamorphosis. 2. In the investment of the body by a huge fold of the skin, or mantle, that encloses an atrial, or peribranchial, chamber. 3. In the outgrowth that arises from the hæmal surface of the head to form the stalk or pedicle. 4. In the occurrence of a reversing circulation. 5. In the presence of a parietal, tri-occellate eye. 6. In the presence of an exoskeleton, which in the one, consists of a calcified, chitenous secretion of the ectoderm; in the other of a substance resembling cellulose; each has a complex and unusual structure, but one that is essentially the same in both. 7. In the tunicates, the enteric pouches have perforated the body wall; the old mouth is permanently closed, and a new one has opened on the anterior hæmal surface of the head. On the other hand, in the cirripeds the gut pouches may have an arrangement in transverse rows similar to that in the tunicates; the old stomodæum often closes up and ceases to function, while the cephalic navel may form a temporary opening into the enteron, in the place where the new tunicate mouth is formed; and in the parasitic cirripeds the region of the cephalic navel may actually serve for the absorption of nutrition.

Thus many important conditions essential to the evolution of tunicates are present in cirripeds, and on the whole the present structure of the tunicates is more like that of cirripeds than that of any other known animals.

III. The Echinoderms.

The echinoderms must be assigned a position in our scheme because they appear to be in some way connected with the enteropneusta, and hence with the tunicates and with the main phylum from which the chordates arose. The problem is a difficult one. It demands some explanation of the apparent resemblance between echinoderms, enteropneusta, and tunicates, and if there is a real resemblance, indicating genetic relationship, it calls on us to harmonize the probable origin of the echinoderms with the explanation we have given above for the origin of the other chordate phyla. The key that unlocks this series of problems and places at our disposal a consistent and ever ready explanation of the multitude of details involved, must indeed be the master key.

The echinoderms are notable for their contrasts and contradictions. Their outward appearance and their pronounced radial structure distinguish them from all other animals, and at first sight suggest a very primitive organization similar to that of the cœlenterates. On the other hand, they display a high degree of histological and anatomical specialization that is in marked contrast with their low grade of organic efficiency. They begin their early embryonic development with a bilaterally symmetrical body and with clear indications of metamerism, only to change it in the later stages for one that is radially symmetrical, and in which all outward traces of metamerism have disappeared. After a short free swimming larval existence they attach themselves, neural side down, by means of larval appendages and a cephalic outgrowth; they then turn neural side up, and remain so attached for life; or, in some cases, they give up their sessile existence and again become free, moving slowly about, neural side down.

There are, therefore, three chief characteristics of the echinoderms that demand our first consideration: The early, bilateral symmetry and metamerism; the sessile life and mode of attachment by cephalic outgrowths; and the asymmetry. There appears to be but one explanation for these remarkable conditions, which is as follows: The early development of bilateral symmetry and metamerism in the echinoderms, and the presence of a telocœle and telopore in place of the more primitive gastrula and blastopore, clearly indicate that they had their origin in bilaterally symmetrical animals of the acraniate type, that had already acquired a considerable degree of complexity. These ancestral forms probably belonged to the cirriped group, for before the latent asymmetry becomes effective the young echinoderm larva resembles a cirriped in its form, mode of attachment, and subsequent metamorphosis, more than any other animal.

The radiate structure of the later stages was due to a persistent local defect, or to the absence of a definite part of the embryonic formative material, which in turn created a condition of unstable organic equilibrium, the result of which is that the whole side, following the path of least resistance, bends toward the defective area, forming an arch that increases in curvature till an approximate equilibrium is again attained by the union of its two ends to form a circle. The original half metameres and segmental organs are then arranged in radiating lines, thus creating a new radiate type and a new set of internal conditions that dominate the future growth of the organism.

If we assume that a strongly marked asymmetry, like that which occurs so frequently as an abnormality in Limulus, or even as a normal character in the bopeiridæ and paguridæ, was a fixed feature of the hypothetical ancestral cirripeds, and was capable of a successful organic adjustment, we shall have a perfectly simple and natural explanation of the origin and structure of the echinoderms, and of their resemblance to the tunicates, enteropneusta, and to the other chordate phyla.

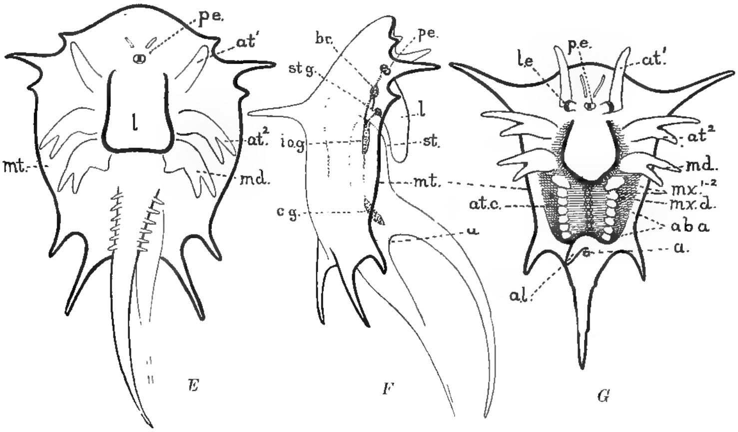


FIG. 289.—Cirriped larvæ. *E*, Early nauplius stage, seen from the neural surface; *F*, from the side; *G*, metanauplius sage. Semi-diagrammatic.

* * * * * * * * *

The Echionderm Larva.—A young echinoderm larva may be represented in a generalized diagrammatic form as shown in Figs. 291, 293. In form and structure it is much like the familiar cirriped nauplius, but differs from it in general appearance, largely because it has no chitenous covering, and because it begins its free swimming existence (the absence of yolk demanding an early liberation of the embryo) with the aid of cilia instead of appendages. But in both larvæ there is the same enormous labrum, *l.*; the same caudal lobe, *al.*, with its similarly placed anus; the same lateral thoracic folds enclosing a central depressed area; a similarly located adhesive disc, and the same simple, U-shaped, alimentary canal.

The ciliated band is one of the characteristic features of the echinoderm larva. It has been compared with the prototroch of annelids and molluscs, but it is of an entirely different nature. Its main course is longitudinal, and when completed it surrounds the neural surface only (Fig. 293, *mt.*) on the other hand, the prototroch is always equatorial, extending around the long axis, across both neural and hæmal surfaces. (Fig. 267, *pt.*)

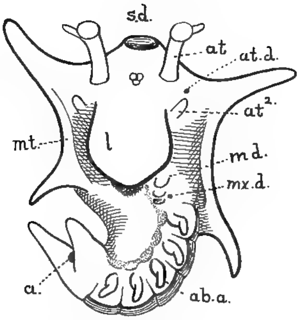


FIG. 290.

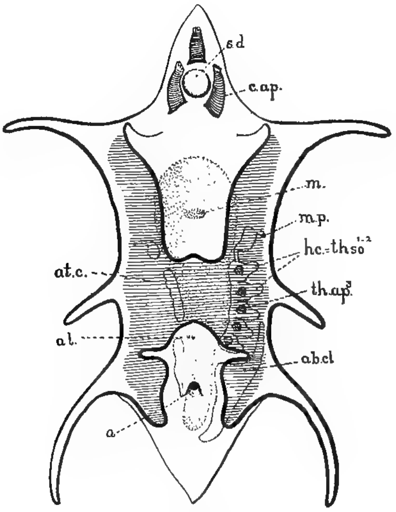


FIG. 291.

FIG. 290.—A hypothetical cirriped-like larva, in which the posterior part of the trunk is taking on a false radial symmetry due to the absence of the left half of the middle group of metameres. The figure is designed to illustrate the probable origin of radial symmetry in the echinoderms.

FIG. 291.—Diagram of a late stage in the development of a star-fish larva. The asymmetrical metanauplius stage, before the asymmetry has produced the characteristic radial structure of the later stages.

The ciliated band of the echinoderm larva is merely an adaptation, or modification, of the thickened and sensory margins of the thoracic folds and of the preoral and caudal lobes. In embryonic arthropods, the margins of the thoracic folds, and to a less degree those of the preoral and caudal lobes, are studded with rows of minute hairs, many of which are sensory. Long before the folds are actually formed, or any chitenous covering is secreted, their future location is clearly indicated by a deeply stained, thickened band of ectoderm. In Limulus the band is first formed as two lateral thickenings, which extend forward and backward, unite, and form a continuous girdle around the neural surface. (Figs. 140–142.)

When the echinoderm larva grows older, the ciliated band is thrown into folds, or tentacle-like lobes (Fig. 292), the larger ones corresponding, approximately, to the marginal outgrowths so characteristic of the cirripeds. (Figs. 289 and 290.)

The apparent difference between them, therefore, is largely due to the absence of chiten in one case and its presence in the other.

The Larval Cephalic Appendages.—The ciliated lobes of the echinoderm larva must not be confounded with primitive appendages, with which they have nothing in common. The true larval appendages appear in the same place as the cephalic appendages of the nauplius, that is, on the neural side of the head in front of the mouth, and in the angle between the lateral margin of the thorax and the preoral lobe. (Figs. 290, 291, 292, *c.a.p.*) There appear to be two pairs; or at least when they have attained their full development and have taken up their final position on the projecting surface of the head, there are three appendages, an unpaired one lying beyond the adhesive disc, and one on each side of it. (Fig. 291, *c.a.p.*) Each appendage is thick-walled and muscular, with a long basal portion and a short terminal knob studded with small adhesive papillæ. At this time they greatly resemble the three cephalic appendages of a tunicate larva (Figs. 284, 285), or the minute adhesive antennæ of the cirripeds and parasitic crustacea. (Figs. 274, 278, 280, 283.)

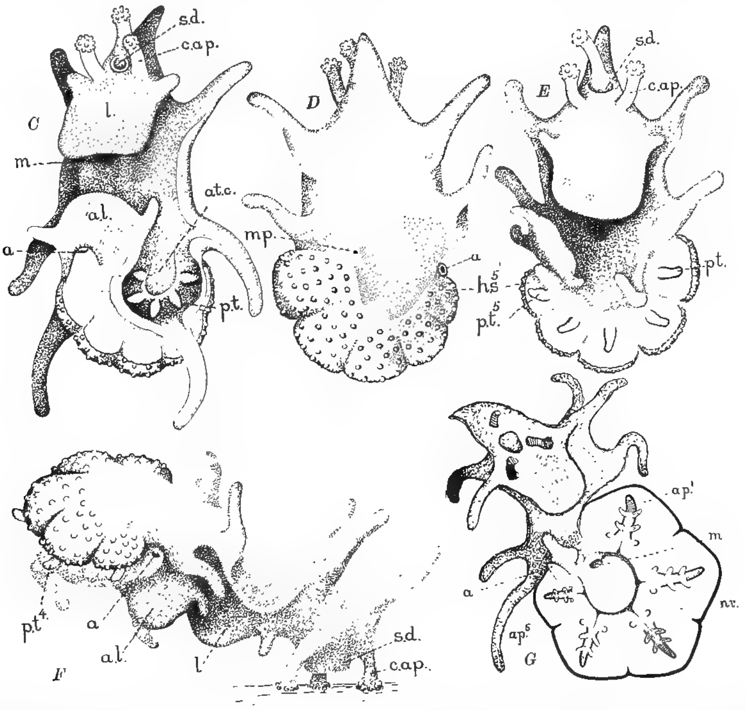


FIG. 292.—Star-fish larvæ, seen as opaque objects, illustrating the mode of fixation and the metamorphosis. Semi-diagrammatic.

Attachment.—The young star-fish larva is said to attach itself voluntarily at first and for a short time only. Later it becomes permanently attached, head first and neural side down, in the same remarkable manner as a young cirriped, both the cephalic appendages and adhesive disc taking part in the process. (Fig. 292, *F*.) In the more primitive echinoderms, such as the crinoids (Antedon), the metamorphosis is even more illuminating. The larva attaches itself wholly by means of the cephalic disc, as the adhesive appendages appear to be absent. Its first position is with the neural, or oral surface down, as in the cypress stage of the cirriped. (Figs. 274, *A* and 295, *D*.) The disc then elongates, forming a slender cephalic stalk, or peduncle, and the larva turns a somersault, bringing its neural side uppermost. Meantime the vestibule, or peribranchial chamber, which at first is small and temporarily closed, enlarges, then ruptures, and the five appendages project from the cup-like head, in typical cirriped fashion. (Fig. 295, *G*.) The cirriped stage (pentacrinoid) is, however, a transitory one, and the young Antedon becomes a free swimming feather-star, by the breaking down of the stalk and the elongation of the appendages.

There are many other representatives of the more modern echinoderms in which the fixed stage is temporary (asteroidea) or appears to be omitted altogether (ectinoidea and holothurioidea), and the young echinoderm, after its metamorphosis, again acquires a limited power of locomotion. But in the most primitive echinoderms, such as the stalked crinoids, blastoids, and cystoids, a permanent attachment by an elongated cephalic stalk, in typical cirriped fashion, was the almost invariable rule, and no doubt represented the primitive condition for the whole class. When an echinoderm does become free, it acquires only a very limited power of locomotion and of coordinated movement. Its characteristic lack of efficiency in this respect is due, not so much to its simple or primitive structure, as to the fact that its freedom was gained at a late period in the phylogeny of a very ancient group, where sessile inaction was the prevailing condition.

Early Embryonic Development.—Let us now return to the early embryonic stages to trace the beginning of the metameres, cœlomic cavities, and thoracic appendages. These structures, when definitely formed, have the same or a very similar structure, location, and mutual relation that they have in the arthropods; but they make their appearance in a somewhat different manner, and at relatively different times, owing largely to the absence of yolk, which has here, as elsewhere, an important influence over the method and relative rate of development.

The Telocœle—After cleavage, which resembles that of the cirripeds, a blastula is formed; from its walls many mesenchyme cells arise, comparable with those which in so many arthropods wander into the yolk from the blastoderm. They are usually more numerous at the point where later the so-called "gastrula" infolding takes place. But this infolding is formed at the caudal end, and extends forward, like the products of all teloblastic growth; and it finally closes in the anal region, not the oral. (Fig. 293.) We have already seen (p. 219), that the real gastrula is always developed at the head end; that the resulting endoderm grows from its point of origin backward, never forward; that the true gastrula opening always persists, if at all, as the oral opening; it is always associated with the stomodæal infolding; it never gives rise to cœlomic epithelium; and is never coincident with the anus.

It is evident, therefore, that the terminal infolding of the blastula in the echinoderm, *tp.*, is in nowise comparable with the true gastrula of molluscs and annelids. It does represent, however, the apical infolding of arthropods (telocœle and telopore) and gives rise, as it does there, to the main mass of the postoral mesoderm and endoderm, but which are here temporarily united to form a continuous layer. Whatever remnant of the true gastrula is preserved in the echinoderms must be looked for at the anterior end of the neural surface, at the point where the primitive mouth arises.

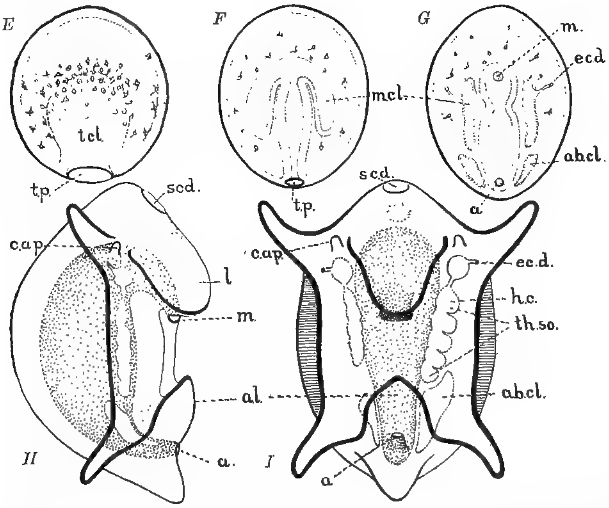


Fig. 293.—Semi-diagrammatic-figures illustrating the development of echinoderm larvæ.

The Mesoderm and the Cœlom.—After the telocœle is formed, the primitive mesoderm and endoderm that form its walls separate, the latter giving rise to the enteron, the former to the paired anlagen of the mesoderm (hydro-enterocœle). The peculiar way in which these two layers separate is merely a specialized process of differentiating the lateral bands of mesoderm and endoderm, and is peculiar to segmented animals with a very small percentage of yolk, and which develop with extreme rapidity (Amphioxus, Balanoglossus, etc.).

The mesodermic vesicles thus formed then break up on each side into two or three main divisions. They are not to be regarded as primitive mesoblastic segments, but as groups of imperfectly divided ones, corresponding probably to the three groups, or tagmas, so commonly present in the arthropods, one belonging to the head, one to the thorax, and one to the abdomen. (Figs. 293, 294.)

The middle section of one side then divides imperfectly into the five chambers of the hydrocœle, *h.c.*, which represent five thoracic somites. If any segmentation occurs in the other vesicles of either side, it is imperfect, and of short duration.

The thoracic somites, as in the arthropods, remain relatively small and without lateral plates, and do not expand laterally onto the hæmal surface.

The more posterior division of the mesoderm, *ab.cl.*, probably represents several abdominal somites and lateral plates which have combined to form the general body cavity, or cœlom. Like the corresponding structure in the arachnids (Fig. 138), it extends rapidly in a cephalic, hæmal, and caudal direction, till it meets the opposite cœlom. (Fig. 294, *E.F.*) The mesentery formed by this union naturally lies to one side of the median hæmal line owing to the unequal growth of the two chambers.

Thus the principal difference between the mesoderm in a young echinoderm, as shown in mercator projection (Fig. 294, *F.*), and that of an arachnid (Fig. 138), lies in the asymmetrical development of the mesoderm and in the absence of segmentation in the abdominal cœlom.

Thoracic Appendages.—Sometime after the five chambers of the hydrocœle appear, finger-like outgrowths of the ectoderm are formed over the thoracic somites. They are the five primary tentacles, or tube feet, which represent five modified thoracic appendages, *th.ap.* An outgrowth of the underlying somite grows into each appendage, in typical arthropod fashion, but instead of breaking up into separate muscles for the appendage it remains permanently in the form of a membranous diverticulum of the hydrocœl, and becomes the distal end of a radiating water vascular canal. Only the distal end of the original appendage separates from the body as the primary tentacle; the remainder of the appendage, however long it may eventually become, may be regarded as lying in the surface ectoderm, developing on either side, as it increases in length, paired cirri that become the double row of tube feet for each arm, and into each of which a prolongation of the water vascular canal extends. (Fig. 294, *G.*)

Excretory Organs.—A portion of the cœlom, probably belonging to the cephalic division, undergoes a special modification. A narrow dorso-lateral outgrowth arises from it that unites with an ectodermic infolding on the anterior aboral, or hæmal surface. From it develops the stone canal and the madreporite. (Fig. 294, *ec.d.*) The ectodermic opening places the hydrocœle in communication with the exterior, so that the organ has often been compared, in whole or in part, to an annelid excretory organ or nephridium. It is, however, more like one of the typical excretory organs of the head region of the arthropods (shell gland, green gland, coxal gland) which consists of thin-walled cœlomic sacs, with a thick-walled tubular outgrowth of varying length, united to a short duct, infolded from the ectoderm. The hæmal location of the external opening to the duct in the echinoderms is no doubt due to the same causes that have carried the corresponding, or at least adjacent, cephalic appendages to the hæmal surface, not only in the echinoderms, but in the entomostraca, cirripeds and tunicates.

The Formation of the Disc.—By the time the larva is attached, the asymmetry of the thoracic region has become very pronounced, due to the fact that practically all the growth is now taking place on the right side of the thorax. In the cephalic and caudal regions the asymmetry is less apparent. (Fig. 294.) As the right half of the oral surface of the thorax takes on a circular form, its hæmal surface divides into five thickened, tubercular, and calcareous plates, each plate corresponding to one of the thoracic appendages and representing the right half of a thoracic tergite. (Figs. 290, 292.) Each of the five plates, or half tergites, becomes the aboral surface of a starfish arm. The cephalic and caudal ends of the thorax finally unite, forming the five-rayed body of the new animal. (Figs. 294, 292, *G.*) The mouth, *m*, is drawn into the center of the neural surface, and is surrounded by the remnants (right half?) of the nerve cord, while the five pedal nerves form the radiating nerves of the arms, and the thoracic cœlomic chambers form the circular and radiating water vascular canals. The anus and madrepore are crowded toward the center of the hæmal surface.

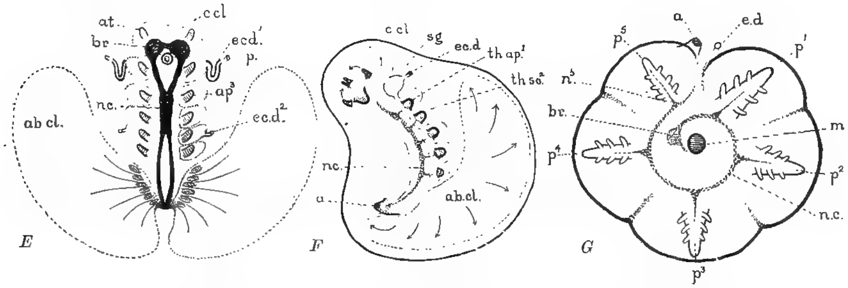


FIG 294.—Diagrams illustrating the probable origin of the echinoderms from asymmetrical, cirriped-like larvæ. The larval organs are seen from the neural surface, in mercator projection. *E*, Hypothetical symmetrical larva; *F*, hypothectia asymmetrical larva; *G*, the radially symmetrical echinoderm.

When the circle is completed, the head of the larva is either gradually drawn into the disc and absorbed, or according to Corens and Danielson, it is amputated, and for a short time may lead a separate existence after its separation from the posterior part of the body, thus recalling the amputation thatoccurs in Sacculina near the close of its metamorphosis, except that here it is the head alone that survives; the abdomen dies.

The Vestibule, or Peribranchial Chamber.—In the starfish, during the formation of the appendages, the neural surface of the thoracic region is depressed and partly enclosed by the thoracic folds, forming a rudimentary atrial or vestibular chamber into which the primary tentacles project like the appendages of an arthropod into the peribranchial chamber. In Echinus and Antedon, the right peribranchial chamber deepens at a very early period and forms a closed vestibule, from the floor of which the five primary tentacles develop in the usual way. (Fig. 295, *D.*) Finally the membranous roof of the vestibule ruptures, allowing the appendages to protrude (Fig. 295, *G*), as they do in a cirriped, or in a polyzoan, (Fig. 301.)

Asymmetry.—The morphology of the echinoderms is dominated by a strongly marked asymmetry. While asymmetry of originally symmetrical animals is no doubt common enough as an embryonic abnormality, it is rarely retained to any marked extent as a permanent feature of the adult. It is, however, a familiar occurrence in the bopeiridæ and paguridæ, although in the last two cases it affects only the terminal metameres, producing various degrees of curvature, but in no wise disguising their morphological characters.

In Limulus, a considerable number of half embryos are always present in material that has been produced and developed under apparently normal conditions; such emboryos probably occur in other arthropods more frequently than we have supposed. The half embryos, in their readjustment to the new conditions of growth, inevitably take on a bow-shaped, spiral, or semicircular form, and may live for several months, although I have never known them to develop beyond the trilobite stage.

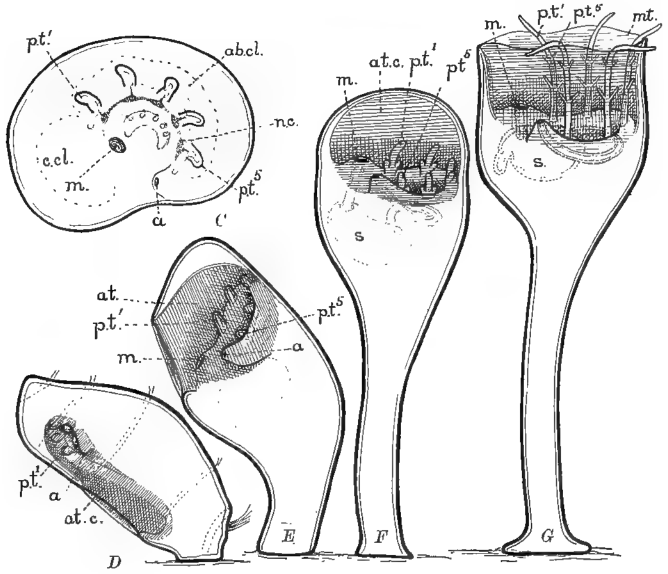


FIG. 295.—Diagrams illustrating the development and metamorphosis of a crinoid (Antedon). *C*, Plan of an early stage seen from the neural surface in mercator projection; *D*, *E*, *F*, *G*, larvæ seen from the side, as semitransparent objects, illustrating the mode of fixation, the revolution, formation of the atrial chamber and of the cephalic stalk.

We assume that half embryos of this nature occurred frequently in the arthropod ancestors of the echinoderms; that they were capable of an organic readjustment that enabled them to survive, and that they became the prevailing form. Whatever animals are assumed to be the ancestors of the echinoderms, it is obvious that half embryos have been produced by them, they have survived, and they have given rise to a new class of animals.

It is a significant fact for the student of creative evolution that the absence of growth on one side of an originally bilateral animal, whatever may have been the cause of that, inevitably compels the remaining side to assume a new form, and thus creates, at almost a single stroke, a new class of animals. In other words, a negative character at one point can create a new character at a different point.

Echinoderms and Cirripeds. Summary.

1. The echinoderms are descended from cirriped-like arthropods in which, as a result of some unknown condition, the absence, or degeneration of organs on one side of the middle section of the body had become a frequent or fixed character.

The five half metameres corresponding to the five defective ones, assumed in consequence, a new architectural arrangement, forming a closed ring with the segmental organs arranged in radiating lines, instead of a double linear series of parallel lines. The five half metameres successfully established a new condition of organic stability, and gave rise to a new kind of body, and a new class of animals; the bilaterally symmetrical head and tail ends of the old body either atrophied completely, or were reduced to structural insignificance.

2. The relation of the echinoderms to the arthropods is shown by the absence, or imperfect repetition of a true gastrula stage; by the conspicuous development of a telopore and telocœle; by the development of a nauplius-like larval form, or naupula; and by the mode of development of the mesoderm, mesoblastic somites, cœlom, and excretory ducts.

3. The echinoderms more particularly resemble the cirripeds in the form of the larvæ, and in their mode of attachment and rotation; also in the mode of growth of the mantle, atrial chamber, appendages, and cephalic stalk; and in the peculiar sessile mode of life that is so characteristic of practically all the more primitive members of the class.

CHAPTER XXIII.

THE ENTEROPNEUSTA, PTEROBRANCHIA, POLYZOA, BRACHIOPODA, PHORONIDA AND CHÆTOGNATHA.

IV. The Enteropneusta. (Figs. 296, 297, 298.)

The resemblance between the larvæ of the enteropneusta and echinoderms has been frequently emphasized, and it is generally assumed that it indicates a common origin for both classes in some worm-like ancestors. We shall show that the resemblance between these larvæ is largely superficial; that between them there are underlying differences, so great as to preclude a direct genetic relation of one to the other, and that neither one nor the other resembles the larva of annelids.

The enteropneusta have also been compared with the vertebrates, because of their aboral nerve cord, perforated gill sacs, "enteric" cœlom, and "notochord." The first two points are of real significance, and together with other evidence, indicate an intimate relation with Amphioxus, tunicates, and other acraniates, but not with vertebrates. The last two points, the "enteric cœlom" and "notochord" have a purely artificial value that has been created by a false interpretation of the early processes of development, for the "archenteron" and the "gastrula" that lie at the bottom of the whole system, have no existence.

The Enteropneusta and the Echinoderms.—The early development of the enteropneusta is very significant. We have already seen that when the gastrula is retained in an essentially unmodified condition, and has the significance originally attached to it, it always gives rise to the endoderm only, its cavity remains as the cavity of the enteron, and its external opening remains as the neurostoma; or the latter is formed at the point where the gastrula opening, or blastopore, closed. These conditions prevail in the annelids and molluscs. Wherever the two inner germ layers arise from a caudal infolding that gives rise to both mesoderm and endoderm, to mesocœle and endocœle, and that in closing gives rise to the anus, not to the mouth, we are dealing with a highly modified process of development that is only remotely comparable with gastrulation, and the presence of which is prima facie evidence that the animals in which it occurs are descended from arthropod ancestors.

It is the latter type of development that is characteristic of the enteropneusta, hence it is apparent at the very outset that their simple structure is not a primitive condition but a secondary one, and that the location of the functional mouth on the hæmal, instead of the neural surface, the formation of an ento-mesocœle in place of a gastrula, and the presence of a telopore in place of a blastopore, definitely excludes the enteropneusta from both the molluscs and annelids, and places them among the descendants of the arthropods.

With these facts in mind, if we compare an echinoderm larva with that of Balanoglossus, it will be seen that the resemblances between them in general form, and in the arrangement of the ciliated bands, are not of special significance; or at least they can be explained on the assumption that both echinoderms and enteropneusta are descended from arthropods, and that their larval forms are similarly adapted to a temporary pelagic existence.

The differences are more fundamental, for in the echinoderm the mouth lies on the primitive neural surface and is still surrounded by the nerve cord, or a remnant of it. Although the larval mouth of the echinoderms is said, in some cases, to disappear, or to close for a time, it opens again, or a new one is formed very close to where the old one was last seen. There are no indications that the permanent mouth of the echinoderms is a hæmostoma, and there are no indications that a functionless remnant of a neurostoma is present. In the enteropneusta the case is different. The permanent mouth lies on the hæmal surface, and outside of the medullary plate; it cannot, therefore, be compared with the functional mouth of the echinoderms, annelids, molluscs, or arthropods. Moreover, in the enteropneusta there are definite indications of a primitive infolding of the neural surface that perforates the medullary plate where the primitive mouth should be located. This opening is not comparable with the hydropore, because it lies on the neural side, not the hæmal. It is, however, comparable in position and development with the neurostoma of annelids and arthropods, and probably represents the subneural gland of the tunicates, and the infundibular tube of true vertebrates. (Compare Figs. 43, 44, 284–297.)

The Enteropneusta and the Arthropods.—The enteropneusta are probably descendants of primitive arthropods in which the essential features of the class were definitely developed. Through one of those inexplicable internal conditions that are exemplified in other sub-phyla of the acraniates, the enteropneusta have failed to develop to their full extent many of the characteristic structures of segmented animals. The power of growth is vigorous enough, for the dwarfed forms of other phyla do not occur here, but the power of organic definition is feeble, producing animals without conspicuous appendages, or outgrowths of any kind, and without a sharp definition or specialization of the organs ordinarily segmentally arranged, such as neuromeres, myotomes, sense organs and cœlomic chambers. We have frequently seen this condition in the abnormal embryos of Limulus, where certain individuals appear, as it were, to have passed through a flame that softened or partly melted the usual surface details (Fig. 184), or that reduced a whole group of metameres to a single appendage, or to an ill-defined unspecialized mass of cells. (Fig. 186.) A somewhat similar condition is familiar enough in the maggot-like larvæ of many insects and arachnids, and especially in those forms where these conditions become more and more accentuated in the later stages, as in Pentastoma, and in innumerable parasitic crustacea.

The initial factor in these cases is, no doubt, a defective germinal structure that determines the character of the older stages and rigidly prescribes the mode of life for the adult. These germinal defects are manifestly cumulative in their results for, as a rule, only the older stages are so modified by them that practically all traces of the initial organs are obliterated. The adult parasitic crustacean with its worm-like body, devoid of metameres and appendages, and with sense organs, nerves, muscles, heart, mouth, and alimentary organs either imperfectly developed, or altogether absent, could not have been recognized as arthropods, with highly specialized ancestors, if it were not for the absolutely conclusive testimony of the embryonic and larval stages.

In the enteropneusta we have a precisely similar condition, except that the particular form of reduction characteristic of these animals is not dependent for its perpetuation upon a parasitic mode of life; and the loss of organic definition extends farther back into the ontogeny, modifying and disguising the embryonic and larval stages, almost as effectually as it does the later ones. Nevertheless, certain characteristic conditions have been retained that demonstrate with reasonable certainty that the enteropneusta are descended from arthropod stock.

Structure and Development.—The *cleavage* is total and the resulting blastomeres are of remarkably uniform size. A deep infolding is formed at the caudal end, representing a typical telocœle, or mesentocœle. The telopore soon closes, but opens again as the anus, or the anus forms at the point where the telopore closes. (Fig. 270, *A.C.*)

The Gastrula and the Telocœle.—At a very early stage a large portion of the inner tube is constricted off, and a funnel-shaped outgrowth extends from it toward the anterior neural surface, where a median ectodermal infolding is formed that unites with it, putting the inner chamber into communication with the exterior.

The history of the important events that take place at this point is by no means clear or conclusive. The early opening in the median neural surface of the proboscis has been called the proboscis pore and has been compared with the hydropore of echinoderms, but the difference in their location is apparently irreconcilable, one being on the hæmal side and the other on the midneural side. Moreover, the primitive proboscis pore does not appear to be the same thing as either the single unsymmetrical proboscis pore, or the two pores that may be present in the adult.

A more satisfactory explanation may be given, it seems to me, and is as follows: The anterior section of the inner tube represents the remnants of the gastrula, and consists of the primitive cephalic mesoderm and endoderm, at first united with the walls of the telocœle, later separating from them as the so-called "proboscis cœlom." (Fig. 270, *g.*) The point of union with the procephalic lobes represents the remnants of the blastopore, and the coincident ectodermic infolding, the neurostoma, and primitive stomodæum, *n.st.* The latter closes and loses its connection with the cephalic endoderm, but leaves for some time a faint central depression that marks its original location. (Fig. 296, *n.st*). The definitive proboscis pores arise later, close to the neurostoma, and open into the proboscis cavity or cavities, which may now be regarded as the definitive cœlomic cavities of the procephalon. (Figs. 296 and 297.)

The Mesoderm and Cœlom.—It is clear that the primitive proboscis cœlom, or cephalic vesicle, is not comparable with the paired cœlomic vesicles of the collar and trunk, for the cephalic vesicle arises at a very much earlier period; it consists of a special type of rounded cells not seen elsewhere, and from them arise the first mesenchyme. It is unpaired, located on the neural side of the head and widely separated from the cœlomic vesicles of the trunk. The latter are paired, have a posterior lateral position, are thin walled, and arise either as evaginations, or as solid outgrowths of the telocœle wall, or as segments of mesodermic bands of teloblastic origin.

The cells forming the primitive proboscis vesicle (Fig. 270, *B.*), are comparable with those that in arachnids (Fig. 141, *ac.*) arise from the inward proliferation of the anterior primitive cumulus, or with those formed in the region of the cephalic lobes in insects. In both cases, and this condition prevails no doubt in many other arthropods, two distinct infoldings or solid ingrowths are formed, the anterior or cephalic one representing the gastrula, the posterior, the teloblasts or telocœle. (Fig. 269.) The anterior one, *g*, gives rise to a mass of cells at the point where the stomodæum is forming, or where it will appear later. From them arises the mesoderm of the procephalic lobes, and the endoderm which either forms the anterior portion of the enteron, or is scattered through the yolk and degenerates.

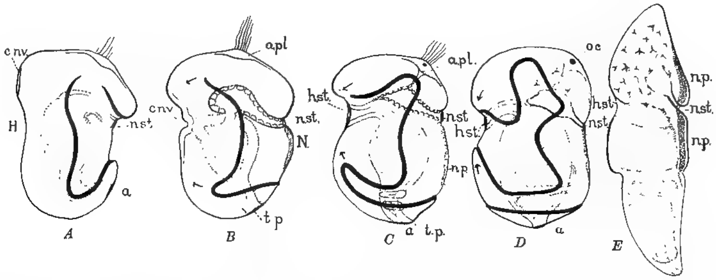


FIG. 296.—Diagrams to illustrate the larval development and metamorphosis of Balanoglossus.

The Larva.—The young larva, at about the time of hatching, is covered with cilia and has somewhat the appearance of that in Fig. 296, *B*. It may now be compared with an echinoderm larva, or with a legless, ciliated nauplius. (Fig. 296, *A*.) The main longitudinal, ciliated band represents, as it does in the echinoderms, the free margin of the thoracic fold, and the margin of the caudal and preoral lobes. The typical tornaria arises as a result of the contraction and subsequent infolding of the anterior hæmal surface of the head. We have studied this process and the part it plays in the formation of the cephalic navel of arachnids, and in the formation of the mouth and the closing up of the hæmal surface of the head vertebrates. Chapter XIV, p. 253. Here we may again recognize the same process. The cephalic navel first appears as a thickened depression of the hæmal surface, *B*.

An outgrowth of the enteron extends toward, and then unites with it, to form the hæmostoma; meantime the surrounding hæmal surface is greatly shortened by the drawing together of the anterior and posterior ends, the progress of the contraction, which may be compared with the reversed curvature commonly seen in arthropod embryos during the formation of the "dorsal organ," being indicated not only by the general shape of the larva, but in a specially striking manner by the changes in the form of the ciliated band, *B*, *C* and *D*.

Metamorphosis.—During the *metamorphosis* the ciliated bands disappear, and the larva rapidly takes on the form of the adult. (Fig. 296, *E.*) The preoral region elongates and forms the proboscis, or procephalon, the middle section forms the collar, or thorax, and the posterior one, the abdomen, or tail.

Cephalic Cæcum.—Meantime a median outgrowth, or cephalic cæcum, arises from the anterior end of the enteron, that marks the beginning of the so-called "notochord" (Fig. 296, *E.*) But neither in structure, nor origin, nor in its anatomical relations, has it any resemblance to a notochord, for we have seen in Chapter XIX, that the notochord is a modification of the middle cord, that it arises from the ectoderm, and that it is never connected with or forms a part of a functional alimentary canal. It is therefore obvious that an organ cannot be regarded as a notochord merely because it is a diverticulum of the gut. In fact, such an origin or connection may be accepted as conclusive evidence that the organ in question is not a notochord.

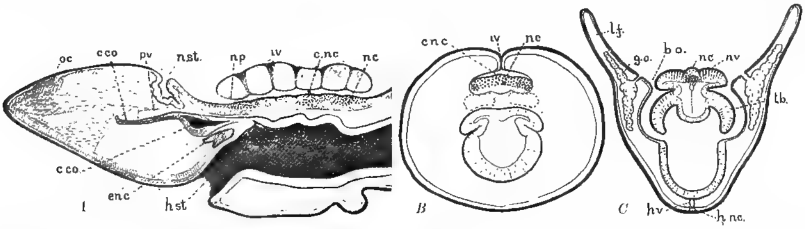


FIG. 297.—Diagrams illustrating the structure of Balanoglossus. *A*, Sagittal section through the procephalon (proboscis) and mesocephalon (collar, thorax); *B*, transverse section of the mesocephalon; *C*, transverse section of the abdominal, or branchial region.

The cephalic cæcum of Balanoglossus, in its minute structure and location is not essentially different from the cæcal outgrowths of the foregut which are so common in arthropods, as for example in cirripeds (Figs. 275 and 277), entomostraca (Fig. 282, *A*), phyllopods (Fig. 273), cladocera (Fig. 10), and arachnids (Fig. 43).

The cephalic cæcum of the enteropneusta probably represents the remnants of that part of the foregut that originally opened into the primitive stomodæcum and neurostoma.

The Late Larval and the Adult Stages.—In the later stages the principal events are: The further differentiation of the main subdivisions of the body, that is, of the procephalic, thoracic, branchial, and caudal regions; and the development of the gill slits, lateral folds, endocranium, excretory ducts, and nervous system.

The relations of these various parts to one another are shown in a diagrammatic way in Fig. 297, which represents a sagittal section of the head and thorax, and in Fig. 298, which represents the entire animal viewed from the neural surface. At this stage Balanoglossus may be compared to a naked phyllopod-like arthropod, with the basal portion of its abdominal appendages infolded in the typical arachnid method to form respiratory sacs, the distal portion persisting as the tongue bar. The gill sacs eventually unite with, and then open into, corresponding cæcal outgrowths from the gut, giving rise to the new type of respiratory organs characteristic of the vertebrates and of several other phyla of the acraniates.

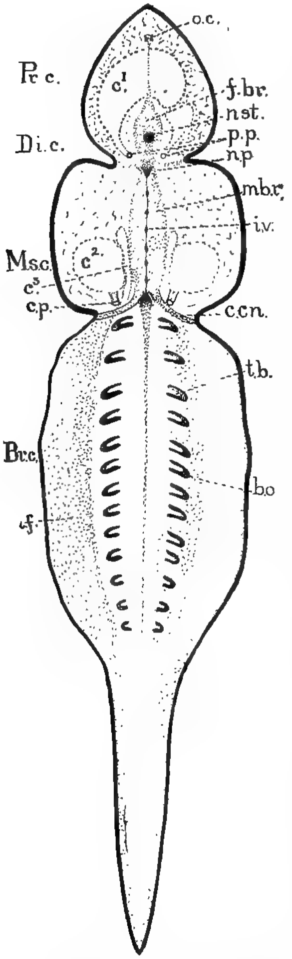


FIG. 298. —Diagram of Balanoglossus, seen from the neural surface.

New respiratory appendages and branchial clefts arise in varying numbers behind those already formed, in the usual manner for segmented animals. The wing-like *lateral folds* (Figs. 297 and 298, *l.f.*), that are so characteristic of the adults, may be compared to the pleural folds on the abdominal metameres of a trilobite, arachnid, or crustacean (Figs. 2, 11), or with the lateral folds of the trunk in a primitive vertebrate. (Fig. 232.) In all these cases the pleural folds represent the extended lateral margins of the neural surface, they lie lateral to the appendages and are turned in a neural direction. (Fig. 297.)

The Endocranium.—We have seen that the endocranium forms a most characteristic structure in the arachnids, and in primitive crustacea related to the phyllopods. In its simplest condition, as in Apus and Branchipus, it consists of a transverse bar, or plate of cartilage, lying in the anterior thoracic region, just back of the neurostoma, and on the hæmal side of the nerve cord. The main body of the endocranium is of mesodermic orgin, and often contains two kinds of cartilage-like tissues that differ in structure and in their reaction to stains; one is a dense fibroid tissue with small flattened nuclei irregularly distributed; the other has more the appearance of hyaline cartilage, and contains large rounded cells, in the peculiar grouping characteristic of certain kinds of primitive cartilage. In a few cases, notably Apus, paired ectodermic ingrowths are formed, lined internally with chiten, which unite with and form an integral part of the endocranium.

These facts have an important bearing on the origin of the enteropneusta, where the endocranium has a similar form and location. Here it is a flattened plate, lying on the hæmal side of the cephalic cæcum, with two slender arms extending backward on either side of the pharynx. (Fig. 297, *en.c.*) The body of the endocranium consists of a sharply defined mass, consisting of clear, concentric "chitenoid" lamellæ, said to arise from the basement membrane of the cephalic cæcum and the pharynx, and in some cases containing cells lodged between the lamellæ. The lateral portions are less clearly defined and consist of a cartilage-like matrix, containing small clusters, or nests of cartilage cells, said to be derived from the epidermis.

Whatever may be the origin of the endocranium in the enteropneusta, it certainly bears a strong resemblance in its location, form, and histological structure to the endocranium of the arachnids and phyllopods.

Muscles.—The arrangement of the muscles in the collar and trunk supports the interpretation indicated above. We have shown (p. 230) that in the arachnids practically all the somatic, or intersegmental, muscles are absent in the thorax, this condition being either the cause or the result of the fusion of all the thoracic and cephalic tergites into one cephalothoracic shield. The muscles that remain belong to the appendages, or to the forward extension of longitudinal abdominal muscles that are attached to the posterior portion of the endocranium. There is, therefore, a marked difference in the arachnids as well as in many other arthropods between the musculature of the thorax and that of the abdomen. According to Ritter there is in Balanoglossus a similar difference between the musculature of the collar (thorax) and trunk. He states that circular somatic muscles are wholly wanting in the collar. Here the principal muscles are radio-longitudinal, attached to the posterior wall of the collar at one end, and at the other mainly to the "notochord" and nuchal skeleton, but also to the walls of the œsophagus. The muscles of the branchial and caudal regions, both longitudinal and circular, are always strictly somatic.

The Cœlom consists of three main divisions. (Figs. 279, 298, $c.^{1-3}$.) That in the proboscis, c^1, may be regarded as the remnants of the procephalic cœlom, and is drained by one or two excretory ducts, comparable with the antennary ducts of crustacea, or the cheliceral ducts of the arachnids (Galeodes). The collar cœlom, c^2, represents that of the thorax, and its excretory duct represents one of the posterior thoracic ducts, *i.e.*, the so-called shell gland of the phyllopods or the coxal gland of the arachnids. The trunk cœlom represents that of the abdominal and post abdominal segments united to form a continuous chamber, and is devoid of excretory ducts as it is in the arthropods generally. (Compare with Fig. 279.)

The Nervous System. The Neural and Hæmal Cords.—The nervous system of arthropods forms: 1. A "ventral" medullary plate consisting of parallel, ganglionated, segmented cords, perforated by the primitive stomodæum. It coincides with the primitive axis of growth and differentiation, ontogenetically and phylogenetically. It is the primary nervous system because it is the oldest, and because it is always associated with the oldest sense organs, muscles and appendages, which develop side by side with it on the neural surface. It rarely keeps pace with the growth of the body, usually concentrating at the anterior end, around, or close to, the stomodæum.

2. The hæmal nerve cord is unpaired, never distinctly segmented, and never associated with important sense organs or appendages. It is the last part of the nervous system to develop, and is associated most intimately with the heart and the hæmal and somatic musculature, which are the last parts of the embryonic body to develop. The hæmal cord extended primarily from end to end of the trunk and was united with the neural cord by segmental, circular nerves. It likewise fails to keep pace with the growth of the body; its point of concentration, however, is never in the anterior cephalic region, but in the cardiac and respiratory region, which tends to shift farther and farther back, beyond the oral and thoracic, and finally into the abdominal region. (See Chapter XII.) Its principal connection with the neural system is with the stomodæal nerve centers at the head end, and with the respiratory neuromeres of the abdominal region. But even the former connection is lost, or greatly reduced in the highest types, leaving only the segmental cardiacs of the vagus and respiratory neuromeres as a means of connecting the main hæmal nerve with the nerve cords on the opposite side of the body. (Limulus).

The principal parts of the nervous system of the enteropneusta correspond with those of the arachnids as outlined above, the most important point being the identity of the primary neural surface of the arthropod with the principal neural surface of the enteropneusta. In the arthropods, it is true, the medullary plate is on the oral side, while in the enteropneusta it is on the aboral side, but it is the mouth that has changed, not the neural surface with all its fundamental relations. The hæmal mouth is a new formation, while the old mouth may still be recognized in its proper place in the median depression of the cephalic lobes. (Fig. 297, *n.st.*) The medullary plate of the proboscis represents the remnants of the supra-œsophageal ganglion, and is still connected with the small eye spot, *ac.*, which probably represents the remnants of a parietal eye. (Figs. 296–298.)

The thoracic neuromeres form the principal part of the nervous system, and at an early period are bodily infolded to form the floor of a canal or tube. The latter usually remains open at either end, and a variable number of vertical canals, or strands of tissue, persist over the median line and appear to mark the point where the medullary folds are imperfectly united (Figs. 296, 297, *iv.*), recalling the vertical strands of ectoderm between the compacted thoracic neuromeres in the insects and arachnids. (Figs. 221, 229 and 231.)

In cross sections the thoracic or collar neuromeres form a thick band of small nerve cells with an underlying layer of "punct substanz." The general appearance of the cord is similar to that of a young scorpion, the more so since the nerve cells, for a time, may be arranged in radiating lines around minute cavities (Harrimania, Ritter) like those so characteristic of the embryonic cords of the arachnids. (Figs. 15, 16 and 227.)

The posterior end of the thoracic nerve cord is united by nerves of considerable size with the median hæmal nerve (Fig 297, *h.nc.*), the latter representing the median cardiac nerve of the arachnids. (Compare Figs. 78, 115 and 117.)

V. The Pterobranchia. (Figs. 299, 300.)

The pterobranchia have been shown to have a structure so much like that of the enteropneusta in respect to the location of the functional mouth, medullary plate, gill pouches, cephalic cæcum, cœlomic chambers, and excretory ducts, that the fundamental features in the morphology of both groups must be, without doubt, interpreted in the same manner. If this is done, then it is apparent that the features which are more specially characteristic of the pterobranchia, such as the six pairs of appendages, the short, branchial region, the U-shaped intestine with the anal end bent toward the posterior neural surface, and with the genital ducts opening in the neural surface of the branchial region, give a decidedly arachnoid character to the adults, and strengthen and confirm the interpretation we have given for the enteropneusta.

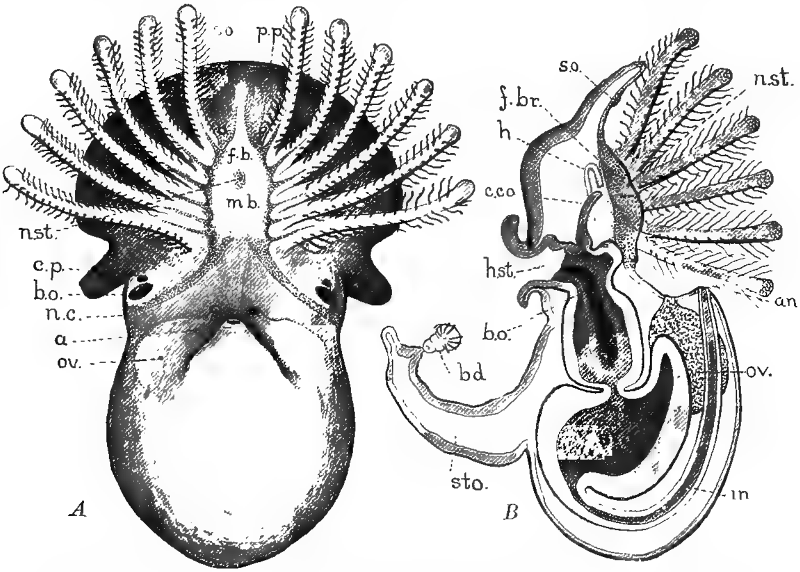


Fig. 299.—Diagrams of Cephalodiscus. *A*, Neural surface; *B*, side view, in optical section.

Cephalodiscus may therefore be regarded as a naked arthropod-like animal with a closed neurostoma, the location of which is indicated by the pit in the anterior portion of the neural plate (Fig. 299, *n.st.*), and by the cephalic cæcum, *di*, that probably united the primitive stomodæum with the enteron. The cephalic disc with its procephalon, thoracic appendages, and thoracic neuromeres, *m.b.*, represents the cephalothorax; the excretory ducts, opening to the exterior by the proboscis pores and collar pores, *p. p.* and *c. p.*, represent respectively the cephalic and thoracic ducts of arthropods; and the single pair of gill sacs, *g.p.*, represent a pair of invaginated respiratory appendages of the vagus region. The genital organs and ducts have approximately the same location as in many arachnids and crustacea, that is, just behind the vagus region.

The thoracic appendages of Cephalodiscus develop in an approximately regular order, from before backward, like those of arthropods. (Fig 300, *C*,*D*.) In Rhabdopleura, the arms probably represent a single pair of enlarged, antenna-like cephalic appendages. (Fig. 300, *A*,*B*.)

Attachment is effected, as in the tunicates, by a postoral hæmal outgrowth probably representing a special modification of the posterior part of the cephalic navel. (Figs. 299, 300.)

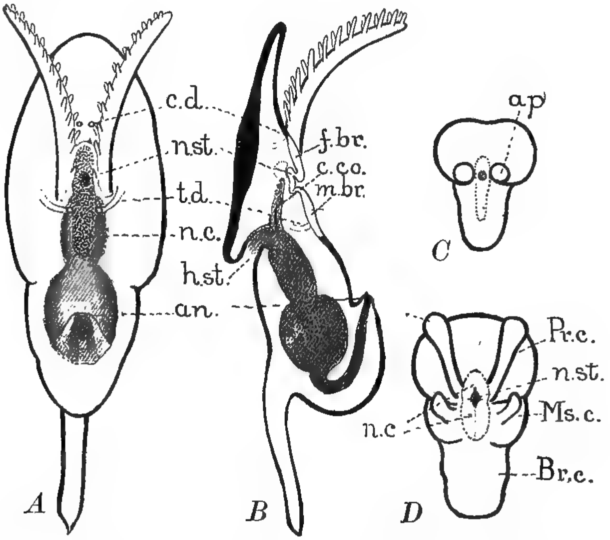


FIG. 300.—Diagrams of Rhabdopleura. *A*, Adult, from neural surface; *B*, from side, in optical section; *C*, *D*, larvæ of Cephalodiscus, from the neural surface.

It will be recalled that the cephalic navel is a center of convergent growth, and that the location of the center, and the nature of the events that take place there is largely dependent on the volume of the yolk sphere and the rate at which the growing tissues spread over and enclose the hæmal surface. The conditions created at the closing area, where the advancing lines of equal growth and differentiation tend to meet and annul one another, may result, at the cephalic end, in an ingrowing tube, the opening of which becomes the hæmastoma, and at the caudal end, as in the tunicates and Pterobranchia, in a stolon-like outgrowth that retains an indefinite power of growth and that becomes the seat of successive generations of new buds.

VI. THE POLYZOA.

The polyzoa likewise may best be interpreted as descendants of primitive arthropods of the cirriped type. They do not develop a clearly marked metameric structure, and they are disguised by the loss of important larval organs, the result of an extensive degenerative histolysis; but in the structure and development of the larvæ and in their attachment and metamorphosis, indications of arthropod affinities may be recognized.

The entoprocta have undergone the least modification, and one of them, Pedicellina, will best serve to illustrate the salient characters of the group.

The young, as in so many other acraniates, undergo the earlier stages of development within the brood pouches of the atrial or vestibular chamber. There is a total and nearly equal cleavage, and the flattened, hollow blastula is infolded

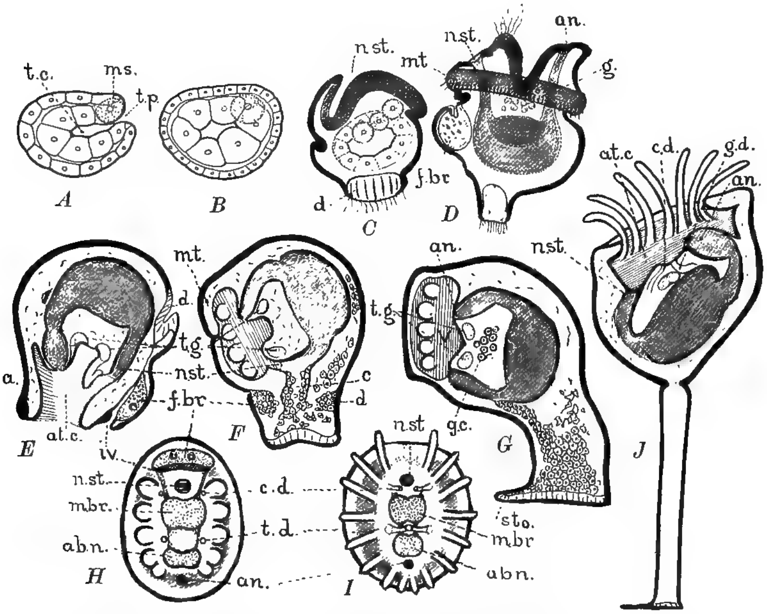


FIG. 301.—Development of an endoproctous polyzoan (Pedicellina). *A–D*, Formation of the telocœle, and the early larval, or naupula, stages; *E–G*, mode of attachment, and metamorphosis; *H–I*, early and late larval stage, seen from the neural surface. The most significant features are the absence of a true gastrula; the conspicuous mantle, its formation of a vestibular, or atrial, chamber that encloses the appendages and the whole neural surface of the body; the attachment of the larva by means of a large cephalic stalk; the rotation; and the degeneration of the prosencephalon. Semi-diagrammatic. (In part after Hatscheck, Harmer, and Barrois.)

at the caudal end to form a telocœle. (Fig. 301, *A*.) The telopore closes and an independent ectodermic infolding at the head end unites with the enteron, forming the primitive stomodæum and neurostoma, *n.st.* A typical gastrula stage, and a blastopore, therefore, does not occur. The larva is a naupula, not a trochosphere, as shown by the prominent labrum, by the longitudinal ciliated band representing the thickened margin of a branchial fold, and by the telocœlic method of forming the germ layers. The enteron is U-shaped, with the concave side turned toward the neural surface. There is a conspicuous apical disc, *d*, and a large preoral ganglion, or forebrain, that is probably united by circumoral commissures with the rudiments of a ventral nerve cord. The latter appears as two thickenings separated by a deep infolding, one next the anterior wall of the stomodæum, the other in front of the rectum, *t.g.* The two ganglia may be regarded as representing the postoral and the anal group of ganglia of the nauplius. (Fig. 272.)

On either side of the stomodæum is an excretory duct (Fig. 301, *H. I. c.d.*), that corresponds approximately with the cephalic excretory duct of the nauplius. The genital cells and genital ducts appear to arise from the deep infolding between the postoral and postanal ganglia, in a position, therefore, that corresponds to the location of the same organs in the nauplius, in Cephalodiscus, and in the adult stages of many arachnids.

The early development of the relatively large brain and nerve cord definitely locates the primitive neural surface, and gives us the necessary data for the proper orientation of the larva. The latter comes to rest in the typical naupula fashion, neural side down. (Fig. 300, *E.*) A large cephalic outgrowth is then formed, and as it elongates, it straightens out and lifts up the body, which meantime turns a half somersault, bringing its neural surface uppermost. The edges of the pleural folds, about the time of attachment, unite to form a closed vestibule, or atrial chamber, *at. c*, within which the appendages make their appearance, *F.* During the revolution of the larva, they elongate, rupture the vestibule, and finally protrude from it in the same manner as the legs of a cirriped, or the arms of a young crinoid. (Figs. 274, 295.)

During the early stages of revolution, the brain and apical disc separate from the ectoderm and break up into a mass of loose cells that nearly fill the cavity of the cephalic stalk. (Fig. 301, *F.*) They appear to increase in numbers and to receive accessions from other sources. The anterior wall of the enteron, or vestibule according to Harmer, then breaks down, and its walls, surrounding an ill defined space, merge with the degenerating cells in the stalk. Later some of the cells undergo still further degeneration, whether by being bodily enclosed in the cavity of the enteron as seems probable, or not, does not appear. In either case the rupture in the walls of the enteron closes over and the amorphous mass of degenerating cells decreases in volume. Some cells appear to persist in the stalk as star-shaped, connective tissue cells.

The point that appears to be clearly established is the disappearance of the forebrain and apical disc by a process of histolysis, that seems also to affect other adjacent tissues, including the anterior wall of the enteron. The fate of the free cells thus produced is not clear. It is obvious that the whole process, even in the way it affects the forebrain and apical plate, is very similar to those which occur on the hæmal surface of the thorax, and in the cephalic navel, or dorsal organ, of cirripeds and parasitic copepods, and it occurs in a corresponding region, that is, on the anterior hæmal surface of the head, at the point where attachment takes place. (Figs. 274, 282, 283.)

It will be recalled that the cephalic navel of arthropods is an area on the anterior hæmal surface of the cephalothorax, where extensive degeneration of embryonic tissues takes place. The degenerating cells are derived from two principal sources, the hæmal blastoderm and the hæmal musculature of the anterior part of the thorax. They concentrate at a definite point on the hæmal surface of the head, where they are invaginated en masse into the yolk, and thence into the enteron where they are absorbed.

The hæmal blastoderm cells are always invaginated into the yolk and absorbed. The degenerating lateral plate cells of the thorax certainly do not, as a rule, undergo this fate, although it is difficult at times to distinguish between them and those derived from the hæmal blastoderm. The vast majority of them either degenerate in situ, become free blood-corpuscle-like cells, or regenerate into scattered muscle cells. See Chapter XIII, p. 230.

The cephalic navel of arthropods is regarded as furnishing the initial conditions that lead to the formation of a hæmostoma. Pedicellina is the only case known to me where the seat of degeneration appears to be in temporary communication with a definitely formed enteron.

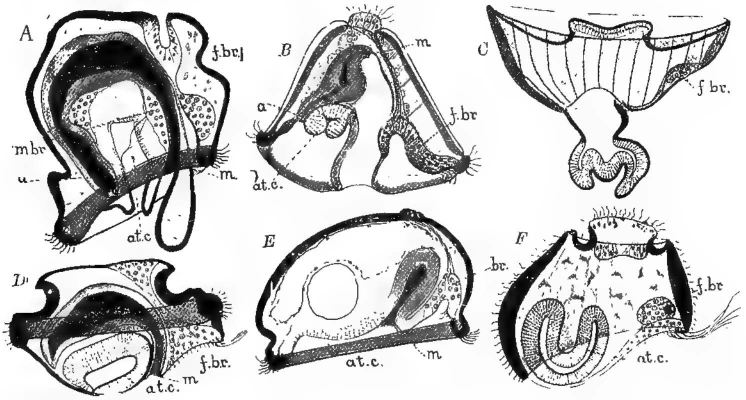


FIG. 302.—Larvæ of polyzoa in the naupula stage, illustrating the degenerative, or pauperitic development of the first generation. *A*, Pedicellina; *B*, Cyphonautes; *C*, Lepralia; *D–E*, Ctenostomidæ; *F*, Bugula. (After Barrois, Prouho, and Harmer, slightly modified. Semi-diagrammatic.

Conclusion.—The main features in the structure and development of the entoprocta agree with those of primitive arthropods, and not with those of the molluscs, or annelids, or with any other worm-like animals. In place of the gastrula, blastopore, and trochosphere that are typical of annelids, we have the telocœle, telopore, and naupula that are typical of the arthropods.

The larva resembles that of cirripeds, in passing its early stages of development within a brood pouch; in its subsequent mode of attachment and rotation; in the mode of growth of its cephalic stalk and mantle, and in the histolytic changes in the region of the cephalic navel; and in the location of the genital cells and principal ganglia.

The Ectoprocta.—The ectoprocta may be regarded as modified derivatives of the more primitive entoprocta. They present an extraordinary diversity of larval forms, methods of metamorphosis, egg formation, budding, and degeneration. It is not our purpose to discuss these interesting but exceedingly intricate processes; we merely wish to point out what we consider to be the chief morphological features of this particular division of the acraniates.

One of the controlling factors in the morphology of the ectoprocta is an extreme exaggeration of those initial defects in germinal material that have been observed in all the acraniates. The result is that the first generation of zoids are, at the very outset, unusually deficient in the various organs that are normally present at those periods. These defective embryos fail to develop beyond the larval stages, as practically all their organs undergo degenerative histolysis. After the attachment, practically nothing is left of the original larva but a shapeless sac filled with a mass of indifferent cells. A second factor in their morphology is that a new generation of zoids arises from a bud-like infolding on the hæmal surface of the first larva. This new product is not to be regarded as the completion of the development of the first zoid, but as a new zoid, representing a second generation that arises from the formless remnants of the first. But while the first generation of larvæ conform in the main, as far as they go, with the larvæ of the entoprocta, the second generation develop into a new type, due to the fact that its primary, or oro-anal axis, is bent double, in exactly the opposite direction from that in the entoprocta. That is, in the ectoprocta the body is bent so as to bring the caudal end to a point just in front of the head instead of behind it, elongating and making convex the primitive neural surface, and greatly shortening the hæmal surface, thus reversing the conditions in the entoprocta. (Compare Figs. 301 and 303.) In the ectoprocta, the resulting elongation of the body is therefore in a hæmo-neural direction, and it appears to be brought about in the same manner as in Phoronis (Fig. 305), by the evagination of the middle section of the enteron through the space between the divergent, postoral nerve cords. The latter, owing to the very unequal growth of the hæmal and neural surfaces, appear to be transferred to the hæmal surface, but in reality undergo but little change of position. The primitive, preoral ganglion, or forebrain, apparently fails to develop, or it subsequently atrophies, as in the entoprocta and phoronida. Consequently the so-called circumoral nerve ring of the ectoprocta does not represent the original nerve ring connecting the pre- and postoral ganglia, but the ventral cords and their transverse commissures. (Fig. 303, *B*.)

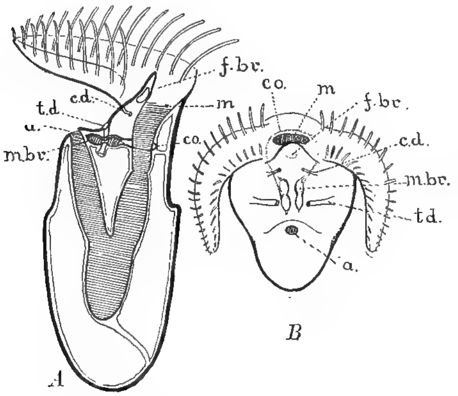


FIG. 303.—Diagrams of an ectoproctous polyzoan. *A*, Seen from side; *B*, from neural surface.

The lophophore on this interpretation may be regarded either as a single pair of greatly enlarged cirrate appendages, comparable with those of brachiopods, or as the laterally extended row of many minute appendages.

It will also be observed that the entoprocta are attached by stalk-like outgrowths from the hæmal surface of the head, in typical acraniate fashion (Fig. 301, *J*), while the adult ectoprocta of the second generation, like Phoronis, are attached by the evaginated neural surface. (Fig. 303, *A*.)

VII. THE BRACHIOPODS.

Our knowledge of the development of the brachiopods is fragmentary and the data we do possess are lacking in detail and precision. The evidence, so far as it goes, indicates that the brachiopods belong with the acraniates and that their structure is best interpreted as a modification of the arthropod type. In fact, they appear to have retained some of the characteristic features of the cirripeds in a less modified form than any other group of acraniates, while their own distinctive features constitute a natural transition to the condition realized in the phoronida and polyzoa. As in cirripeds, the eggs pass through their early stages of development, in some cases the whole larval development (Stringocephalus, Zittel) in brood pouches formed by folds in the mantle chamber.

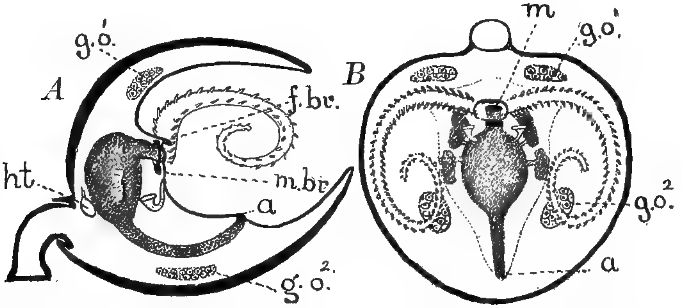


FIG. 304.—Diagrams of a brachiopod. *A*, Seen in optical section; *B*, from the neural surface.

Cleavage is total and almost equal, giving rise to a hollow blastula that is infolded to form a telocœle. The telopore closes, the mesoderm separates from the entoderm as two cœlomic chambers, and the body is divided by two transverse constrictions into what appear to represent the cephalic, thoracic, and abdominal regions.

The details of the method of attachment and of the subsequent metamorphosis are not clearly understood, but they appear to be essentially the same as in Pedicellina. A hæmal outgrowth serves for the permanent attachment of the larva and a voluminous mantle fold encloses the body in a typical atrial chamber. The mantle secretes a thick shell, resembling in its somewhat complex minute structure, the simpler forms of the mantle skeleton in the cirripeds.

The two valves are usually spoken of as dorsal and ventral, but morphologically they are better designated as either cephalic and caudal, or anterior and posterior, corresponding approximately with the rostrum and carina of the cirripeds.

The stomodæum arises at a comparatively late period and is without doubt formed on the primitive neural surface, as indicated by the location of the nerve ring itself and by the position of the simple sac-like heart on the opposite side of the enteron, *h*.

The genital cells are located in the walls of the mantle, one pair in the cephalic, *g.o.*[1], the other, *g.o.*[2], in the caudal lobe, recalling the arrangement of ovaries and testis in the cirripeds.

The nervous system, in spite of the relatively large size of the animals, is rudimentary in the extreme, the central portion consisting of a slender circumoral ring with a small, postoral ganglion.

The forebrain, considered as a nerve center, may be regarded as practically absent, since the preoral portion of the ring consists of little more than a slender commissure. The fact is significant, in view of the absence of the preoral ganglion in the polyzoa and phoronida owing to its histolytic degeneration during the metamorphosis, and in view of the extremely rudimentary condition of the forebrain in all other members of the acraniates.

VIII. The Phoronida.

In the ectoprocta we can only infer from the condition that obtains in the adult, that the metamorphosis of the second generation of zoids takes place in the manner described above, for the embryonic processes by which this result is attained are not clearly defined. In the phoronida, however, where the adult condition is apparently very similar to that in the ectoprocta, the successive steps in the metamorphosis of the larvæ are sharply differentiated and are sufficiently well known to supply this deficiency.

The eggs are nearly yolk free and undergo the early stages of development in the recesses of the lophophore. The cleavage is nearly equal, forming a hollow, nearly spherical blastula that is infolded at one side to form, apparently, a nearly typical gastrula (Fig. 305, *A*), the blastopore remaining open as the mouth, and the infolded cells forming the permanent enteron. The latter extends in a caudal direction, the anus forming at the point where it unites with the ectoderm. The mesoderm arises as isolated cells at various points from the walls of the blastoderm and especially in the vicinity of the anus. It is, apparently, not formed in conjunction with the endoderm, nor does it separate from the later as definitely formed cœlomic chambers.

There is a prominent apical plate, *a.pl.*, that probably represents the beginning of the forebrain, or supra-œsophageal ganglion.

A thick, longitudinal band, *ab*, is formed at an early period, that contains the anlagen of the larval appendages and probably such portions of the postoral nerve cords as are represented.

The preoral lobe corresponds roughly to the labrum and procephalon, and the region covered by the diagonal ciliated band, to the thorax of the naupula. The abdominal region, as in the ectoprocta, is represented by an imaginal disc-like infolding that grows, in a measure, independently of the rest of the larva, *C*, *ab*. After a while, the thickened floor of the infolding, that has become irregularly folded, ruptures its amnion-like covering, and is violently everted, carrying a U-shaped fold of the enteron with it. Meantime the anal end of the larva is drawn in a hæmal direction, the diagonal band ruptures, the forebrain, preoral and marginal lobes break down, and the fragments pass into the enteron through the mouth. The short permanent appendages, which are lined with a prolongation of the cœlomic epithelium, assemble in the oral region, forming the basis for the lophophore.

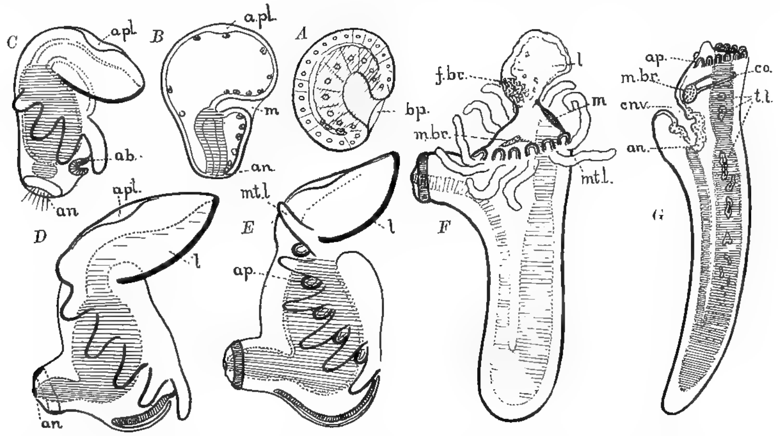


FIG. 305.—Diagrams illustrating the development and metamorphosis of Phoronis. (In part, after Selys-Longschamps.)

The primitive cerebral ganglion, or forebrain, disappears with the preoral lobe, and the permanent ganglia appear to be derivatives of the ventral cords, transferred to the hæmal surface with the permanent appendages. As in the ectoprocta, these ganglia are connected with each other by a circumœsophageal band that probably represents the remnants of the transverse commissures, which have been greatly elongated by the hæmal migration of their appropriate ganglia.

Fusiform Cells.—At about the close of the metamorphosis, many peculiar spindle, or fusiform cells make their appearance, that probably represent the remnants of the disintegrating, or the unformed, thoracic musculature. In their histological structure, general appearance and distribution, they agree closely with the fiber cells of Limulus and of many other arthropods. See Chapter XIII, p. 232.

In Phoronis, they are mingled with the vaso-peritoneal tissue, or float freely in the cavity of the body. They have been regarded as modified blood cells, but their origin and fate has not been definitely determined. According to Selys Longchamp, they have a distinct longitudinal, usually spiral striation, and apparently a small eccentric nucleus. When alive they are flexible, but become hard and brittle when fixed. Their color and appearance is suggestive of muscular substance. Similar cells occur in Lingula (Yatsu) and are said to occur also in the annelids (Nereis). Their significance in the annelids is not apparent. In the arthropods they are associated with special forms of muscle building and with muscle degeneration. They are significant in the acraniates (phoronida and polyzoa), for they are indicative of the occurrence of extensive muscular degeneration, and of the secondary character of the anatomical structure of these animals.

Selys Longchamp figures a deep infolding that is formed in the middle of the hæmal surface at the close of metamorphosis. It is not described in detail, but it appears to be the seat of extensive degeneration, similar to that in the cephalic navel or "dorsal organ" of arthropods. (Fig. 305, *G*, *c.nv.*)

IX. THE CHÆTOGNATHA.

The chætognatha are clearly to be regarded as the modified descendants of primitive arthropods, for they retain, even in the adult stages, some of the more important characters of that group. The head (Fig. 306, *A. B.*), with its rudimentary appendages, mantle (prepuce), and organs of special sense, represents the modified remnants of the nauplius; while the trunk, which is a voluminous but very simple caudal outgrowth from it, represents the imperfectly developed thoracic and abdominal tagmata, *I*, *Brc.*, and *ab.* They show no recognizable division into metameres, and are used mainly for locomotion and for the retention of sexual cells. There is no distinct larval stage, no period of fixation, and no striking metamorphosis; the adult is to be regarded merely as a sexually mature naupula adapted for, and leading throughout its whole life, a pelagic existence.

Development.—The eggs are relatively large (2 mm. in Sagitta), transparent, and contain a considerable amount of yolk. They are discharged in the early morning, and develop very rapidly, the young escaping from the egg membranes between 6 and 8 o'clock on the evening of the same day. Cleavage is total and nearly equal, resulting in the formation of a spherical blastula with a small cleavage cavity. The so-called "gastrula" is in reality a typical telocœle, and is formed at the caudal end by the infolding of the teloblasts and primitive germ cells. Two primitive sexual cells may be recognized at an extremely early stage on the posterior neural surface of the blastula, *D*, *g*, in a position that corresponds with their early location in many different arthropod embryos. (Lernæa, hymenoptera, coleoptera, etc.)

The apical infolding carries with it the mesentoblasts and germ cells, the latter finally lying at the anterior extremity of the telocœle, *E*. With the closure of the telopore, which appears to take place on the posterior, neural surface of the embryo, the mesoderm, endoderm, and germ cells begin to separate from one another. The endoderm forms the walls of the primitive gut, *F*, *en*, and the mesoderm forms sac-like diverticula on either side, *m.s.* In the next stage, *G*, the mesoderm has divided into two pairs of mesodermic chambers, one for the head, *c.m.s.*, and one for the trunk, *th.ms.* The anterior end of the primitive gut unites with an ectodermic infolding at the cephalic apex, that gives rise to the mouth and stomodæum, *n.s.t.*; the posterior end extends backward and ultimately unites with the caudal apex at the point where the anus is formed later. Meantime the two primitive germ cells have divided into four cells, two on either side of the free end of the enteron. The two anterior ones are the anlagen of the ovaries, *ov.*, and the two posterior ones of the testis, *t.*

In the next stage, *H*, the mesocœles break down, the mesoderm forms a practically solid mass, and the post-anal section of the body develops. During the early cleavage stages, a large nucleus appears in association with the cells that give rise to the mesoblasts and germ cells, *C*, *x.* Later it is transferred to the primitive germ cells, and finally breaks up into fragments and disappears. It appears to represent the "yolk nuclei" so characteristic of arthropod eggs containing a large amount of yolk.

In the newly hatched young, *I*, three regions may be recognized, the head, *Pr.c.*, consisting of what appear to represent the rudiments of one, possibly three pairs of appendages. It is partly enclosed by two lateral folds, *mt.t*, that may be regarded as the remnants of a bivalve shell of the naupula.

The trunk, *Br.c.*, contains very large, paired ventral ganglia, *m.br.*, and the ovaries, *ov.* A membranous partition separates the trunk from the caudal region, *a.b.*, in which are located the testes, *t.*

The three divisions of the body indicated at this early period are not comparable with metameres; they represent three tagmas, or three imperfectly developed body regions, head, thorax, and abdomen, such as are commonly seen in many primitive arthropods, or in the embryonic stages of the more highly developed forms. In the chætognatha, either these regions have never been definitely divided into metameres, or if so, the metameres have disappeared through the regressive or degenerative processes that are so prevalent in the acraniates.

The Adult.—The newly hatched young, without any strongly marked larval stage, pass directly into the adult form. The most noteworthy fact in their development is the relatively enormous size of the ventral ganglion in the younger, as compared with the older stages, indicating a certain amount of degeneration in the history of the group.

The integument may be very thick and surprisingly complex for animals of such a low grade of development. It consists, in some genera, of a complicated irregular network of interlacing trabeculæ, recalling the vacuolated or cancellous ectoderm of the cirripeds, branchiopods, and tunicates.

Excretory organs are not definitely known to occur, although the ducts opening near the base of the mandibles, *d*, may be connected with such organs. They are regarded by Moltchanoff as the nephridia-like ducts of the first metamere.

There is no heart, and no circulatory organs, and there are no indications of a cephalic navel. The body and the alimentary canal are straight, that is, there is no marked neural or hæmal curvature, and no multiplication by budding, agreeing in these respects with the cephalochorda and the enteropneusta.

The trunk of the adult is elongated, spindle-shaped, flattened on the neural and rounded on the hæmal surface, with broad pleural, or thoracic folds, of various forms in different genera. The caudal portion is provided with a telson-like terminal lobe.

The head of the adult undergoes but little change over that seen in the young larva, the most conspicuous features being the prepuce-like mantle folds, representing the bivalve shell of the nauplius, *pr*, and the pair of large muscular lobes or mandibular-like appendages, *md*. They are provided with a group of sensory, or glandular follicles, *fo.*, and armed with stout movable spines consisting of a chitenoid material, apparently perforated with typical pore canals and enclosing a conspicuous pulp cavity. The structure of the follicles and spines gives the appendages a decidedly arthropod appearance.

The Endocranium.—The mandibles and their spines are moved by powerful adductor muscles, in which is imbedded what appears to be a small median fibroid, or cartilaginous plate, *en.c.*

It was this plate that Grassi referred to as an organ of unknown significance, but which might possibly prove to be a "precious jewel" in the eye of the morphologist.

In his description of the muscles in question, he states (p. 42.): "Esso e dentro l'involucro chitinoide del complesso mediano. Questo musculo, siccome dissi, ha forma d'arco concavo anteriormente; in un suo-seno, sotto al punto di massima concavità dell'arco, riposa un corpicciolo ovale, appiattito nel senso dorso-ventrale, fatto di cellule neucleate piuttosto piccole ed a contorni piu or meno decisi; esso e coperto di fibre muscolari da ogni lato, eccetto il dorsale e l'anteriore, dov'è separato dall' esofago per l'involucro chitinoide del musculo. Questo involucro e la musculatura lo separano dalla commissura nervosa boccale. Ho riscontrato l' organo in discorso in tutte le specie, eccetto la Claparedi; piu voluminose sono le specie, piu compare grosso. Per quanto indagassi non riuscii ad intenderne la significazione fisiologica e morphologica. Posso congetturare soltanto che si tratti di un organo o nascente o rudimentale, e percio di una pietra, forse preciosa agli occhi del morphologo."

The plate in question no doubt represents a small endocranial cartilage, or sinew, serving for the attachment of the mandibular muscles. It has a special significance for us because we have seen that a similar cartilage is imbedded in the mandibular muscles of many primitive arthropods, as in Branchipus, Apus, and many others, and that it forms the starting point for the cartilaginous endocranium of the higher arthropods and of the vertebrates. See Chapter XVII, p. 312.

Nervous System.—The chætognaths are the only acraniates that retain in the adult a comparatively large forebrain, with the full equipment of stomodæal ganglia, nerves and cephalic sense organs, *B*, *f.br.*

It sends nerves to three sets of cephalic sense organs, to the stomodæum, mantle, and to the oral appendages and their follicles. It is connected with the ventral ganglion by double circumœsophageal commissures, and probably includes the rudiments of the primitive forebrain and one or more segments of the diencephalon. In its general appearance, it resembles the brain of a primitive arthropod more than that of any other invertebrate. This is shown by the internal arrangement of the commissural fibers, medullary substance, and nerve cells, as well as by the arrangement of the principal sensory nerves, and the distribution of the voluminous stomodæal nerves and ganglia. The lateral stomodæal ganglia,

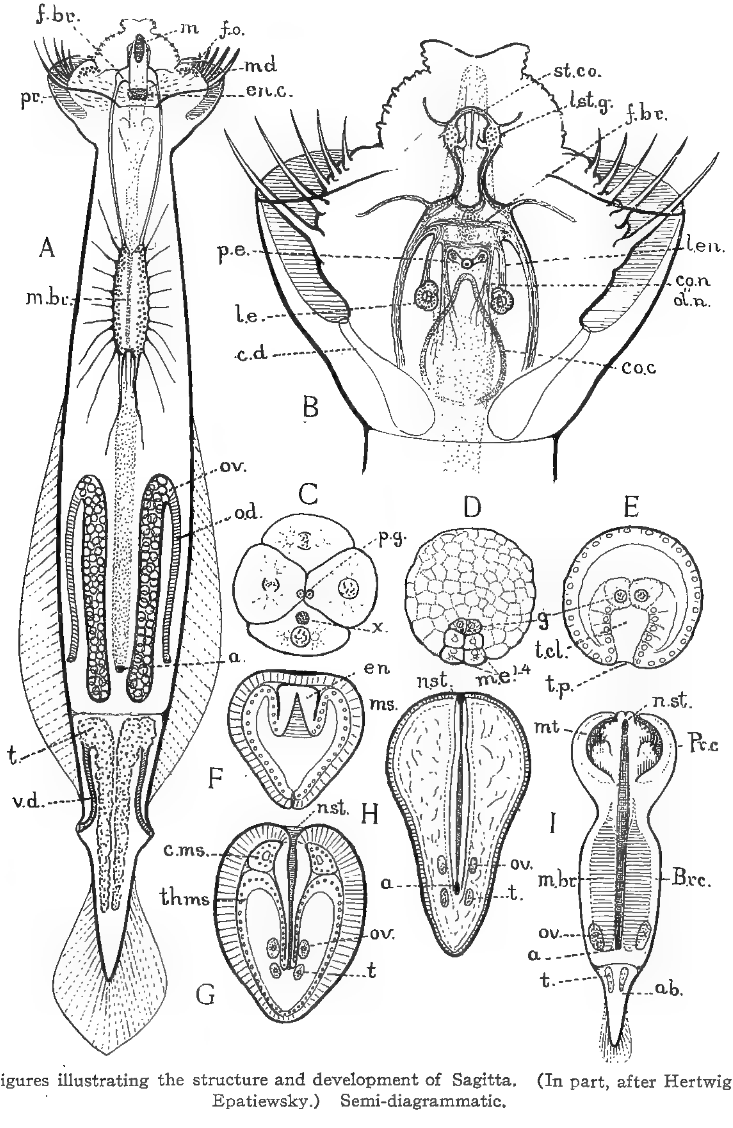


FIG. 306.—Figures illustrating the structure and development of Sagitta. (In part, after Hertwig, Grassi, and Epatiewsky.) Semi-diagrammatic.

l.st.g., are more widely separated from the forebrain than in most arthropods, but otherwise they have a similar relation to the stomodæum and forebrain. They are united with each other by the same highly characteristic cross commissure, *st.co.*, that passes over the anterior hæmal surface of the stomodæum, and that forms such an important landmark in the brains of insects, arachnids, and phyllopods. Moreover the lateral stomodæal ganglia, judging from the figures of Doncaster, appear to arise, as they do in the arthropods, independently of the forebrain, from lateral thickenings, or evaginations of the walls of the stomodæum. See Chapter IV, p. 60.

Cephalic Sense Organs.—The cephalic sense organs consist of two compound lateral eyes, *l.e.*, a parietal eye, *p.e.*, and the frontal or olfactory organs ("corona ciliata"), *co.c.* These important sense organs have the same general arrangement, innervation and structure that is so characteristic of the cephalic sense organs of all primitive arthropods. Chapter VIII, p. 125.

The lateral eyes, *l.e.*, consist of three retinulæ, or three small optic cups, united to form a single organ. The rhabdoms are terminal and nearly upright, that is they are directed outward toward the optical center of each cup and toward a centrally located refractive body consisting of three sharply defined segments These eyes represent the compound lateral eyes of arthropods in a rudimentary or elementary condition.

The parietal eye ("Fossetta Retrocerebrali" of Grassi), including its two appendages, is a tri-lobed sac, lying on the posterior median margin of the forebrain. Except for the absence of the black pigment that ordinarily makes the parietal eye so conspicuous, it is very similar to the parietal ocellus of the nauplius of Apus, Branchipus, or Lernæa.

The eye sac consists of a median portion opening freely to the exterior, and representing the unpaired ocellus with its short epiphysis and pore, while the two paired ocelli lie in the diverging blind sacs on either side. The globules and glistening granules described by Grassi, that are contained in these sacs, no doubt represent the vesicular retinal cells filled with the white pigment so commonly present in the degenerate parietal eye, *e.g.*, Limulus and Petromyzon. The eye lies directly on the posterior surface of the brain, as in Apus, and appears to be connected with it by short but indistinct nerves.

The Olfactory Organ.—Between the parietal and lateral eyes are two large nerves, *co.n.*, one on either side, that represent the frontal-organ nerves, or the olfactory nerves of arachnids, phyllopods and entomostraca. They terminate diffusely, that is, in widely distributed, subcutaneous branches, as is characteristic of these nerves in the above mentioned forms, in a large sensory area enclosed by a prominent ciliated groove, "corona ciliata" of Grassi. This area, the surrounding ciliated groove, and the appertaining nerves (two pairs?) represent the frontal or olfactory organs of the craniata. See Chapter X, p. 160.

The Ventral Ganglion.—The ventral ganglion is relatively large and complex. Its minute anatomy has not been carefully described, but it appears to have the typical structure of the ventral nerve cord in primitive arthropods. Whether or no it consists of distinct neuromeres, secondarily united, will probably be manifest on a more careful examination of its transverse commissures.

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Conclusion.—The chætognatha are unquestionably primitive arthropods, somewhat degenerate. They are adapted to a permanent pelagic existence and reach sexual maturity without passing much beyond the nauplius stage. Their relation to the arthropods is shown by the presence of a typical telocœle; cœlomic pouches; the early appearance and the location of the sex cells in the segmenting egg; the division of the body into head, thorax, and abdominal regions; the location of the ovaries in the thoracic region, and the testis in the abdominal region of the adult; the character of the jaws; the lateral or pleural folds; the bivalve mantle folds of the head (prepuce); the prevalence of chiten; the fibro-cartilaginous plate in the jaw muscles (endocranium); the structure of the brain and the arrangement of stomodæal nervous system; and finally the structure and distribution of the lateral and parietal eyes and "frontal organs."

The history of the chætognatha is profoundly significant, for it shows us a group of animals that combines in a convincing manner some of the important anatomical characters of adult arthropods, such as those above mentioned, with the more striking embryonic characters of typical acraniates, such as the telopore and telocœle and cœlomic pouches. Their structure and development justifies the conclusions already reached in other ways, that the telocœle and cœlomic pouches are secondary, not primary characters, and that they have been acquired from arthropod ancestors, partly as a result of degeneration, loss of yolk, and a consequent rapid process of early development.

The chætognatha resemble the cephalochorda and the enteropneusta in their straight, elongated body and intestine, but differ from them in the presence of an open neurostoma and the absence of a hæmostoma and gill clefts. They are definitely excluded from the nematodes, annelids, molluscs, and rotifers—with which they have been affiliated by various authors—by the absence of the gastrula and trochosphere stages, by their highly modified development, as well as by the peculiar structure of their brain, stomodæal ganglia, and cephalic sense organs. They are clearly acraniates, but are not closely affiliated with any other subdivision of the group.

CHAPTER XXV.

SUMMARY AND CONCLUSION.

We have shown in the preceding chapters that the great trunk line of animal evolution is the vertebrate-ostracoderm-arthropod-cœlenterate stock. The recognition of this fact is of great importance, for it enables us correctly to locate several other important phyla, whose position in a natural system of classification it has been heretofore impossible to determine. For the first time it opens to us the great creative period in the evolution of vertebrates; lays before us in detail the successive stages in the upbuilding of their physical structure and functional organization; reveals the important factors that create and control the process, and the critical events incident to its consummation.

This reconstruction of the phylogeny of the animal kingdom adds enormously to our perspective of evolution, both as to the length of time, and the number and variety of graded animal forms involved. For the first time it places us in a position to study the rate and direction of organic evolution on a grand scale and to observe in action the forces that direct and control the process, for all the great systems of organs that find their fullest expression in the vertebrates were in a nascent condition in the arthropods; here their qualitative material basis, their relative locations, and their modes of growth were established, and the conditions were already present that made possible the characteristic structures of man.

This new point of view shows us that the primary creative factors in organic evolution lie within the organism, and that growth itself not only creates the conditions that produce the framework of living things, but marks out the boundaries within which organic evolution is possible. External environment, natural selection, and heredity are of little or no importance in this process. They cannot be considered as active factors in evolution till after the underlying framework of the organism has been created.

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I. THE EVOLUTION OF A CREATIVE ENVIRONMENT.

Cosmic, Organic, and Social Environments.—It is evident that we may not consider environment as something apart from and independent of the things environed, for, as we have seen, the mere process of growth, or of continued being, literally creates new environments for all the constituent parts, whether we are dealing with proteids, or protoplasm, or a group of cells, or a vast community, or society of organisms; and the new environments, likewise, literally create new structures and new organisms. Structure, organization, and environment therefore, are evolved simultaneously and inseparably, and they become more and more complex, interlocked with one another and with their innumerable constituents, with the lapse of time.

It is important to distinguish, more sharply than is usually done, between the various kinds of environment, and the parts they play in the production of new structures and organisms; between the environments that create, and those that are prohibitory, or exclusive, or merely permissive.

Consider, for example, a simple case, such as ice. There are three essential factors involved in its production, or creation: 1. The inherent nature of the hydrogen and oxygen of which it is composed; 2. the relation of the two elements to each other as to time, space, and quantity, and 3. the conditions as to pressure, temperature, etc. When all three factors, *i.e.*, materials, time, space and quantity relations, and environment, are in a definite adjustment, ice appears, or is produced, or created. If some animal, or other agent, devours or destroys the ice as fast as it is created, or prevents the act of creation, we may add a fourth factor as essential to the creation or the existence of ice, namely 4. the absence of an excluding, or destructive agent.

The first and second factors include the materials and their distribution; the third and fourth are external, and are primarily distinct from the materials or their distribution; they constitute the environment. Only one factor may be assumed to be permanent, or at any rate relatively permanent, that which constitutes the quality or nature of the materials, or simply the materials themselves. All other factors are constantly changing or fluctuating. The second and third factors may be properly considered creative factors in the sense that when they prevail, ice, a different thing from what previously existed, appears. In no sense can ice be said to have been present in, or to have pre-existed in either the materials, H and O, or in the creative conditions. The fourth class of factors may be neutral or permissive, exclusive or prohibitory, but under no conditions creative.

Thus, reduced to its simplest terms, the command of materials and of their relations to each other as to time, space, and quantity, and the command of environment, constitute creative power.

All aggregations of material create for the aggregate, and for each of its components, new directive and controlling conditions. This is true whether we are dealing with the aggregation of elements to form water, or proteids, or mixtures of proteids. The aggregation of cosmic materials to form the earth has produced new conditions that created the land, and sea, and atmosphere, rivers, mountains, valleys and soil, and gave to each in turn its power to direct and control, and to create anew. All vital, organic growth is of this nature, except that its income and outgo are more accurately balanced and its sphere of activity more minutely localized.

The geologist interprets the growth of the earth by its change of form and by the distribution of its materials, and seeks to correlate its structure at a given time with the conditions which at that, or some previous time, prevail, convinced that one is the formal expression of the other. We have used the same method in the interpretation of organic growth. We have shown that the mere process of radial and apical growth, or the aggregation of organic materials around a given center, or along a given line, or surface, automatically creates regularly graded zones of unlike conditions that are coincident with the distribution of unlike materials or organs We conclude therefrom that the basic structure of plants and animals is automatically created by the process of growth itself, or that growth automatically creates special local conditions, which are expressed in the structures that appear at those points.

The principal factors, therefore, that create organized structures are primarily internal and are sharply localized; they are the result of the environment of its several parts, and they change with the process of growth. The medium external to the organism as a whole, its cosmic environment, such as the sea water and its contents, pressure, temperature, light, gravity, etc., is practically unaffected by local growths and remains approximately constant.

Historically speaking then, the evolution of the external environment did not keep pace with the evolution of the internal environment. Primarily the external environment was purely inorganic, or cosmic, broadly permissive, or neutral. In the early stages of organic evolution there was no dependence of one organism on another, no social organization, no social environment, no organic competition, or selection, or elimination, for all alike drew their materials from the surrounding inorganic media.

As primitive organisms became more complex, the balancing points of internal environments became more precisely located, and were expressed in more stable, more sharply defined differences in the structure of the resulting forms. The growth of individual organisms was accelerated, or short circuited by the fusion, or union, or absorption, of one form by another, giving simultaneous rise to organic nutrition, sexual reproduction, social environment, and social competition.

Thus we again reach the conclusion that the continual aggregation of like units to form a homogeneous whole is an impossibility, for aggregation creates unlike conditions, that create new things, new organs, new organisms, new societies, and new organizations of old societies.

II. Crises in Organic Evolution.

The evolution of organisms does not proceed at a uniform rate, but at a variable one; now slow, now fast, retreating, diverging, advancing; now by innumerable minute steps, now by leaps and bounds; because the ever shifting relations of part to part, organ to individual, and individual to society, are of unlike nature and of unequal value.

These inequalities in the potential value of organic readjustments form the true basis of a natural system of classification. They create the critical periods in organic evolution; they produce actual gaps in the mosaic of adult forms which constitutes the ideal genealogical tree of the animal kingdom; their advents create the real subdivisions, and mark the starting points of divergent evolution for phyla, classes, and for the innumerable smaller branches. The gaps in a natural system of classification therefore do not always mark the periods of lost records or the areas of densest ignorance.

Hence organic readjustments, according to their import, mark the periods of relatively rapid phyletic changes that are of value in classification. Let us consider some of those organic changes that are recognizably correlated with differences in bodily form, and that have been instrumental in fixing or guiding the course of evolution in the arthropod-vertebrate stock.

A. The Evolution of Metamerism and Bilateral Symmetry.—It has been shown that a local exaggeration of radial growth results in apical growth, and that under the existing conditions apical growth inevitably creates bilateral symmetry and a double series of graded unlike conditions and structures, one series extending in a cephalo-caudal direction giving rise to metamerism, the other in a neurohæmal direction, giving rise to the graded series of conditions and organs on the right and left half of each metamere. (See Fig. 157.) These conditions are probably resident in all coherent, organic growth, for we see essentially the same conditions repeated wherever apical growth prevails, whether in plants or animals.

It was, no doubt, some local exaggeration of radial growth in a cœlenterate ancestor that initiated the craniate stock. The craniates began as minute animals (trocosphere stage) consisting of a relatively large head that was built on a radiate plan, and that represented the ancestral cœlenterate body. From this primitive head, a local outgrowth arose that gave rise to a new body. The latter gradually increased in volume, and as a result of its characteristic mode of apical growth, bilateral symmetry, metamerism, and the difference between the neural and hæmal surfaces, became gradually and permanently established.

The old body, or primitive head, decreased relatively in volume and was finally represented almost solely by its nervous elements, the primitive forebrain, and by the oral opening into the alimentary canal. The new trunk increased in volume by the spasmodic production of new groups of metameres, alternating with prolonged periods of phylogenetic inactivity. Each new group of metameres always differed from the preceding ones, and after a varying period of greater or less organic independence, was incorporated with them as a subordinate part of an increasingly complex head. Even in its most elaborate condition, as seen in the higher vertebrates, the head still shows distinct traces of the successive generations of metameres of which it is composed.

Each notable increase in the size of the body due to the addition of a new group of metameres, disturbed the pre-existing organic equilibrium, bringing about the shifting of the organs of locomotion, excretion, circulation, and digestion, to regions farther and farther back in the body. Outgrowths of nerve fibers from the old sensory and nervous centers then established coordinating relations with them.

The special characteristics of apical growth in the craniate stock are the precise limitation to its extent; the sharp differences between the metameres of different groups, or generations; and the differences between the various parts of the same metameres. This is specially notable in the arthropods where many of the subphyla, such as the insects, arachnids, etc., are notable for a small, definite number of metameres, and for the sharply graded step-like differences between them. This is in marked contrast with the leaf-like, homogeneous body of the platyhelmenthes; the voluminous and elaborate, but short bodied mollusca; the indefinitely elongated series of similar metameres characteristic of the annelids; and finally with the small size, feeble definition of organs, but unlimited power of budding so commonly manifested by the acraniates.

One of the striking features of apical growth that is manifest through the entire range of the arthropod-vertebrate stock is the vigorous and persistent power of producing new metameres that are varied in character, and that have a well marked power of mutual adaptability. It is this adaptability that ultimately leads, especially in the older, more anterior metameres of the higher forms, to the almost complete disappearance of metamerism, and to the substitution for it of a linear arrangement of unlike functions and organs where the location of an organ in the series is determined by its right of historic precedence and by the degree to which the performance of its functions depends on location.

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On the other hand, the acraniates are universally characterized by the lack of this vital vigor, and the contrast between the method of growth and differentiation in these two great subdivisions of the animal kingdom is most instructive. Although the acraniates apparently started at the same time as the craniates, with a very similar structure, and under similar external conditions they gave rise to a multiplicity of feeble, defective, often degenerate subphyla, whose most characteristic features are the degenerate or extremely small size of the neuromuscular systems, the feeble power of apical growth, and the indistinct metamerism. We may attribute this lack of organic definition to some inherent defect in the constituent materials common to them all, and which lies quite beyond our reach. Another great difference between the two groups is the absence of a fixed internal environment in the acraniates, due to the absence of an impervious exoskeleton. Without it, development is apparently more diffuse, or vegetative, and is marked by an unlimited power of budding. At the same time there is clearly some fundamental defect in their neuromuscular system which checks its development, or leads to its almost complete degeneration.

B. Asymmetry as a Creative Factor.—While bilateral symmetry, with its accompanying arrangement of unlike parts in linear and transverse series, is apparently an inherent product of apical growth, and is the normal condition in the arthropod-vertebrate stock, it is subject to modifications of unknown origin that produce various degrees of asymmetry. Where there is a measurable quantitative difference between corresponding right and left organs, the other parts of the body promptly respond by a change of form, or position, which tends to restore the lost equilibrium, producing thereby a more obvious deformity or asymmetry.

It is often assumed that asymmetry is the result of a sessile or parasitic mode of life. But it is altogether more probable that the reverse is true, for comparatively few sessile or parasitic animals are asymmetrical, and extremely asymmetrical forms would be likely to find a sessile or parasitic mode of life the only one open to them, because these conditions are less exacting.

The initial cause of asymmetry is usually some event that occurs within the egg itself, probably at a very early period. It has been shown, for example, that under normal conditions, such an ancient and stable type as Limulus produces a surprisingly large number of asymmetrical embryos. When one side is entirely absent, the remaining side is thrown out of its original straight line into the form of a bow, a half circle, or a semi-spiral. These forms may live several months and appear to be perfectly healthy, but apparently they never develop beyond the larval stages.

Extreme asymmetery in the embryonic development of some cirriped-like arthropod probably initiated the great class of echinoderms, for the echinoderm larva, which in its structure, metamorphosis, and mode of attachment, resembles that of a cirriped, is at first quite symmetrical. When the organs on one side degenerate, or fail to develop, the remaining side bends till its two ends meet and form a ring; the segmental organs are then arranged along the radii of a circle, instead of in parallel lines. These changes are similar to those that occur in Limulus embryos, except that they are carried farther and give rise to animals capable of surviving in their new form.

Thus such a negative character as the absence of one side of the body has created a new condition, a new organic environment, that has in turn created a new type of radiate structure, and at a single stroke initiated the evolution of a new class of animals. Organic readjustment, during this crisis, was no doubt extremely rapid. But after the essential changes took place, elaboration toward a more active neuro-muscular existence practically ceased. The history of this ancient phylum indicates that it never completely recovered from the effects of this radical metamorphosis, for no other large group of animals, with an equal grade of organic complexity, shows such a low grade of neuro-muscular adjustment to its environment.

C. Chiten and the Exoskeleton as Creative Factors.—Chiten is one of the most characteristic features of the arthropods, and like the cellulose wall of the plant cell is a creative factor of very great significance.

It is tough and flexible, but inelastic; it is capable of great hardness and forms for the entire external surface of the body a water- and air-proof covering, unaffected by any chemical changes likely to occur in the surrounding media. More perhaps than any other factor it controls the form of the body, its method of growth, the distribution and attachment of muscles, the character of the appendages, and of the sensory and respiratory organs. Its chief significance therefore lies, not in its occasional and purely incidental usefulness, especially in the higher forms, as a material to construct supplementary organic instruments, or weapons of offense and defense, but in its compelling influence on form, and in its creation of an internal organic environment distinct from that of the surrounding medium.

Chiten appears at a precisely defined period in arthropod embryos, as the result of some chemical transformation that takes place on the outer surface of ectoderm cells. Its presence is at once recognized by the way in which it prevents the penetration of stains and other chemical reagents. There is no reason to doubt that it appeared in the ancestral arthropods with corresponding rapidity, and that it had an immediate and persistent transforming effect on those animals in which it occurred. From the earliest period, therefore, every member of the arthropod stock has been a practically closed mechanism. Its sensory, respiratory, and excretory relations with the exterior were necessarily confined to precisely located, and definitely constructed points, or openings. The location and attachment of muscles, and the movements of one external part on another, were controlled by the location of flexible, hinge-like joints in the armor; and no notable increase in volume or in organic activity could take place without special provisions for the circulation of a blood-like plasma that should serve at the same time as a uniform internal environment, distinct from the external one, and that was suitable both for cell growth and as a means of transporting nutritive and waste substances to their place of consumption or point of discharge.

The presence, therefore, of a chitenous exoskeleton in the arthropods may be regarded as one of the primary causes of their slow growth in volume and of the early historic appearance of precisely located sensory, motor, excretory, circulatory, and respiratory organs; and of their sharply defined, closely knit, and potentially sound organization.

These conditions are in sharp contrast with those in the naked, soft bodied cœlenterates, and in many worms, molluscs, and acraniates, where the surface of the body is more uniformly exposed to external agents, and the external medium has great freedom of access to the interior.

The sudden loss of a chitenous exoskeleton, after a longer or shorter period of control, is no less significant than its initial formation. When some comparatively insignificant change in its chemical composition, or in its mode of growth, led to a radial change in its physical properties, or to its complete disappearance, the body was again released from its control and a new set of form-creating factors arose, but on a different level from the old. The change from a chitenous armor to one of cellulose was a powerful factor in the creation of the tunicate type; and the almost total absence of chiten in Balanoglossus, Cephalodiscus, Amphioxus and the polyzoa; the substitution for it of a heavy armor of isolated calcareous plates in the echinoderms; and the predominance in it, of a heavy calcareous deposit in the cirripeds, were all factors of great importance in controlling the mode of life, the method of growth and the direction and progress of evolution in these phyla.

In the craniates, the characteristic chitenous exoskeleton of the arthropods is doomed to extinction, owing to conditions created by its own mode of growth. It has been shown, for example, that in Limulus a peculiar and exceptionally vigorous method of growth in the skeletogenous tissues gives rise to a system of subdermal, interlocking trabeculæ that probibits the subsequent periodic removal of the exoskeleton. A condition is thus produced that compels the permanent retention of the chitenous products within the tissues of the animal, and which initiates the formation of a new type of exoskeleton that is largely subdermal, cellular, and fragmented. This permits a new mode of growth for the animal as a whole, differing from the old in much the same way that the growth of an endogenous stem differs from that of an exogenous one; and it ultimately liberated the arthropod stock from the bondage of an increasingly restrictive, burdensome, and menacing armor. This new type of skeleton itself practically disappears in the higher vertebrates, giving place to the new framework of cartilages and bone that constitute the internal skeleton.

D. **The Increasing Volume of the Yolk Sphere as a Creative Factor.**—The local retardation of growth caused by the presence of yolk in the developing ovum has long been recognized by embryologists, but they have not recognized the form controlling conditions created by apical growth on a spherical surface.

The gradual increase in the size of the yolk sphere throughout the arthropod and lower stages of the vertebrate stock creates a new set of conditions that greatly modifies the process of development; for the growth of an embryonic metamere over the surface of a yolk sphere is a different problem from the growth of a new metamere added to the apex of a mature animal. One spreads film-like in mercator projection over an approximately plane surface, the other grows as a solid body round a central point. When the size of the yolk sphere is increased, the number of metameres so affected is increased, and the effect on each metamere will depend on its location in the series, that is, whether it lies at the head or tail end, whether it has to grow round the equator, or round the poles of the sphere. In this way the size of the yolk sphere controls the structure and mode of growth of the heart, the belly navel, and germ wall, and has created the phenomenon of concrescence.

Thus, owing to the difference in the location of metameres on a yolk sphere of variable dimensions, inevitable differences arise in the conditions under which these metameres are compelled to grow, and these differences are increased, or exaggerated, with the increasing volume of the yolk sphere. These differences in conditions coincide to a large extent with the morphological and physiological differences that characterize the corresponding regions of the body, and may be assumed to be the causes that have brought them about.

E. **The Increasing Volume of the Brain as a Creative Factor.**—A conspicuous feature in the evolution of the arthropods is the steady increase in the volume of the sensory and nervous centers located in the more anterior metameres of the head and trunk, and the corresponding decrease of the lateral plates, together with the alimentary, locomotor, and mesodermic elements belonging to the same metameres.

Structural changes of very great moment are inevitably brought about by these conditions. Owing partly to the presence of yolk, from which all the growing tissues can draw their sustenance without the intervention of an alimentary canal, the nervous system attains a very considerable volume, and becomes functional long before the stomodæum is called into action. This delay in its development, its unfortunate location, and its comparatively delicate epithelial walls, places the stomodæum under a heavy handicap in its competition for space with the nervous system. The result is that the increasing size, precocity, and more intimate union of the cephalic neuromeres during early embryonic development, leads to a gradual narrowing of the nerve ring surrounding the œsophagus, making in many arthropods, for a longer or shorter period, a fluid, or semi-fluid diet (*i.e.*, blood-sucking, parasitic, or scavenging) more and more imperative. The same increase in volume and in precocity of the cephalic neuromeres also led at an early embryonic period to the invagination of the entire brain, so that with the closure of the neural crests and palial fold, the old mouth, which opens into the floor of the brain chamber, became completely shut off from the outside world, and could no longer perform its normal functions.

The increasing precocity of the cephalic neuromeres and the diminishing volume of the corresponding lateral plates also lead to the formation of a more and more prominent head fold, and to the transfer of the oral arches, which in the arthropods are neural or lateral in position, to the hæmal surface of the head. (Figs. 32, 33, 157.) There they converge toward the old dorsal organ and cephalic navel that constitutes the center for the formation of the new mouth.

The actual closure of the old mouth, the opening of the new one, and the transfer of the jaws to the hæmal surface of the head, were, therefore, brought about in a large measure by the action of the same forces. These events, by the final upsetting of a long established organic equilibrium, took place rapidly, the consummation of one event probably accelerating the other; they also led to a rapid readjustment in other parts, and to important changes in the mode of life, especially in the mode of feeding and in the position of the body in locomotion.

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F. **The Creation of a New Environment for the Eyes.**—The location of the vertebrate eye in the walls of a hollow brain has caused much discussion. We have shown that these so-called cerebral eyes did not originate in situ as the result of the stimulating effect of light acting on the brain through the body walls of a transparent ancestor, or by use, or natural selection. They are merely the ancient median and lateral eyes of the arthropods in a new position. They have been forced into the brain chamber by an accident, as it were, because they happened to be located near the margin of the rapidly infolding neural plate. One may observe in the arthropod stock the steady approach of this inevitable disaster to the visual organs, brought about by the increasing precocity of the embryonic brain and optic ganglia. It is important to observe that under the existing conditions there is no half-way position for the eyes; they are either carried wholly inside, or remain wholly outside the brain, and that once inside there is no escape for them. But the very slight difference in the physical conditions that finally precipitates the eyes into the brain cavity, creates at once an immense difference in the physical conditions under which the eyes, the brain, and indeed the whole anterior part of the head must complete its development. At one stroke the lateral eye is changed from the superficial type seen in the invertebrate to that which, in the vertebrate, lies in the walls of the cerebral vesicle.

The actual closing of the old mouth and the opening of the new one, the transfer of the oral arches to the hæmal surface of the head, and the transfer of the lateral eyes to the interior of the cerebral vesicle, brought about a great crisis in the evolution of the arthropod-vertebrate stock; and the successful consummation of these internal organic changes constitutes the most important event in the evolution of the animal kingdom.

The organic adjustments referred to above were necessarily rapid in their progress and revolutionary in their effect. But the evolution of the conditions that led up to them was extremely slow, consisting of a long series of cumulative internal events that had no immediate bearing on the use or the character of the organs that in the end were most vitally affected. In the arthropods, we may follow in detail through an immensely long period of time, and in a long series of animals, the steps that led up to this inevitable crisis. The rapid succession of readjustments that followed gave rise to a sharply defined, remarkably short-lived, transitional phylum, the ostracoderms. After that stage is passed, the organs in question remain practically stationary through the whole vertebrate series from fishes to man.

The Significance of a Natural System of Classification.

A consideration of the facts discussed above, to which many more might be added, throws a new light on variation and environment and on the meaning of a natural system of classification.

A natural system of classification is an attempt to represent in graphic form a genealogical tree of the animal kingdom, and in so far as it is a true record of evolution and descent, it should reflect the guiding and controlling factors that have created it.

If natural selection and external environment are the important factors in creative evolution that they are frequently assumed to be, then there should be reflected in a natural system of classification a broad correlation between structure and environment that could be used as an aid in the making of it. But this is not the case, for we do not usually divide animals, according to their mode of life or environment, into those for example, that live in fresh or salt water, or in the air, or on the land, etc.

If variation, from whatever cause, is invariably minute and of equal specific value, then a perfect record of the past, that is, the genealogical tree, should show a continuous system of branches composed of a uniformly graded series of animals.

But while it may be possible to arrange the members of certain small subdivisions of the animal kingdom into minutely graded linear series, it is usually exceedingly difficult to determine which end of the series is the base and which is the apex, because a considerable gap usually exists between the offshoot and the presumably parent stock.

The speculative zoologist often attempts to fill this gap with hypothetical forms having the desired intermediate characters, on the assumption that connecting adult forms, as numerous and finely graded as on any of the modern terminal branches, once existed, but are now either extinct, or unknown, or both extinct and unknown. Some morphologists assume, for example, that the vertebrate stock had its origin in such forms as the annelids, echinoderms, tunicates, or enteropneusta, and that the enormous series of animals necessary to fill the gap between them and the vertebrates are now extinct and will remain forever unknown.

But there is no evidence to show that the true genealogical tree is, or should be, a minutely and uniformly graded series of animal forms. On the contrary, we have shown that the internal creative factors are of very unequal value and that they are exceedingly variable at different times, giving rise to well defined periods in phylogeny during which many large and important changes of form take place. Hence while some of the apparent gaps in our imperfect genealogies may be filled by the discovery of new forms, it is evident that the ideal phylogenetic tree of the animal kingdom must be in reality a loosely articulated system, consisting of slender, interrupted, or vanishing basal stems, expanding into top-heavy branches. In other words, it was minutely graded in certain places only, notably on the older terminal branches. There the differences may well be either the minute so-called continuous variations of Darwin, or the sharper, discontinuous mutations of De Vries.

But the larger natural subdivisions of the animal kingdom, in some cases at least, appear to be separated by real gaps, much larger than any known mutations, and that are not due to defective records. They represent periods, varying in intensity and in duration, of rapid transformation in definite, predetermined directions, followed by periods of slow development along more varied, but less revolutionary lines. These gaps can never be filled by the discovery of new forms, for in reality they represent changes of pace in evolution, or periods of greatly accelerated evolution, which in perspective, and by comparison with other periods, appear as gaps.

A phyletic metamorphosis of this character I have named a methallosis.[1]

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[1] To rush after, to leap from one ship to another.

It may be defined as a marked change of pace in phylogeny; or a rapid succession of important embryonic variations due to the upsetting of a long-established condition of organic equilibrium; or to some organic change, insignificant in itself, but which at once creates new conditions for the growth of the organs so affected, or of other organs. The extent of a methallosis maybe measured by the extent of the variations and by the length of the period in which they occur.

During ontogeny there are well-marked periods of accelerated development, quite independent of growth or increase in size, during which there is a rapid succession of profound structural changes, followed by longer periods of slow development. These periods of accelerated development are well known as metamorphoses, or transformations. When seen in perspective, they appear as gaps separating distinct periods of life. They represent no doubt the ontogenetic repetition of periods of accelerated race development, the accelerated period, in the latter case, representing the real gaps between the larger subdivisions of the animal kingdom.

If the variations that have given rise to new animal forms are indiscriminate, diverging in all conceivable directions from the parent stock, then the actual genealogical tree that is the result of such indiscriminate variation, and as controlled by natural selection, should show a recognizable correlation between the structure of a given group of animals and its surroundings. But this is so to a very limited extent only, and only in regard to minor or superficial features of organs that have long existed under other conditions.

The underlying basic structure of the organism is in no way modified by the mode of life or by the surroundings, for all segmented animals, whether they live in the air, in water, or on the land, agree in their mode of growth and in the relative positions of the principal organs, such as the central nervous system, alimentary canal, heart, eyes, olfactory organs, etc. The same thing is true of the whole great class of vertebrates, where the basic structure of the jaws, gill arches, the brain, and principal sense organs, is immutable, and identical for every member of the class. This established structure has rigidly defined the possibilities of evolution in the past and it will control the actual development of the future.

The power of articulate speech, for example, depends on the structure of the lips, jaws, tongue, larynx, and the respiratory organs, and upon a definite nervous association of these parts. It is a highly characteristic faculty of man, yet the organic basis of the entire complex mechanism preexists, and the framework is already set up in the fishes, where the rudiments of all these organs are known to occur and where they have in the main, the same mode of growth, interrelations, and nerve connections they have in man.

In the same broad sense, the basic structure of the arthropod rigidly determines that of the fishes, and the fishes that of man. The main highways of evolution are therefore mapped out by the initial structure of the most remote ancestors. To that extent, evolution is direct, orthogenic, predetermined. It

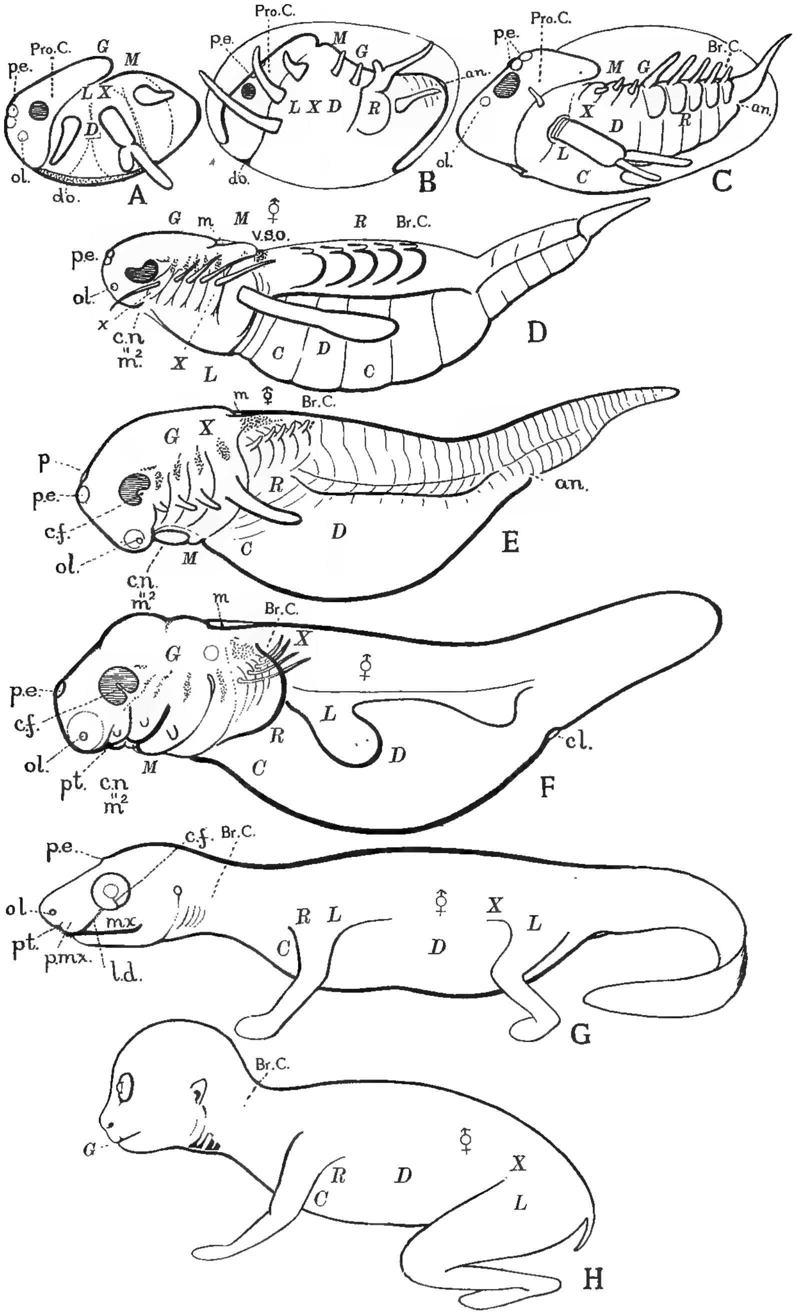
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FIG 307.

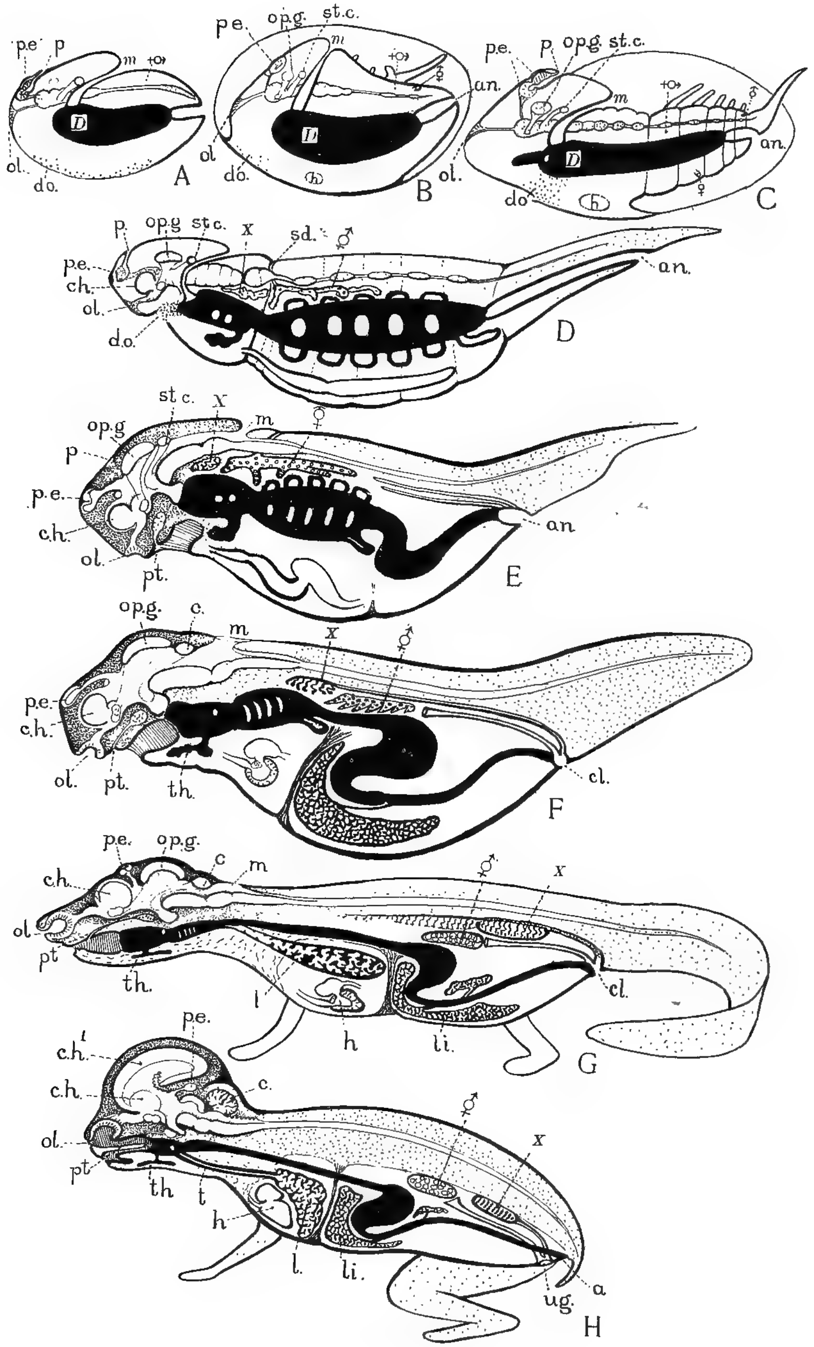
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FIG. 308.

is dependent on antecedent structure, and that is automatically created in the process of growth and organic readjustment.

* * * * * * * * *

There are therefore various aspects of evolution; some are over-emphasized by one school of biologists, and ignored by others, because the creative factors have widely different values at different periods of evolution, and in different fields of investigation.

There is no master key to evolution. It does not always move in the same way; not always by continuous, nor always by discontinuous variations; it is not always direct, orthogenic, determinate; not always indeterminate; heredity is not always a controlling factor, nor does it always control in the same way; neither does the external environment, nor use, nor disuse, nor natural selection. All are real factors and all have doubtless played some part in the grand total of results, but each has a different value, more here, less there, and these values have changed with the progress of evolution. They are as varied as life itself.

FIG. 307, 308.—Diagrams illustrating the principal stages in the evolution of segmented animals (syncephalata). They illustrate: *a*. The spasmodic increase in the number of metameres, the advent of each new group (tagma) marking a distinctly higher level in evolution, of class, sub-class, or divisional value. *b*. The approximate historic period at which new functions and organs, demanded by the new internal conditions, make their appearance; *e.g.*, circulatory, respiratory, locomotor. *c*. The initial location of the most important functions and organs. *d*. The most important changes in the location of functional centers, due to the transfer of organs to other regions, or to their degeneration or atrophy, and the appearance of new organs elsewhere to take their place. The substitution of new organs and functional centers for the old is apparently always in a hæmad, or caudad, direction, never cephalad, or neurad. The most striking change in the location of old organs is the transfer of the appendages and associated parts (visceral arches, nerves, muscles, and ganglia in an anterior hæmal direction, the process beginning with the oral or anterior thoracic arches of primitive crustacea and attaining completion in the mammals, with the transfer of all the branchial arches to the anterior hæmal surface of the head. One of the principal causes of this change in the position of organs is the atrophy of all the organs on the corresponding hæmal surface of the head. The most striking illustrations of local atrophy, and the formation in the younger, more posterior metameres, of new organs or parts of organs serving the same purpose are shown by the locomotor, *L*, sexual, ⚥, excretory, *X*, digestive, *D*, and circulatory organs, *C*. *e*. The substitution of one organ for another. The most striking illustration is the closing of the old mouth and stomodæum, and the formation of a new opening into the mesenteron in the region of the "dorsal organ," *i.e.*, on the hæmal surface of the procephalic and anterior diacephalic region. Other examples are the substitution of lungs for gills; and of local expansions of the lateral or pleural folds of the trunk, that serve as balancing, supporting, and locomotor organs, in place of the cephalic appendages. *f*. The permanency and very great antiquity of the more anterior cephalic organs is strikingly shown by the procephalic structures, such as the median and lateral eyes, olfactory organs and their ganglia, the primitive "hemispheres," cerebellum and stomodæum. *g*. The most striking innovation is the perforation of the walls separating gill sacs and enteric diverticula. *h*. The rise and decline of metamerism. Metamerism is never complete or perfect at any phylogenetic or embryonic period, or in any region. It attains its highest expression in the mid-body region of the higher arachnids and is but very incompletely expressed in the anterior cephalic and caudal regions. The decline of metamerism begins in the higher arachnids, ostracoderms, and primitive vertebrates, and makes its appearance first, and in the most marked degree, in the oldest or most cephalic regions, and more on the hæmal than the neural side. That is, it follows the primary axes of growth and structural differentiation. *i*. Result. Each new local growth, atrophy, transfer, substitution, or innovation, of parts is interlocked with all the others, inevitably creating new conditions pregnant with new structures and activities. The process is most conspicuously manifest in the gradual creation of the mammalian "head" and "body," with the old structural units in a totally new and different organic relation from the initial one. The final, permanent relation of part to part, and of the new to the old, is a logical, inherently necessary one, the most important internal factors in bringing it about being priority of origin, the imperative demands for intercommunication and distribution of products, mechanical balance, coherency, and stability.

The following capital letters signify the location of the principal functions: *C*, Cardiac, or circulatory; *D*, digestive; *G*, gustatory; *L*, locomotor; *M*, masticatory; *R*, respiratory; *X*, excretory; ⚥, sexual. Other letters as before: *A*, nauplius stage; *B*, ostracode; *C*, cladoceran; *D*, merostome; *E*, transitional; *F*, larval fish; *G*, amphibian; *H*, mammalian.

In the creation of the great phyla of the animal kingdom, natural selection, external environment, heredity, use and disuse, have played an insignificant, subordinate part. They may check, or stimulate, or eliminate in a quantitative manner, but they are not primarily creators of structure or of organization.

The familiar "Deus ex machina" of heredity and natural selection, may be summoned to account for the absence of organs that ought to be present, or to account for the elimination of mechanisms that will not work, but they are powerless to explain the method by which a given change in one organ or organism creates a change in some other organ or organism.

The creative power of internal environment is always present, always active, always changing. But the basic chemical elements of life are the same as they always have been; and the cosmic, inorganic environment has changed but little since the dawn of organic evolution. It is the internal, organic environments, and the social and communistic environments that have gained in power with the progress of evolution, and that are the most important expressions of it.

The foundations of organic structure are therefore laid down and locked up within the narrow bounds of internal environment, forming a self contained system that grows and creates from within, and which is essentially unmodified by changes in the external environment, except those that are absolutely prohibitive of all life.

Social and communistic environment are later, secondary products, that lend effectiveness to selection in proportion to their own evolution; that is, according to the degree to which the life at large of one group of organisms is interwoven or interlocked with that of others.

Creative evolution is the progressive interlocking of one activity with another, to a common end, each moulding the other, and all moved by the mainspring of a common external medium. It is expressed in a perpetual flow of newly created organisms, and the form and action of each one, and of its constituent parts, can alone indicate the nature of the forces that have created them.

Hence comparative morphology and phylogeny must always constitute the fountain head whence comes our knowledge of creative evolution. Such problems as the phylogeny of vertebrates are therefore the most important ones the biologist has to deal with, for on their solution depends our conception of the way in which evolution actually has taken place.

Comparative morphology has no value except in so far as it points out the historic sequence of organic forms and functions, and reveals to us the trend of evolution and the causes that direct and control it. In that morphology stands supreme, for the thin red trail that marks the orbit of evolution is the only index we have of life as it was and shall be. If our reconstruction of phylogenetic lines is hopelessly wrong, then indeed will ontogeny be a false guide, and we shall be left the hopeless task of reconstructing the life history of eons from the contents of a test tube, or the products of the breeding pen; or tricked into the hope of stemming the tide of evolution with a scalpel, a rule of conduct, or a dietetic formula.

It is not surprising that the large expectations of the outdoor naturalist, the cytologist, the experimental evolutionist, and the animal breeder have not been realized.

The cytologist is too intent on the raw materials of life; his field of operation is both too remote and too narrow to give either measurable detail or perspective. To discover the immediate causes of any given stage in the evolution of the nervous system, or of the endocranium, by a study of chromosomes, or of protoplasm, or by juggling with imaginary hereditary units is as hopeless a task as it would be for the geologist to explain the delta of the Ganges by an appeal to the composition of cosmic matter.

The naturalist is bewildered by the amazing detail of the finished product, and so much absorbed in the social organization of the present moment, or in the relation of one plant, or animal to the other, and to the environment at large, that he fails to acquire an adequate historic perspective.

The experimental evolutionist, for a few hours, or months, arbitrarily narrows the environment of an organism, and measures the results, if any, with instruments of precision, or with the aid of the higher mathematics; but he generally ignores, or looks with contempt, on the vast experiments already performed for him, where the laboratory is nature, and the results are expressed in species, genera, and classes.

The comparative morphologist aims, not merely to trace the identity of changing structures under the disguise of new forms, but to measure the rate of these changes, and to seek out the underlying causes that have brought them about. He is heavily handicapped by the lack of materials that can be precisely measured or controlled. But on the other hand there is a certain advantage

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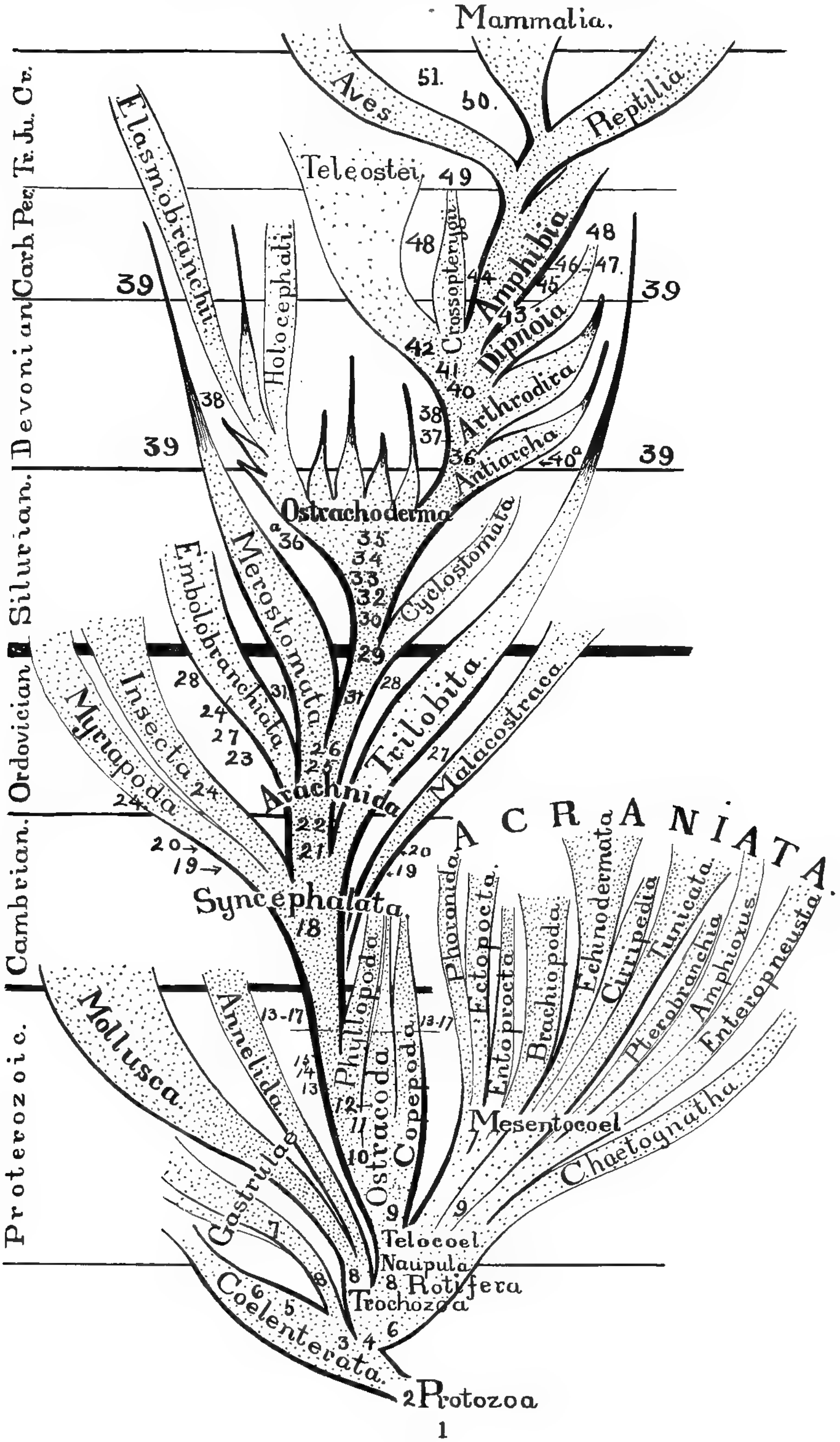
Fig. 309.—Diagram illustrating the phylogeny of the principal subdivisions of the animal kingdom. The numbers indicate approximately the periods at which some of the more important events in the evolution of structures and functions have taken place.

51, Fixation of balanced internal temperature; 50, decline of yolk volume, and perfection of uterine gestation; 49, maximum size of yolk sphere; 48, decline of exoskeleton and notochord and perfection of endoskeleton; 47; evolution of larynx, cochlea, ear-bones; 46, decline of gills, closure of gill clefts; 45, pectoral and pelvic appendages, supporting and digitate; 44, lungs; heart, three-chambered; 43, second migration to land; 42, elongation, and jointing of pectoral fins; 41, air bladder; 40, median fusion of paired jaws; fixation of maxillæ; 39, decline of metamerism; 38, decline of cephalic appendages and rise of lateral folds and paired fins; 37, merging of endo- and exoskeletal elements, and calcification of endo-skeleton; 36, vertebral rings; heart two-chambered; 36*a*, decline of predatory life; 35, gill sacs unite with, and perforate the gut; 34, leg-jaws; three pairs transferred to the hæmal side; 33, neuron continuous; tubular; infolding of the lateral eyes; 32, closure of neurostoma; rise of hæmostoma; 31, increased size of forebrain and cephalic sense organs; 30, increase of endo-skeleton, endocranium, notochord and gill cartilages; 29, new generation of caudal metameres; new trunk and tail flexible laterally; 28, postanal concrescence of the germ wall; 27, increase in size of eggs and in the volume of yolk; 26, exoskeleton thickened, trabeculate, cellular, fragmented; 25, notable increase in size and improvement in locomotor and predatory organs; carnivorous; 24, first invasion of land; 23, respiratory appendages, forming infolded sacs; 22, parietal eye enclosed in forebrain vesicle; 21, endocranium; 20, leg-jaws, multiple, paired, neural; 19, tagmatism, and linear distribution of function; 18, metamerism perfected; number small; 17, heart; internal circulation; 16, rise of excretory organs; 15, body plasma; separation of internal and external media; 14, exoskeleton, water proof, chitenoid, non-cellular; 13, cœlom, telocœl; 12, metamerism perfected; 3 to 7 in number; 11, pursuit and capture; 10, appendages become locomotor, grasping, respiratory; 9, cephalic sense organs, median and lateral eyes and olfactory organs; 8, bilateral symmetry; 7, gastrulation; 6, radiate symmetry; 5, neuron circumoral; 4, enteron opening directly to exterior; 3, early evolution of tissues; 2, evolution of cells; 1, evolution of protoplasm.


Mammalia.
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Devonian
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Proterozoic.
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Teleostei
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Holocephali
Crossopterygii
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Trilobita
Malacostraca
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Insecta
Myriapoda
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Arachnida
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ACRANIATA.
Syncephalata
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Phoronida
Ectoprocta
Entoprocta
Brachiopoda
Echinodermata
Cirripedia
Tunicata
Pterobranchia
Amphioxus
Enteropneusta
Mollusca
Annelida
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13-17
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Phyllopoda
Ostracoda
Copepoda
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Mesentocoel
Chaetognatha
Gastrulae
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9
9
Telocoel
Naupula
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8 Rotifera
Trochozoa
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4
Coelenterata.
2 Protozoa
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FIG. 309.

inherent in the very size and remoteness of his problems, that is absent in the brief laboratory experiments that have taken place under the eye of man. His problems must be viewed from a great distance, but one that gives a large perspective, and draws a vast range of structural changes into a single horizon where sporadic details disappear, and only those events catch the eye that are massed around some central cause or are ranged with monotonous regularity along some common line of physiological upheaval.

* * * * * * * * *

In so far as we may judge from the teachings of morphology, the perfection of physical organization is reached in man. The structural differences between him and the higher mammals are insignificant; but the potential differences created by his upright gait, his use of the hand as a tool, his power to make his experience the property of another, to look into the past at what occurred before his existence, and to predict what will occur when he has ceased to exist, are faculties of great creative power, which in a true biological sense constitute the supreme crisis of organic evolution, and mark the advent of man as the beginning of a new class of animals.

Organic evolution is progressive differential growth, in more intricate, ever narrowing environments. It is primarily concerned with obtaining, preparing, and distributing the raw materials of life; in perfecting the coordinate action of the great bodily functions; and in establishing more economic biologic and cosmic relations. In man, growth and the internal organic adjustments to the above indicated ends have reached their optimum level, and progress in that direction has practically ceased. Further progress must be in the extension of man's contact with, and control over nature by the creation of instruments of power and precision; in the development of his intellectual, artistic and sympathetic faculties; in perfecting the social organization of humanity, and in the creation of social consciousness.

EXPLANATION OF THE LETTERING.

a	Anus; bony axial rod supporting the cephalic appendages.
ab	Abdomen.
ab.a	Abdominal or branchial appendages.
ab.cl	Cœlomic chambers of the abdomen.
a.bm	Abductor branchial muscle.
ab.t	Abdominal temperature organs.
a.c	Anterior cornua; atrial or peribranchial chamber.
a.card	Anterior cardinals.
a.d	Anterior dorsal plate.
a.dl.	Anterior dorso lateral plate.
a.dp	Row of teeth on anterior margin of mandible.
a.f	Ant-orbital foramen.
ag	Argentea.
a.h.co	Anterior hæmal commissure.
a.h.p	Anterior hæmal process.
a.l	Anal lobe.
a.l.m	Alary muscle.
a.m	Anterior marginal line of canal organs.
an	Anus.
an.c	Anterior commissure.
an.n.co	Anterior neural commissure.
an.p	Anterior neuropore.
an.pl	Anal plate.
a.n.s	Anterior neural spine.
ao	Aorta.
ao.ar	Aortic arch.
ap	Apical plate; appendages.
a.p	Anal plate.
a.pl	Apical plate.
a.p.r	Anterior bony entapophysis.
a.s	Anterior sclerotic plate.
at	Atrium; antennæ.
at.c	Atrial chamber; vestibule.
at.d	Excretory duct to antennal segment.
at.r	Anterior triangular recess.
au.o	Auditory organ.
a.v	Anterior median ventral.
a.v.l	Anterior ventro-lateral plate.
ba	Basilar plate to the cephalic appendages
b.c	Blood cells.
bd	Bud.
bl	Balancers.
bl.c	Blood corpuscles.
b.nv	Belly navel.
b.o	Branchial opening.

b.pl	Basilar plate.
br	Brain; brain chamber; procephalic lobes.
bran	Branchiæ.
br.c	Branchiocephalon.
br.ct	Branchial cartilage.
b.t	Branchial temperature organs.
b.t.hm or **b.t.m**	Branchiothoracic or hypobranchial muscle.
b.th.n	Branchiothoracic nerve.
b.v	Blood-vessel.
c^{1-3}	Lines of canal organs.
c	Cancellæ; corneal membrane; cœlom.
c.ap	Cephalic appendages.
cap.b	Capsuligenous bar of the endocranium; chilarial bar.
card.g. or **cd.g**	Cardiac ganglion.
card.m	Cardiomeres.
card.s	Cardinal sinus.
c.c	Canalis centralis; colar cœlom.
c.ca	Conical pulp cavities.
c.d	Cephalic disc. Cephalic duct.
c.cl	Procephalic cœlom.
c.cn	Collar nerve.
c.co	Cephalic cæcum.
cer	Cerebrum.
cerbl	Cerebellum.
cer.p	Cerebral peduncles
c.f	Cranial floor.
c.g	Corneagen layer; cephalic ganglia; caudal neuromeres.
chila	Chilaria.
ch.g	Cheliceral ganglion.
ch.H.c	Chelicero-hemisphere cells.
ch.H.tr	Chelicero-hemisphere tracts.
ch.l	Cheliceral lobe.
chl.b	Chilarial cartilage bar of endocranium.
chlic	Cheliceræ.
ch.pl	Chilarial pleurite.
ch.t	Chitenous tubule.
cl	Cloaca.
c.l	Cancellous layer.
c.ms	Cephalic mesoderm.
c.n	Procephalic neuromeres; cancellæ.
c.nar or **c.nv**	Cephalic navel; dorsal organ; hæmostoma.
cn.c	Neural canal; neurocœle.
cnl	Canaliculi.
co	Commissure.
co.c	Cerebral commissure cells; corona ciliata.
co.f	Cerebral commissural fibers.
co.n	Nerve to corona ciliata.
cort	Cerebral cortex.
cox	Coxal spurs.
c.p	Collar pore.
cr	Branchial cartilage of embryo

c.r	Root-like cephalic outgrowths.
cran	Cranium.
cr.g	Cranial ganglia.
cu.d	Cuvierian duct.
cut	Cuticular layer.
c.w	Circle of Willis.
cx.g	Coxal glands.
cx.t	Coxo-tergal muscles.
d. and **d**^{1}	Dorsal plate; dentine, or dentine-like chiten.
d.bl	Dorso-branchial line of canal organs.
d.c	Sensory and glandular ducts.
d.end; or **d.e**	Ductus endolymphaticus.
d.f	Dorsal fins.
d.fd	Dorsal portion of anal frill.
di.c	Dicephalon.
di.enc	Diencephalon.
d.o	Dorsal organ; dorsal opening in cephalic shield; cephalic navel.
dor.o	Dorsal organ.
d.s	Dorsal sclerotic plate.
dt. and **dt**^{1}	Denticles or denticle-like spines.
e. and **e**^{1}	Mesethmoid; enamel layer or enamel-like chiten; ocelli.
e.b.m	External branchial muscle.
ec	Ectoderm.
ec.d	Excretory duct.
ec.pa.e	Ecto-parietal eye.
el	External labials (Drepanaspis); extra-laterals; suborbitals.
en^1	Primitive gastrula; cephalic endoderm.
en	Endoderm of trunk.
en.ch	Endochondrites.
encl	Endocœle.
en.cx	Entocoxal nerves.
en.me.cl	Endomesocœle.
en.pa.e	Endoparietal eye.
ent	Entapophyses.
ep. or **eph**	Epiphysis; parietal eye tube.
e.t	Parietal eye tube.
ex.p	External pores.
ext.g	External gills.
f.br	Forebrain.
flab. or **fl**	Flabellum.
f.p	Fringing plates.
f.r	Free nerve endings; frontals; fleshy portion of the rostrum
g	Gills; gastrula; germ cells.
g.ar	Gill arches.
gast	Gastrula
g.c	Germ cell.
g.ctr. or **g.c**	Gustatory center; gustatory tracts.
g.c.tr	General cutaneous tracts.
g.cut	General cutaneous nerves.
g.g	Gustatory ganglia.

g.h	Cephalic gastro-hepatic gland.
g.i	Intraganglionic infolding of the middle cord.
g.iv	Invagination for optic ganglia.
gm.c	Germ cells.
g.n.c	Gustatory nerve roots.
g.o	Gustatory organs; genital organs.
g.p	Gular plates.
gr	Groove between olfactory organs.
gt.p	Gut pouch.
g.tr	Gustatory tracts.
gust.n	Gustatory nerve.
gust.o	Gustatory organ.
g.w	Germ wall.
h	Hypodermis.
h$^{1-2}$	Bony plates covering the hyoid arches.
H.as	Hemisphere association cells.
H.as.tr	Hemisphere association tracts.
h.c	Haversian canals; hepatic cæca.
hc	Hydrocœle.
h.co	Hæmal commissures.
h.l	Hæmal lamina of cephalic shield.
h.m	Hyo-mandibular.
h.m.n	Hyo-mandibular line of canal organs.
h.n.c	Hæmal nerve cord.
h.ne.n	Hæmo-neural nerve.
h.n.m	Hæmo-neural muscle.
h.pr	Hæmal processes.
h.r$^{1-5}$	Hæmal roots.
h.ri	Horn ridges.
h.s	Tergal plates of the abdominal half-segments.
hst	Hæmostoma.
ht	Heart.
h.tr	Hæmal tracts.
hy	Hyoid.
hyp	Hypophysis.
i	Intestinal nerves (1–10).
i.ent	Inter-entapophysial muscle.
i.g	Inter-ganglionic infolding of the middle cord.
i.g.s	Inter-ganglionic spaces.
i.l.m	Gill muscle.
i.n.l	Inner neurilemma; neuroglia.
int	Intestinal nerve.
i.og	Post-oral or mesocephalic neuromeres.
i.o.l	Infra-orbital line of canal organs.
i.p	Internal pores.
i.pl	Intestinal plexus.
i.r	Transverse ridge-plate on inner surface of the premaxillæ
i.sh	Inner neurilemma sheath.
i.v	Infoldings leading to neural canal.
iv.l.e.g	Invagination for lateral eye-ganglion.
iv.ol.l	Invagination for olfactory lobes.

iv.op.g	Invagination for optic ganglion.
l	Lacunæ; lateral plate; labrum.
l.ab.m	Longitudinal abdominal muscle.
l.ab.n	Longitudinal abdominal nerve.
la.f	Lateral fold.
l.ch	Lemmatochord.
l.c.n	Lateral cardiac nerve.
l.co	Longitudinal connectives.
l.cord	Lateral cord.
l.e	Lateral ethmoids; lateral eye.
l.e.n	Lateral eye nerve.
l.ey	Lateral eye.
l.ey.g	Lateral eye ganglion.
l.ey.n	Lateral eye nerve.
l.f	Lateral fold.
lg.	Lung.
lg.b. or **l.b**	Lung book.
l.h.tr	Longitudinal hæmal tract.
l.l	Lateral line of canal organs.
l.lo	Lateral lobes to the olfactory recess.
l.l.ch	Lateral bands of the lemmatochord.
lm	Lamellæ.
l.m.pl	Nerve plexus of longitudinal abdominal muscle.
l.n	Lateral nerve.
lns	Lens.
l.n.tr	Longitudinal neural tract.
l.p	Lateral process; lateral subdermal process to the mandibular plates.
l.pl	Small bony plates in the fleshy sides of rostrum.
l.pl.t	Lateral plastro-tergal muscle.
l.tr	Lateral tracts of brain.
m	Mouth; muscles.
man	Mandibles.
max	Maxillæ.
m.br	Midbrain.
m.c	Merochord; segment of the lemmatochord; marginal cells.
m.cd.n	Median cardiac nerves.
m.ch	Middle chord; median nerve; notochord.
m.cl	Mesencœle.
md	Mandibles.
m.d	Mullerian duct.
mes.c	Mesocephalon.
mesen.c	Mesencephalon.
met.c	Metacephalon.
meten.c	Metencephalon.
m.f	Median furrow.
m.l	Median line; marginal line of canal organs; mantle layer.
m.lch	Median portion of the lemmatochord.
m.lo	Maxillary lobes.
m.m	Muscle markings.
m.n	Median nerve (mouth).

m.n.co	Median neural commissure.
m.oc	Median ocellus.
mp	Malpighian tubules; madreporite.
m.pl	Medullary plate.
m.r	Marginal wall or ridge.
ms	Mesoderm.
msc	Mesenchyme.
ms.en	Mesentoderm.
m.s.p.ent	Mesoplastro-entapophyseal muscle.
m.t	Motor nerve tubes.
mt	Mantle.
mx	Maxillæ.
mx.d	Excretory duct to maxillary segment.
mxl	Maxillaria.
n. or **n.c**	Nerve cord; neuron; neuromere.
n.ch.c	Neurochordal canal.
n.co	Neural commissure.
n.cr	Neural crests.
neph	Nephridia.
neu.p	Neuropore.
n.l	Neural lamina of cephalic shield.
n.n	Neural nerve.
noto	Notochord.
n.p	Neuropile; neural process; neural plate; neuropore.
np.d	Nephric duct.
n.r	Nerve ring.
n.st	Primitive mouth; neurostoma
n.tr	Neural tracts.
n.v	Neural vessel.
o.b	Opening to branchial chamber.
oc	Ocelli; occipital plate.
o.c	Occipital line of canal organs.
oc.f	Occipital foramen
od	Oviduct.
oe	Œsophagus.
ol	Primitive olfactory organ; frontal organ.
ol.l	Olfactory lobes.
ol.l.n	Lateral nerve of olfactory organ.
ol.m.n	Median nerve of olfactory organ.
ol.np	Olfactory neuropile.
ol.o	Olfactory organ.
ol.r	Olfactory recess.
ol.v	Ventricle of olfactory lobes.
o.m	Circumoral membrane.
op	Operculum.
o.p	Postorbital valley.
op.g	Optic ganglion.
op.neu	Optic neurones.
op.pl	Optic plate; opercular pleurite.
op.s	Opercular segment.
op.tr	Optic tracts.

op.tr.h	Optic tract to hemispheres.
o.r	Lateral eye orbit.
os	Cardiac ostia.
o.sh	Outer sheath.
ov	Ovaries.
p	External opening of parietal eye tube; epiphysis; anterior neuropore; opening to endolymphatic ducts; penis thoracic appendages.
pa	Parietals.
p.ap	Pectoral appendage.
pa.ey	Parietal eye.
pa.ey.g	Parietal eye ganglion.
pa.ey.n$^{1-2}$	Roots to parietal eye nerves.
p.b	Posterior branchial line of canal organs.
p.b.c	Peribranchial chamber.
p.c	Paccinian-like corpuscles.
p.c	Pore canals; proboscis cœlom.
pc.a	Pectoral arch.
p.ca	Pulp cavity of denticle.
p.card	Posterior cardinals.
p.ce	Prosencephalon.
p.d	Pericardium.
p.dl	Posterior dorsolateral plate.
p.d.p	Posterior mandibular dental plate.
p.e	Parietal eye.
p.e.n	Parietal eye nerve.
pec	Pectines.
ped.g	Pedal ganglion.
p.e.p	Pits on inner surface of postorbital plate; posterior parietal eye pits.
per.c	Pericardial nerve.
p.e.t	Parietal eye tubercle.
p.g	Polar globules.
ph	Pharynx.
p.h.co	Posthæmal commissures.
pit.f	Pituitary foramen; passage-way for primitive stomodæum.
pl.ap	Pelvic appendage.
pl.cx	Plastro-coxal muscles.
pl.ent	Plastro-entapophyseal muscle.
pl.f	Pleural fold.
pl.t	Plastro-tergal muscle.
p.m	Posterior marginal.
p.m.v	Posterior median-ventral plate.
p.n	Pedal nerve.
p.n.co	Posterior neural commissure.
p.np	Posterior neuropore.
p.o.c	Preoral chamber.
p.p	Posterior process; parietal eye plate; proboscis pore.
pr	Prepuce; cephalic mantle.
pr.mx. or **p.mx**	Premaxillæ.
pr.n or **pro**	Pronephros.

proc	Procephalon.
prosen	Prosencephalon.
pr.s	Primitive sheath.
prt	Protoplasm.
ps	Posterior sclerotics; pancreas.
p.s.o	Primitive sense organs.
pt	Pituitary gland or duct.
p.t	Primary tentacles.
p.t.r	Posterior triangular recess.
p.v	Posterior median ventral plate; postorbital line of canal organs.
pv.l	Pulsatile vessel.
p.v.t	Mass of bony trabeculæ below the postorbital valley.
r	Ridges; roots to spinal nerves; rostrum.
r.d	Visual rods.
r.l	Rostral line of canal organs.
rost	Rostrum.
r.s	Shelf plate on the inner surface of the rostrum.
s	Scales; sulcus on the floor of the procephalic lobes; stomach.
s.c	Superficial canals; sensory canals.
s.c.n	Segmental cardiac nerve.
s.c.no	Subcortical neuropile.
s.d	Sucking disc.
s.g	Shell gland.
s.l	Superficial layer.
s.l.c	Cells derived from sheath of lateral cords.
s.lch	Sheath to lemmatochord.
s.m.n	Sheath to median nerve.
sn.c	Sensory canals.
s.o	Suborbital plates; sense organs.
s.o.l	Supra-orbital line of canal organs.
sp	Spindle-shaped dilatation on the sensory tubes; subdermal process on lateral margin of premaxillæ.
st	Stomach; stomodæum.
s.t	Sensory tubes.
st.c. or **st.co**	Stomodæal commissure.
st.g	Stomodæal ganglion.
st.n	Stomodæal nerves.
sto	Stomodæum; stolon.
t	Terminal joint to cephalic appendages; testis.
t.b	Tongue bar.
t.cl	Telocœle.
t.cx	Tergo-coxal muscles.
t.d	Tear duct; thoracic duct.
telbl	Teloblasts.
telen	Telencephalon.
tel.o	Telopore.
t.g	Groove (for tentacle?).
tg.prpl	Tergo-proplastral muscles.
th	Thyroid.
th.ap	Thoracic appendages.

th.n	Thoracic nerve cord.
th.so	Mesoblastic somites of thoracic metameres.
t.l	Remnants of ingested larval tentacles.
t.l.n	Thoracic temperature organs.
t.p	Telopore.
tr	Trabeculæ
tr.c	Trabeculæ cranii.
t.st	Tendinous stigmata.
u	Point of union of vascular canals.
v	Ventricle; subneural gland; vestibule.
v.c	Vascular canals.
v.d	Vas deferens.
v.dec	Vagus decussation.
v.fd	Ventral wall of anal frill.
vg	Vagus (yellow body).
vg.ap	Vagus appendages.
vg.n	Vagus nerves.
vg.nm	Vagus neuromeres.
v.l	Vascular layer.
v.m	Ventral margin.
w.d	Wolffian duct.
yk.c.h	Yolk cells of head.
yk.c.t	Yolk cells of tail.
yk.nav	Yolk navel.

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