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THE

EMBRYOLOGY OF LIMULUS.

BY

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J. S. KINGSLEY.

CONTENTS.

Historical.

The embryology of Limulus has already given rise to considerable literature, but there still remain many problems to be solved. The first to describe any embryonic stage of this genus was Henri Milne-Edwards, who figured and briefly described ('38, '39, '40) a single larval stage. The next was Samuel Lockwood ('70), who gave an account of the oviposition, and the hatching of the egg, and described several of the larval stages. A. S. Packard followed with a long series of articles ('70^a, '70^b, '70^c, '71, '72, '73, '75, '80, '85), each of which added something to our knowledge. Dohrn ('71), who studied material supplied by Packard, was able to see some points which had escaped the latter. Alexander Agassiz ('78) described the habits of the young after the beginning of a free life, and contributed a figure of the larva to Faxon's ('82) compilation of drawings illustrative of the embryonic stages of Crustacea. The present writer made his first contribution to our knowledge of the development of Limulus in 1884, following it in October of the next year with a more extended paper ('85). In the same month H. L. Osborn ('85) and Brooks and Bruce ('85) published preliminary accounts of their investigations; the complete papers have not yet appeared. S. Watase has made the structure and development of the visual organs the subject of three papers ('89, '90 a, '90 b). William Patten ('89) gave a brief note on the origin of the nervous system and sense organs, while in a later paper ('90), in which an attempt is made to derive the Vertebrates from the Arachnids, numerous facts relating to the early history of Limulus are given. Lastly, I have presented ('90) a brief abstract of some of the results to be described more at length in the present series.

HABITS, ETC.

The American horse-shoe crab (*Limulus polyphemus*) is distributed along our eastern shores, from Maine to the West Indies and the Gulf of Mexico (Vera Cruz, teste J. E. Ives), occurring at certain times and places in large numbers. Its habits have been described with some detail by Dr. Lockwood ('70). During most of the year it frequents deeper water, but during the breeding season — May until the middle of July — large numbers come to the shore for the purposes of oviposition. I have never been able to notice any connection between the hours when they frequent the shore and the state of the tide. Several times on moonlight evenings, in the height of their spawning season, I have sailed over their favorite spawning grounds, but did not see any of the "crabs."

I do not know where the couples meet. When first seen they come from the deeper water, the male, which is almost always the smaller, grasping the hinder half of the carapax of the female with the modified pincer of the second pair of feet. Thus fastened together, the male rides to shallow water. The couples will stop at intervals and then move on. Usually a nest of eggs can be found at each of these stopping-places, and as each nest is usually buried from one to two inches beneath the surface of the sand, it appears probable that the female thrusts the genital plate into the sand, while at the same time the male discharges the milt into the water. I have not been able to witness the process more closely because the animals lie so close to the sand and all the appendages are concealed beneath the carapax. If touched during oviposition, they cease the operation and wander to another spot or separate and return to deep water. I have never seen the couples come entirely out of the water, although they frequently come so close to the shore that portions of the carapax are uncovered.

I have already commented upon the great vitality of the eggs and the young ('85, p. 522), but a few words more may prove of interest. When studying the development in 1884 the eggs I studied were transported 200 miles from the place they were laid. They were six days on the journey, packed in moist sand, but without any addition of salt water. On August 1 I left the shore, taking with me some 200 embryos and about a pint of salt water. By merely supplying the loss by evaporation with fresh water from the city supply I kept some of these alive until November 20, when the last were killed to supply material for study. In 1890 I fertilized some eggs on June 22. Some 200 of these were taken in half a litre of water to Lincoln, Nebraska, 1600 miles from the shore, where they lived from September 7 to the week of November 14–20, when they were killed by an accidental drying up of the water during a temporary absence. As it was, they lived over twenty weeks in confinement. It would not have been possible to keep them much longer, as the stock of food yolk was about exhausted. Adult specimens have been shipped alive to San Francisco, and now one meets occasionally with notices in the Pacific coast papers of the capture of horse-shoe crabs, probably those planted there several years ago by the U. S. Fish Commission. They have also been shipped alive to England and Germany. Professor E. Ray Lankester had three barrels of these animals sent him in London from Woods Holl, a large proportion of them surviving the voyage.[1]

An observation made by Dr. Lockwood upon the retardation and vitality of the eggs should be repeated. He says ('70, pp. 271–272): "At the close of the warm season last year [1869] my jars must have contained not less than 200 young Limuli. . . . Hoping to continue observations upon the growth of my interesting family, the jars were carefully put away. Little regard, however, was paid to temperature, which, on several occasions, went down to the freezing-point. On the 3d of May, 1870, I emptied the jars to see how my charge was getting on, when lo! not one of the last year's hatching was alive! but, won-

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[1] Mr. Vinal Edwards, who made the shipment, informs me that those packed without seaweed or other moist packing survived the journey the best.

derful to say, at least a dozen little fellows, all hatched this spring, and all alive, had taken their place. With these were also at least thirty eggs, in different, but all in advanced, stages of incubation. In some of them the young could be plainly seen revolving." Here was a retardation of development for almost a year!

METHODS.

The observations here recorded were made at the Marine Biological Laboratory at Woods Holl, Massachusetts, during the months of June, July, and August, 1889 and 1890, and in the zoological laboratory of the University of Nebraska. In writing up the results obtained I have been hampered not a little by my distance from the larger libraries, and hence the comparative portion of the paper is sadly deficient — a fact which no one can realize more than myself.

For my material I have relied partly upon the natural nests and partly upon artificial impregnation. With the former method one cannot be certain of the age of his material, for not infrequently two ovipositions become mixed. I have never succeeded in getting the crabs to oviposit naturally in confinement. In artificial impregnation the eggs and milt were sometimes obtained by squeezing individuals taken *in copulo*, or by sucking these products from the genital ducts with a pipette. Very severe squeezing will force out but a small number of eggs, — far fewer than are naturally laid in a nest, — while any attempt to remove them from the body by cutting covers the eggs with a layer of very rapidly coagulating blood (*vide* Howell, '85), which affords an excellent nidus for bacterial and fungoid growths.

The study of the early stages has proved very difficult from the fact that the eggs are the most refractory objects I have ever seen. Until the outlining of the germ there is no means of orientation, so that sections must be taken hap-hazard. The greatest care must be taken in hardening them in order to prevent the yolk becoming too hard for the section knife; and after numberless experiments with every reagent I could think of, I came to rely almost entirely upon killing the eggs by heating them in sea-water to 70°–75° C. and then passing them through successive grades of alcohol, from 30 per cent to 70 per cent, in which they were finally kept. Eggs thus treated afforded at the moment of killing excellent, but evanescent, surface views, as a short immersion in alcohol renders the whole surface one uniform color. Hence, in order to orient these eggs for subsequent section, I marked each one, at the moment of killing, with India ink — not affected by alcohol — and subsequently arranged the egg with reference to the line thus afforded. For staining I used chiefly alum cochineal and Grenacher's borax carmine, while a short stay in osmic acid brought out certain details.

I found it impossible to cut the early eggs in paraffin. Absolute alcohol and the clearing reagents rendered the yolk extremely hard and brittle, while the paraffin refused to penetrate the centre of the egg. So for the early stages I had recourse to celloidin. For the main outlines of the process employed I am indebted to the suggestions of Dr. H. C. Bumpus. The celloidin was hardened with chloroform and cleared with origanum oil or with a mixture of turpentine and carbolic acid *before* cutting. The sections were cut with the knife flooded with the clearing fluid, and then placed in order on the slide. Being already cleared, all that is now necessary is to apply balsam and the cover glass. In many respects this process is identical with that described by Eyclesheimer ('90).

To study the stages after the outlining of the germ, the chorion was removed by needles,[1] and then by careful manipulation the blastoderm was stripped from the yolk, stained, and either mounted *in toto* for surface views or sectioned as usual in paraffin. In the later stages the processes of development so modify the yolk that the whole embryo is capable of being sectioned in the usual manner.

As a result of the difficulties of manipulation the following account of the early stages is exceedingly fragmentary, yet it is hoped that the little here detailed will prove of value, especially as almost nothing is known of the processes involved in the formation of the germ layers. (See Postscript.)

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[1] Owing to the great thickness of the chorion I found it difficult to control the action of eau de Javelle or Labbaracque's solution. Before the chorion was dissolved the solution would frequently affect the egg, interfering with staining and making it very crumbly.

Ovigenesis.

I have made no extended observations upon the origin and development of either eggs or spermatozoa. The gross structure of the ovaries has been described by van der Hoeven ('**38**), Gegenbaur ('**58**), and Owen ('**72**), while Gegenbaur adds a short account of the origin of the egg, presented in abstract by Ludwig ('**75**). Owen gives a line or two to the testis, while Benham ('**83**) describes it more in detail. Packard ('**72**) figured the spermatozoa, Lankester ('**78**) noted the fact that they are motile, and Packard ('**80**) refers to the histology of the testis and speaks briefly of the development of the ovary. Aside from these and one or two older papers, at present inaccessible to me, I know of no published results upon the reproductive organs of Limulus.

In a female Limulus four inches long (not including the caudal spine) I find the ovarian cæca lined with columnar epithelium which secretes a delicate cuticle, and outside of this epithelium a connective tissue tunica propria. As in other higher Metazoa, this epithelium is the ovogenetic layer, certain of its cells becoming modified into primordial ova. These at first lie within and form a part of the parent epithelium, but with growth the eggs pass to the outside of the epithelium and, separating the tunica from the other layer, come to lie between the two. (Figs. 1 and 2.)

The primordial ova are distinguishable not only by their size, but by their more deeply staining cytoplasm, in which the yolk spherules, so characteristic of the mature eggs, are lacking, unless the minute granules are to be regarded as such. Around the cytoplasm of the older eggs, after leaving the epithelium, there is a delicate membrane, the origin of which I have not been able to decide, but I think it a true vitelline membrane. The nuclei of the ovarian eggs vary considerably with age. In the younger ones they are strongly staining bodies of about the size of the nucleoli of older eggs. In these no reticulum is visible. A little later this nucleus is surrounded by a clear space which separates it from the darker and more granular cytoplasm. This clear space shows processes radiating into the surrounding substance. In still older eggs a well-marked nuclear membrane is distinguishable, inside of which is a faintly staining chromatin (?) reticulum and from one or two to five spherical and deeply staining nucleoli. There is no 'yolk nucleus' like that described in certain Arachnids.

As will be seen, the foregoing description differs *in toto* from Packard's brief account and figures ('80, p. 39, Pl. IV, Figs. 8, 8^a). In fact, I cannot determine what he had under the microscope. If I understand Gegenbaur ('58) aright, the eggs in his specimen[1] project into the lumen of the ovarian tube, a difference possibly explicable on account of the mature condition of his material. He was farther unable to recognize any membrane around the egg aside from the epithelial cuticle of the ovarian tube. In other respects there is no discrepancy between our accounts.

Making comparisons now with the Arachnida, we see no little similarity in the structure of the ovary and the relations of the ova. Metschnikoff ('71, pp. 207–208, Pl. XIV, Figs. 1 and 2) and Laurie ('90, pp. 108–111, Pl. XIII) describe and figure almost the same condition in the scorpion. The ovary consists of the same epithelium and tunica, and the eggs, as they increase in size, come to lie between these two layers. The differences are that in Limulus each egg is not enveloped in a separate follicle; but in the scorpion, where the eggs are few, such is the case. In Limulus the epithelium does not form such a well-marked "stalk" connected with the egg as in the scorpion; and the cells of this stalk are columnar, not stratified. Closely similar resemblances can be traced with the Araneida, as epitomized by Ludwig ('75) and the Acarina (Pagenstiecher, '60–'61). In the Crustacea, on the other hand, a similar condition is not found, there being nowhere an ovary with a similar constitution. In short, so far as my observations on ovigenesis go, Limulus agrees well with the Arachnida and contrasts strongly with the Crustacea.

Early Development.

The eggs of Limulus, as they come from the oviduct, vary considerably in size and shape. They are usually more or less oval,

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[1] Twenty-five German inches long. Gegenbaur is in doubt about his specimen. In appearance it was clearly *L. molluccanus*, but so far as he was able to find out it came from the West Indies. As *L. polyphemus* and *L. molluccanus* are easily distinguishable, it is possible that a mistake was made in locality.

being somewhat flattened at first by mutual pressure in the oviduct. The average diameter is perhaps two millimetres. Each egg is enveloped in a tough chorion in which a laminated structure is readily recognizable. I have never been able to discover any opening or pores in this chorion through which impregnation can be effected, although it is certain that fertilization must take place outside the body of the female, and hence after the chorion is formed. The egg proper consists of a large mass of strongly refractive yolk globules of various sizes, and in the egg as it comes from the oviduct I have been unable to find a trace of a nucleus, nor of nuclear material. No matter what stain was employed, I could not recognize any chromatin granules scattered through or upon the yolk, while anything that might be considered as protoplasm was very scanty.

In this my experience is paralleled by that of certain other students of Arthropod eggs. The nucleus can be traced to a certain stage of ovarian development where, as Stuhlmann says ('86), "Später verschwindet das Keimbläschen vor unseren Blicken, bis wir endlich am oberen Eipol der Furchungskern wieder finden." Of course this absence is apparent rather than real, as has been shown by numerous other observations.

I have been equally unsuccessful in my attempts to witness the phenomena of fertilization, nor have I seen any features undoubtedly characteristic of maturation, although I have sectioned many eggs. In one egg, an hour after fertilization, I found on one side a faintly staining structure which I have possibly thought may have been a polar globule (Fig. 3), but the fact that a nuclear stain brought out no chromatin inside the yolk renders this doubtful.

The various steps of development vary in time, not only with the temperature, but with eggs of the same lot exposed to exactly the same conditions. Hence the ages quoted in the following pages must be understood as averages. Thus, in one lot of eggs I have found phenomena occurring at four hours, which in others occurred at twenty-four hours, while in later stages there may be variations of a month or more.

At the time of impregnation, the surface of the egg is covered with dark yolk granules, each granule having a lighter boundary. The granules vary in size, and the egg completely fills the chorion. In fifteen minutes the chorion distends so as to leave a space between it and the egg, and at the same time its outline becomes regular and ellipsoidal. In half an hour the granules begin to break up and become smaller, while the yolk begins to swell, and at the end of an hour completely fills the chorion.

In four hours begin those strange modifications of the surface already noticed by H. L. Osborn ('85) and by Brooks and Bruce ('85). Viewed from the surface the eggs exhibit a number of fissures, usually at one pole of the egg, which strongly simulate cleavage furrows (Figs. 4, 5, 6). I have not be enable to kill such eggs quickly enough to preserve these furrows for section. Even when dropped into hot water the surface would become smooth before death ensued.

Sections of such eggs present some features difficult of interpretation. In the earlier phases near one pole there appears a clear line inside the yolk, concentric with the surface, which marks off a central from a superficial portion; while in older eggs (Fig. 7) the line has extended nearly around the egg. Inside of this line were no features worthy of mention, and in the several eggs sectioned no nucleus was to be found. Outside of the line the yolk becomes broken up into numbers of columnar bodies — like the cells of columnar epithelium — with rounded external ends. These yolk columns are separated from each other by a slightly staining protoplasm (Fig. 8), and the outer ends of these columns are more free from yolk spherules than are the deeper portions. I think, notwithstanding the apparent disparity of dates, that it was an early stage of this process which Brooks and Bruce describe when they say of an egg of twenty-four hours "protoplasmic processes or pseudopodia extend from the [protoplasmic] cap into the yolk, and surrounding and including the substance of the yolk divide this up into a number of yolk balls." After a short time these motions of the external surface cease, and the egg becomes as smooth as before, while in section no change is recognizable except that there is a thin layer of protoplasm — a true blastema[1] — over the whole yolk.

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[1] As I have already indicated ('86, p. 116, foot-note), I use the term blastema in the original sense. Patten defines ('84, p. 564) the blastema as "a thin nucleated layer of protoplasm covering the whole outer surface of the yolk, and not divided into distinct cells." He, however, suggests that it is not impossible that a

I am in doubt as to the interpretation of these phenomena. They are not connected with segmentation. Two possibilities have suggested themselves. One is that they may possibly be compared with those still unexplained polar rings described by Whitman (**'78**, p. 234), on *both* poles of the maturing egg of Clepsine (a suggestion of doubtful value). The other would view them as connected with the formation of the blastema. It is certain that a blastema surrounds the egg of Limulus after this process while none was visible before.

In one egg of about twelve hours I found what I regarded in my preliminary paper (**'90**) as the segmentation nucleus, occupying a subcentral position in the yolk, but I have not succeeded in connecting it with the later stages. In other eggs of the same age I find a thickening of the blastema on one side of the egg, but no stain serves to distinguish a nucleus in it, but still it may be present. The position of the segmentation nucleus has no great taxonomic importance, as in both Crustacea and Arachnida it may be either subcentral or superficial.[1]

Stage A. — Between twelve and twenty hours I have not been able to get any sections showing anything. At twenty hours I found an egg containing eight nuclei. By drawing these in their relative positions and projecting them on a plane (Fig. 9), a marked polarity in their distribution is apparent. As will be seen, the nuclei are much nearer to one pole of the egg than to the other, and had the plane of projection been slightly different this polarity would have been more marked. This condition is intelligble on the view that the segmentation nucleus is subcentral as well as if it be regarded as superficial.

In the next twenty hours there are no phenomena to detail at length. From the surface no changes are visible, while sections reveal a gradual increase in the number of nuclei, the polarity just mentioned persisting in their distribution.

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blastema may exist without nuclei. The term blastema was first used by Weismann (**'63**) for a non-nucleated layer in Musca and Chironomus, and such a layer has been shown to exist in many eggs by various authors, among them Metschnikoff (**'66**) in Aphis, Aspidotus, Cæcidomyia; Witlaczil (**'84**) in Aphis; Locy (**'86**) in Agalena; Heider (**'89**) in Hydrophilus; Voeltzkow (**'89**) in Musca, etc. A blastema, then, is a layer of anucleate protoplasm around the yolk.

[1] *E.g.* subcentral in Cetochilus (Grobben, **'81**), Crangon (Kingsley), Eupagurus (Mayer, **'77**), Porcellio (Reinhard, **'87**), Araneina; peripheral in Nebalia (Metschnikoff), Mysis (Van Beneden, **'69**), Scorpio (Laurie), Acarina (Claparède, **'68**).

In from forty-two to forty-eight hours the eggs, as they lie in the dish, show on their upper surfaces the first traces of segmentation of the yolk. In this there is no regularity as to the direction of the furrows nor uniformity in their extent. At first the furrows are clean cut, with well-defined margins and some depth, but soon they become shallower, and the margins and bottoms become irregular by the formation of numerous yolk spheres of varying size (Figs. 10, 11). Gradually the furrows flatten out, and the yolk spheres become merged in the general yolk of the surface, and the egg is as smooth as before. In from four to six hours this process is repeated, the spaces between the furrows becoming smaller and the furrows embracing more of the egg than before (Fig. 12). This is repeated several times, until at last the whole surface is included in the segmentation (Figs. 13, 14). At each of these divisions there are at first the same clean-cut furrows followed by the same irregularity, and eventually by the apparent obliteration of the planes of segmentation.

Sections plainly show (Fig. 15) that this is a true segmentation of the yolk, the result being to divide the whole egg into a series of cells, each consisting of a mass of yolk (Fig. 18) with a central nucleus. It is also apparent that therewith is connected the appearance of the nuclei at the surface of the egg and the formation of a blastoderm (Fig. 15). In the projection of an egg of forty-eight hours (Fig. 16) twenty-six nuclei were seen. A little later (2¼ days) a higher power shows some interesting phenomena. The nucleus is surrounded by an amœboid mass of protoplasm, sending processes into the surrounding yolk, while the planes of segmentation, as well as the external surface of the egg, are covered with a thin layer of faintly staining protoplasm (Fig. 17), apparently the blastema of the earlier stages. At the time when these furrows seem to disappear (*supra*), this protoplasm regains the surface, but the furrows themselves remain, and eventually the whole egg is divided into nucleated yolk cells (Fig. 18).

At first the central portion divides as rapidly as the peripheral, and in each portion of the egg the cells are about equal in size; at last, however, the central cells enter upon what may be called a resting stage, which condition persists until after the beginning of a free-swimming life. Their divisions occur at infrequent intervals, and the differences in size, from the appearance of the germ until the caudal spine appears, are scarcely noticeable.

Stage B. — The peripheral cells, on the other hand, divide more rapidly, so that in five days from impregnation (Fig. 19) there is a marked difference between the cells on the surface and those deeper in the egg. A more careful study shows that this division of the surface cells has a peculiar character. In each instance (see Fig. 20, which represents a portion of an egg of $5\frac{3}{4}$ days) the first division of the peripheral cells occurs in a plane parallel to the surface of the egg. This is plainly shown in the cases of the cells marked x, where the direction of the mitotic spindle shows the direction of the future division — a view which is confirmed by a study of the other cells. Another feature is noticeable. The products of this division are unequal. There is a deeper and larger cell containing a large amount of food yolk and closely resembling the neighboring yolk cells; and a superficial smaller and flattened cell, richer in protoplasm and containing far less yolk. In this way a blastoderm is differentiated, but the process has in my opinion a deeper significance, for by it the entoderm is separated from the rest of the egg. In other words, in Limulus the two primary germ layers are differentiated by multipolar delamination.

This process is clearly allied to that multipolar delamination which Morgan ('90, '91) has described as occurring in the eggs of certain pycnogonids and Faussek ('91) in phalangids. While I shall discuss it later, I may say here, that it probably has at most a very distant relationship to the Cœlenterate delamination, but has arisen within the Arthropod phylum.

After the formation of the blastoderm, *i.e.* the separation of ecto-mesoderm from entoderm, I have not been able to add much to our knowledge until about eight days after impregnation. The absence of all features which would aid in the orientation of the egg makes it necessary to cut all sections at random, while the opacity renders surface views impossible. In general this time is occupied by a multiplication of the blastoderm cells and a consequent diminution in their size. This multiplication by division proceeds at a more rapid rate at one pole of the egg than at the opposite, the result being that soon a germinal pole may be recognized by the smaller and more columnar cells, those at other portions retaining, until later stages, more the appearance of pavement epithelium.

BLASTODERM CUTICLE.

With the formation of the blastoderm, the blastodermic cuticle is first laid down. Its history need not be given here, as I have already ('85, p. 524) detailed it, and have suggested for it and similar envelopes, Claparède's term "deutovum." The occurrence of these *Blastodermhauten* is frequent in the Arthropod phylum. In Limulus the envelope persists as a protective structure until a late stage in development, but it is omitted from my figures.

EARLY EXTERNAL DEVELOPMENT.

Stage C. — At from six to eight days after impregnation a lighter patch is visible on one side of the egg. Its outline is not distinct, but in general it may be said to be circular. The change which this undergoes in two or three days (eight to eleven days from impregnation) is slight; at the latter date a pit is apparently seen in the centre of the white spot (Fig. 21).

For this lighter patch I have taken the same name which was given by Claparède ('62) to a similar structure in the developing Arachnid egg.[1] The spot is the first appearance of what is to form the primitive streak. At first this spot is circular, but it soon becomes elongate. The next day a second cloud appears immediately adjoining the first and connected with it (Fig. 22). I am not positive in my identification, but believe that the primitive cumulus marks the anterior end of the embryo. At first the posterior, or secondary, cloud is smaller than the primitive cumulus, but it rapidly increases in size, while its outlines become more indistinct than shown in Fig. 23. At the same time the primitive streak extends backward from the spot mentioned above, into the posterior cloud; the anterior spot remaining the widest of the whole. For reasons which will appear farther on I regard the widest end of the primitive streak as marking the position of the future mouth. The posterior cloud continues to grow until the result is as shown in Fig. 24.

Next there appears a transverse line behind the primitive cumulus, cutting the embryo into an anterior, or cephalic

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[1] I retain this term, 'primitive cumulus,' notwithstanding Kishinouye ('90) has shown that it is possible that Claparède has mistaken the order of appearance of his "cumulus primitif" and the 'calotte.'

region, and a posterior or thoracico-abdominal portion, the cephalic being the smaller and more sharply differentiated from the rest of the blastoderm. This occurs on the average about fifteen days after impregnation. Twelve hours later a second line occurs behind the first, cutting off from the thoracico-abdominal region the first somite of the body; and about twelve hours later a third transverse line appears (Fig. 25), and now there is a head region, two body somites, and an undifferentiated caudal region.

This figure (Fig. 25), taken from a blastoderm peeled from the egg and mounted in balsam, shows clearly that this appearance of somites and lines of separation results from the fact that the cells are abundant in certain regions and more scattered in others; in other words, from the outlining of the mesodermic somites. This process continues until six segments behind the head are formed, the sixth consisting of the united sixth 'thoracic' segment and the caudal plate.[1] At first these segments are quite short and correspondingly broad (Fig. 26), but later they increase rapidly in length. I may say in passing that owing to the difficulties of observation it was not possible to be certain of the limits and proportions in certain figures. Each egg had to be studied in strong sunlight, and the use of a camera was impossible. Such was the case with Figs. 22, 23, 26.

MESODERM.

The primitive cumulus is shown in section in Fig. 36. As will be seen, the surface of the egg is covered with a layer of thin, flattened cells, while beneath are the entoderm cells. The cumulus itself is thicker, partly owing to the fact that its component cells are more columnar, and also to the fact that lower layer cells have been formed. The spot in the cumulus, which in surface views (Fig. 21) looks like a pit, is seen in sections to be produced by the greatly thickened centre of the cumulus.

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[1] In a few instances I have seen reason to doubt this. In almost every instance I have seen all six appendages arise at the same time, but in two or three cases, (*e.g.* Fig. 28) but five appendages appear at first, the appendage I being noticeable at a later date. This may indicate that the corresponding segment may be correspondingly delayed; and that the above interpretation is not correct. On the other hand, these instances may belong to some of the many anomalies, which are found in examining a large series of Limulus embryos.

Sections of the embryos shown in Figs. 21–23 show but slight differences from those of Fig. 24, and hence a description of that will suffice. Fig. 37 represents a section through the anterior end of the streak at stage C. In the median line is the streak itself, which shows a median proliferation of cells extending some distance into the yolk, while on either side is a less conspicuous thickening of the blastoderm. All three of these elements enter into the formation of the appearance of a primitive streak as viewed from the surface, and all contribute to the formation of the middle germ layer. At the point of the section the median ridge extends below the others, and the nuclei at its inner extremity show a tendency to spread towards right and left. Farther back (Fig. 38) these same centres of proliferation may be traced, and here the lateral as well as the median band contributes to the mesoderm. From the primitive streak the mesoderm here extends right and left to the margin of the germinal area, where, apparently, it again connects with the ectoderm. In some sections, especially in later stages, other points of connection occur between ecto- and meso-derm, but I have not been able to trace any regularity in these.

This account accords well with that of Patten ('90), except that I have failed to trace, in surface view, the ring of mesoderm extending completely around the embryo to which he refers (p. 375). Probably this is represented by the marginal connection between ectoderm and mesoderm in my figure.

In this method of mesoderm formation a portion of the peripheral part of the yolk is cut off by the outgrowing middle layer, and comes to lie between it and the ectoderm (Fig. 39). This yolk is in such position that it can readily serve as food for the growing ectoderm, and although I have no evidence on this point, I believe that such is its fate.

The subsequent history of the mesoderm and its derivatives will be followed in detail in the next portion of these studies.

Development of External Form.

Stage D. — The next step is the formation of the appendages. So far as my observations go this process would seem to take place nearly simultaneously on all of the cephalothoracic postoral segments in the majority of eggs. Yet this is not the case in all. Figs. 27 and 28 show two modifications which I have witnessed, the latter in two instances. In the first and more normal of these figures the cephalic region is small, and behind it come six somites, each with the outline of a pair of appendages. The sixth appendage is faint, and the segment which bears it is not yet differentiated from the abdominal region. The same state of affairs is shown in the slightly later stage represented in Fig. 29, made from an embryo peeled from the egg, and which also shows several other points to be described later. In this the mesodermic somites are obscured, while the abdominal region is more elongate. On the other hand, Fig. 28, also made from a transparent specimen, shows but *five* pairs of thoracic feet, while in other respects the embryo is much further advanced, as is shown by the existence of appendages VII and VIII (operculum and first gill-bearing appendage) in the abdominal region.

This variation in the time and order of the appearance of the appendages probably explains the difference between Dohrn ('71) and Packard, the former stating that appendage I appears later than the others. This is certainly true in some cases, but out of several hundred eggs examined at about the time of the appearance of the feet, I have seen but two instances, and in my former papers ('85 and '90) I took Packard's position, as at the times when those papers were written I had not seen a specimen without appendage I.

Professor H. L. Osborn ('85, p. 2) gives the following account of the appearance of the limbs in Limulus: "On July 28th, 11.30 A.M. [the eggs were fertilized July 23], a deep semicircular depression showed itself. On the 29th, in the space between the two lips of the depression of the day before, a pair of buds appeared — the beginnings of the anterior pairs of limbs. On the following day two more pairs are added, and in front of the first pair and behind the front lip of the fold a most important structure is for the first time seen: it is a slit elongated antero-posteriorly, — the definitive mouth opening. It is distinctly in front of the first pair of limbs. It is to be noted that the anal opening has not yet shown itself, according to my observations. The stomodæum and the three somites are now included in an area which is plainly marked off from the rest of the egg and surrounded by an oval elevation. On the following day, July 31, there had appeared inside this rim the remaining pairs of cephalothoracic appendages."

Although I have looked carefully for the appearances thus described, I cannot confirm the description. Still, there are so many anomalies in the history of many eggs that it is possible that the conditions witnessed by Professor Osborn may sometimes occur. For instance, in some eggs, after the somites are partially outlined, a deep longitudinal groove appears, transverse to the somites and extending the whole length of the embryonic area. The lips of this groove sometimes even touch each other, and in the tube thus formed the limbs bud out. Again, in other eggs a deep invagination may take place in the abdominal region, carrying in with it the abdominal feet. Such eggs appear later to regain the normal appearance and to develop in the regular manner.

Concerning the later features of external development but little needs to be said. The figures given by Packard Dohrn, and myself are sufficient to indicate most of the features of the growth of body shape and the positions and changes of forms of the various appendages.

Stage E (= Kingsley, 85', Fig. 5; Packard, '72, Fig. 12). — In this stage the edge of the carapax has been differentiated, forming a clear-cut line marking off the ventral from the dorsal surface. The six pairs of cephalothoracic legs retain a post-oral position, while the first pair (operculum) of abdominal appendages is outlined.[1]

Stage F (Packard, Fig. 12; Self, '85, Fig. 6; present article, Fig. 28). — In this stage the embryo is much as before, except that the second (first gill) appendage of the abdomen has made its appearance, while the series of sense (?) organs briefly mentioned by Patten ('89, p. 602) are prominent, especially in mounts peeled from the egg and in osmic acid preparations. These sense organs, to which I shall return later, are six in number on either side of the body. I earlier ('90) described their fates, which are as follows: The first pair give rise to the median ocelli of the adult; the second move to a position in front of the mouth, where near the median line they form a peculiar sense organ as yet undescribed; the third and sixth disappear at a very

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[1] This is not well shown in Packard's figures.

early day; the fourth forms the structure called by Watase ('89 and '90ᵃ) the "dorsal organ," which early reaches a large size and then disappears; while I believe that the fifth gives rise to the compound eye.[1] I now believe that this account will require serious modification. Of the existence of the organs there is no doubt, but their fate is in question.

Stage G (Fig. 32) is characterized by the relative change in position of mouth and the first pair of limbs. At first the mouth is distinctly pre-appendicular (*vide* Figs. 27, 28, 29). At this time its shape is approximately circular. Soon, however, the mouth becomes more elongate, its front margin becoming acute as if the right and left lips were coalescing (Figs. 30, 31). By this process a true ectodermal stomodæum is invaginated, and the mouth is carried backward, as I have already explained and diagrammatically illustrated ('85, Pl. XXXIX, p. 526, Figs. 40–43), so that as a result the first pair of appendages become distinctly post-oral. Other features are the budding of the curious appendix (flabellum Auct.; appendice lancéolé de la hanche, van der Hoeven) upon the basal joint of the sixth pair of appendages; and the outlining of the so-called metastoma upon the sixth body segment. I have already pointed out that this last cannot be regarded as an appendage of a metameric nature (Self, '85, p. 532), since it is borne on the same segment as the true sixth appendage.

In *Stage H*, Fig. 33 (Packard, Fig. 19; Kingsley, '85, Fig. 12), the distinction between cephalothorax and abdomen is evident; the legs are longer and show evident segmentation. (Fig. 33.)

In *Stage I* (Kingsley, '85, Fig. 14; Packard, Fig. 24) the appearance is quite like that of the adult. The body is now much more depressed, the legs are like those of the adult, and the cephalothorax is considerably larger than the abdomen. The abdomen exhibits traces of segmentation, while its margin bears the movable spines upon its margin which are characteristic of the adult. The telson as yet remains as a slight lobe of the middle of the hinder margin of the abdomen.

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[1] This account varies from that of Patten, ('90) if I understand him correctly. According to him the median eye falls outside the category of these organs. The compound eye ("convex eye") "arises from three small sense organs near the third thoracic segment," while the "eye of the fourth segment" is very large, thus putting the compound eye in front of the 'dorsal organ.' Watase, on the other hand ('90ᵃ) places the compound eye behind the dorsal organ. (See Postscript.)

Stage K, Figs. 34 and 35 (Packard, Fig. 25; Self, Figs. 16 and 17) is the last stage previous to the molt which results in the adult form. The abdomen is relatively much larger than before; the opercular lobes have nearly met in the median line, and the animal begins to burrow in the sand, although embryos of this stage are not infrequently taken in the towing net.

Stage L (Packard, Fig. 27) is produced from the last by a single molt. It is characterized by the presence of an elongate telson much like that of the adult. With this stage my studies end.

The following points may also be of interest. The Blastodermhaut is molted at about *Stage F*, the time varying with different eggs. It still persists as an embryonic envelope (vicarious chorion of Packard) until a late stage. Soon after it is shed from the parent cells a second embryonic cuticle is cast, and then the true chorion is shed, and the embryo, encased in the distended Blastodermhaut, escapes from the egg at about *Stage K* or *L*. The Blastodermhaut itself is ruptured, and the animal begins its free existence at the end of *Stage I*.

COMPARISONS.

A. With Previous Accounts. — H. L. Osborn ('85) and Brooks and Bruce ('85) have described some of the phases of segmentation, the latter studying sections. Their account so far as it goes is reconcilable with what I have described, including the pre-segmental movements. They have also noticed the primitive cumulus and interpret it as giving rise to the mesoderm, a point to be discussed later. Neither, however, traces the relationship of the cumulus to the embryo. According to the last quoted paper the blastoderm is to be regarded as ecto-mesoderm, the yolk as at least largely, if not wholly, entoderm.

Packard ('72) has apparently seen some of the phases of segmentation, but it is difficult to arrange his account in its proper order, as it is evident that some of his eggs were addled. In others he figures nuclei which had no actual existence. From segmentation until the appearance of the limbs Packard has seen nothing except the formation of the Blastodermhaut, which he in various papers has compared to the Hexapod amnion — a view which I ('84) showed to be untenable. H. L. Osborn's account of the formation of the limbs, etc., I have referred to above

(p. 50). Patten has incidentally described some of the early stages of Limulus ('90). Packard, Dohrn, Lockwood, *et al.* have described the later stages, and the foregoing brief *résumé* calls for no comparisons with their results. (See Postscript.)

B. With Other Arthropods. — Three types of segmentation of the egg may be recognized in the Arthropods.

In the first, examples of which are furnished by the lower Crustacea, Lucifer, (?) Palæmon (Bobretzky), Phronima, Chelifer, *Gammarus locusta* (Van Beneden and Bessels), Pycnogonids (Morgan), etc., the egg undergoes a regular or irregular total segmentation (holoblastic).

In the second the egg consists of a central nucleus and protoplasm with peripheral yolk. The central protoplasm segments, but until several or many blastomeres result, the yolk remains undivided. This is the type usually called centrolecithal, or endolecithal (Claus) and superficial. I have already pointed out with some detail ('86, pp. 112–138) that these terms are misleading, and would substitute *ectolecithal* therefor. 'Superficial segmentation' as usually described is characteristic only of late stages of ectolecithal or of meroblastic eggs. In these ectolecithal eggs two secondary modifications are noticeable. In the one the yolk is extracellular; it lies between the cells formed by the dividing protoplasm and nuclei, as in Phryganids (Patten, '85), Crangon (Kingsley, '86), and Julus (Heathcote, '86). In the other the yolk itself becomes divided, forming balls (true yolk cells), in the centre of each of which the nucleus and protoplasm occur (examples, most Hexapods).[1] Of these the second is structurally, if not phylogenetically, nearest to the meroblastic type.

In the third or meroblastic type the segmentation is, strictly speaking, superficial, and is at first confined to one side of the egg. Instances are less common among the Arthropods than of the other two, although several have been described; *e.g.* Scorpio (Metschnikoff, '71; Laurie, '90), Mysis (Van Beneden), Oniscus[2] (Bobretzky).

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[1] Mereschowski ('82) has described what he regards as a fourth type, occurring in *Callianassa mediterranea.* It is plainly closely related to the second modification just mentioned.

[2] According to Reinhard's brief note ('87) it would appear as if in Porcellio the segmentation was of the ectolecithal type, and that the meroblastic conditions

Owing to my inability to find the segmentation nucleus, I am unable to say with certainty to which of the types the egg of Limulus should be referred, but all the facts point towards the second modification of the ectolecithal type. However, segmentation is at best an uncertain guide to affinities.

The matter of differentiation of the germ layers is more important. Until recently delamination was believed to be confined to the Cœlenterates and a few other forms.[1] It would appear, however, that delamination is of frequent occurrence in the Arachnid phylum. Morgan finds in the Pycnogonids ('90) a true multipolar delamination, and he uses this as one reason for assigning these forms to a position near the Arachnids. He refers to Chelifer as described by Metschnikoff and to Balfour's account of Agelena, and to these additional references may be given. Locy ('86, pp. 74–75) clearly confirms Balfour so far as Agelena is concerned; Henking ('86) describes a delaminate type of blastoderm formation in the Phalangids, while Faussek ('91), studying the same forms, is in full accord and expressly uses the term delamination in this connection. Schimkewitch ('84 and '87) also clearly describes delamination in Epeira, Pholcus, Agelena, and Lycosa.

On the other hand, the following forms have the yolk at one time free from nuclei, and hence, if delamination occur in connection with the primitive keel, it is not of that type which obtains in the cases mentioned above: Theridion (Morin, '87) at the 128-cell stage; a Japanese species of Agelena (Kishenouye, '90), Scorpion (Kowalewsky and Schulgin, '86; Laurie, '90).

So far as I know, nothing approaching delamination occurs in the Crustacea, while that in the Tracheates, already referred to, is of a character far different from that in the Arachnids. Hence Limulus, in the method of differentiation of entoderm from ecto-mesoderm, finds its closest analogues within the Arachnid phylum.

resulted from a migration of the blastomeres to one pole of the egg. Dr. McMurrich informs me that, according to his observations on both Porcellio and Armidillidium, the segmentation is as I have interpreted it in this note, — a fact which would tend to show that Bobretzky described a stage too late to decide the question.

[1] Balfour ('81), p. 278, compares the origin of the germ layers in most 'Tracheates' to a type which approaches delamination, but he expressly states that there are strong grounds for regarding it as "a secondary modification of an invaginate type."

There can be no question that delamination in these forms is not a direct derivative from delamination in the Cœlenterates. It has rather arisen in the Arachnids and probably from a true gastrulate type. The considerations which lead to this conclusion are these:—

It is at least probable that the Arthropods have had an annelidan ancestry, and in these latter forms delamination does not occur. Hence we must either regard it as having been lost in the segmented worms while it is retained in the Arachnids, or we must consider it as of cænogenetic character in the latter group. I believe that delamination, as it occurs in Limulus and the Pycnogonids, may be traced back to an ancestral invaginate condition; in fact, all stages between a regular embolic gastrula like that of Lucifer and the extreme delamination of the Pycnogonids can be found in the Arthropod phylum, although not in the Arachnids themselves.

The series between Lucifer (Brooks, '82) with an archenteric cavity of large size is easily traced through conditions like those of Astacus and Palæmon, to that presented by Crangon, where the invaginated entoderm is solid, but in which the blastopore is still readily recognized. Crangon, on the other hand, presents many similarities to Theridion (Morin, '87) and the Japanese species of Agelena studied by Kishenouye. In the forms just mentioned there is apparently[1] a time when every nucleus has reached the surface and has participated in the formation of the blastoderm, leaving the large central yolk in an anneliate condition. Later, the blastoderm thus formed becomes thickened by cell proliferation, and from the ridge thus formed cells pass "into the yolk and become scattered without definite arrangement through the entire yolk. These are the entoderm cells" (Kishenouye, p. 62; cf. Kingsley, '86, p. 110).

Now in forms like Astacus, Palæmon, and Crangon the mesoderm arises from the lips of the blastopore and from what may be regarded as its forward continuation in the median line, and from this fact we are justified in regarding the thickening which in the Japanese Agelena and in Scorpio (Laurie) gives rise to mesoderm and entoderm as an obsolescent blastopore homologous with the actual open blastopore in the other forms mentioned.

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[1] Kishenouye could not "detect any nucleus at all in the yolk, thus confirming the views of Morin in opposition to Balfour's" ('90, p. 60).

The transition from the Japanese Agelena and Scorpio to a true delamination is greater than that already traced; and as yet, so far as the literature at hand enables me to decide, it cannot be traced without going outside the limited group of Arachnids. Still the successive stages are readily imagined.

In the ectolecithal egg the blastoderm arises by migration of the primitively central cells to the periphery, and in many forms every nucleus goes through this migration, leaving the yolk at one period entirely free from cells. In others only a portion of the cells reach the surface, the others remaining behind in the yolk. Concerning the fate of these latter, opinions differ. In some forms they are described as playing no part in the building up of the embryo, but rather acting as 'vitellophags,' the sole function of which is to gradually metabolize the deutoplasm, after which they disappear. On the other hand, instances are not wanting in which these yolk cells are to be regarded as true entoderm cells, from which later the epithelium of the mid-gut is to be built up. This is the case with Limulus, as I shall detail later, and apparently also in many Araneina and Hexapods.

With such conditions as are afforded by Crangon, Theridion, etc., it can readily be seen that any acceleration of development which would prevent certain of the central blastomeres from migrating to the surface, only to be immediately returned as entoderm, would be a distinct gain; and this, in my opinion, is the way the peculiar conditions in many Hexapods have been brought about. At least, this view has the merit of rendering intelligible many features of Arthropod ontogeny which otherwise are not readily understood.

A farther step in the same direction is afforded by Limulus, where a farther economy is seen in the cutting off of the peripheral from the deeper ends of the cells, thus at once differentiating an outer ecto-mesodermal layer from an inner entoderm rich in food yolk. The final stage, as we know it, is seen in Tanystylum and Phoxichilidium as described by Morgan ('90). Here the egg is much reduced in size, the blastomeres are fewer, and each cell is at once (apparently) differentiated into entodermal and ecto-mesodermal portions, the result being a condition which closely simulates the multipolar delamination found in Geryonia, made classic by the researches of Fol and

Metschnikoff, but of course without actual phyletic connection with it.

Our knowledge of mesoderm development in the Arthropods is far from complete, and at present it is not possible to point out the peculiarities which characterize the different groups. My account of mesoderm formation, as it occurs in Limulus, agrees well in its major features with the account of Patten ('90), except that he describes at the posterior end of the embryo a "slit-like" primitive streak, and he further regards the proliferated cells as both mesoderm and entoderm (p. 373). The lateral connection of mesoderm and ectoderm he compares with the Keimwall of the Vertebrates — a point upon which I would rather admit analogy than actual homology.

The accounts of mesoderm formation in Scorpio differ. Laurie ('90) describes the inpushing of a mes-entoderm from all parts of the upper (outer) surface of which the mesoderm is afterward proliferated. Patten ('90), on the other hand, describes a median posterior thickening from which cells grow forward and laterally, the median portion forming the sexual organs and botryoidal cord; the lateral, the mesoderm and entoderm.

In the Decapodous and Isopodous Crustacea the mesoderm would appear to grow forward as two bands from the anterior margin and sides of the blastopore. In some Cladocera and Copepods (Grobben, '79 and '81) somewhat similar conditions may be traced, except that the primitive mesoderm cells are *behind* the point of entodermal invagination. In Cyclops, on the other hand (Urbanowicz, '84), mesenchyme is described as budding from the blastoderm cells, and Ulianin ('81) describes the same in Orchestia.

In the Arachnids our knowledge of mesoderm formation is extremely scanty. All agree, so far as the Araneida are concerned, that the primitive cumulus and posterior cloud are concerned in the process, and some show that at first the mesoderm forms a continuous band across the embryo. A comparison of figures (*e.g.* Locy, 86, Fig. 49) of Arachnid embryos with my own of Limulus will, I think, show similarities which cannot be paralleled by similar resemblances between Limulus and the Crustacea.

In the differentiation of the germ the resemblances of Limulus to the Arachnids are striking. So far as I know primitive cumulus and posterior cloud occur only in these forms; and the succeeding stages are almost equally close. As I correllate them, my figures of Limulus are to be compared with those of the true Arachnids as follows: —

LIMULUS.	ARACHNIDA.
Fig. 21	Agelena, Locy, Fig. 1; Kishenouye, Fig. 5.
Fig. 23	Agelena, Kishenouye, Fig. 5; Balfour, Fig. 1.
Fig. 24	Agelena, Locy, Fig. 3; Scorpio, Metschnikoff, Pl. XVII, Fig. 2.
Fig. 25	Scorpio, Metschnikoff, Pl. XVII, Fig. 3 (one less somite); Laurie, Fig. 17 (one more segment and lacks primitive groove).
Fig. 26	Agelena, Schimkewitsch, Pl. XVIII, Fig. 1; Balfour, Fig. 3. Locy, Fig. 6; Scorpio, Metschnikoff, Pl. XVII, Fig. 6.

A slight comparison of these figures will show that previous to the appearance of the limbs there are a remarkable series of parallels. Limulus agrees with the Arachnids and differs from the Crustacea in the external appearance and growth of the germinal disc; in the considerable development of metamerism before the appearance of the appendages,[1] and in the simultaneous appearance of the anterior five or six pairs of appendages. When one of the six is lacking at first, it is apparently the anterior pair which forms later. This has been shown by Balfour, Schimkewitsch, and Kishenouye in Agelena; by Metschnikoff and Laurie in Scorpio, and by Dohrn and myself in the present paper. On the other hand, Claparède (**'68**) describes the sixth pair as lacking in Myobia, and Van Beneden (**'51**) gives the same account of Atax. Limulus agrees with the Arachnids and differs from the Crustacea in the total absence of a nauplius stage.

AUGUST, 1891.

POSTSCRIPT.

Since the foregoing pages were in the printer's hands K. Kishenouye has published his complete paper on the development

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[1] In Chelifer (Metschnikoff, **'70**), the cheliceræ apparently are formed before the somites are outlined.

of the Japanese King Crab (*L. longispina*), which presents some points of difference from the *L. polyphemus* of the Atlantic coast. Some of these variations may be noticed here.

In the external development Kishenouye did not distinguish between primitive cumulus and posterior cloud. In the process of metamerism the first line of demarcation occurs between somites I and II, while the appearance which I have called the primitive streak does not occur until two somites are differentiated from the anterior and posterior areas. In the later stages he finds organs homologous with the flabellum of appendage VI, occurring as transitory rudiments on somites 2–5. These are clearly not homologous with the peculiar (sense ?) organs mentioned on p. 49, since the latter occur outside the ventral disc, while the flabella of Kishenouye are all within that area.

In the internal development the discrepancies are more important. Thus Kishenouye describes the ectoderm as separating from lower-layer cells, and says that the mesoderm has three origins: (1) from the lower-layer cells, (2) from the edges of the primitive streak, which is confined to the posterior portion of the ventral disc, and (3) from cells in the dorsal region which migrate from the yolk. The primitive streak mesoderm is confined to the abdominal region, while that derived from the lower-layer cells gives rise to the tissues of the cephalothorax.

A still farther point of difference is with regard to the metastoma. This Kishenouye regards as a true appendage serially homologous with the other appendage of the body. In this I cannot agree with him. My observations show no metastomal somite and no corresponding neuromere.[1] On the other hand, it seems probable that there is here an error in interpretation, for a study of his figures inclines me to believe that his metastoma is in reality the operculum, and that the following appendages are to be correspondingly changed. The other points of difference will be discussed in the second part of this paper.

TUFTS COLLEGE, MASS., August, 1892.

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[1] See Kingsley, '**85**, p. 532, Pl. XXXVIII, Fig. 22.

LITERATURE.

'78 Agassiz, A. Note on the Habits of the Young Limulus. *Am. Jour. Sci.*, III, xv, pp. 75–76. 1878.

'80 Balfour, F. M. Notes on the Development of the Araneina. *Quarterly Jour. Micros. Sci.*, xx, pp. 167–189; Pl. xix–xxi. 1880.

'81 Balfour, F. M. A Treatise on Comparative Embryology. Vol. I. London, 1881.

'83 Benham, W. B. S. On the Testis of Limulus. *Trans. Linn. Socy.* II, *Zool.*, ii, pp. 363–366; Pl. 38. 1883.

'73 Bobretzky, N. In *Mem. Kiew Nat. Soc.*, iii, pp. 129–263; Pls. i–vi. 1873. (I have used only Hoyer's Abstract in Hoffmann & Schwalbe's Jahresberichte, ii, p. 312. 1875.)

'74 Bobretzky, N. Zur Embryologie des Oniscus murarius. *Zeit. wiss. Zool.*, xxiv, pp. 179–203; Pls. 21–22. 1874.

'82 Brooks, W. K. Lucifer: a Study in Morphology. *Phil. Trans.*, cclxxiii, p. 57. 1882.

'85 Brooks, W. K., and Bruce, A. T. Abstract of Researches on the Embryology of Limulus polyphemus. *Johns Hopkins Univ. Circ.*, v, pp. 2–4. 1885.

'62 Claparède, E. Recherches sur l'Évolution des Araignées. *Natuurk. Verhandl. Utrechts Genootsch.*, D. i, S. i, pp. 92; Pls. 8. 1862.

'68 Claparède, E. Studien an Acariden. *Zeit. wiss. Zool.*, xviii, pp. 445–546; Pls. xxx–xl. 1868.

'71 Dohrn, A. Zur Embryologie und Morphologie des Limulus polyphemus. *Jena. Zeitsch.*, vi. 1871.

'90 Eyclesheimer, A. C. Celloidin Imbedding in Plant Histology. *Botan. Gazette*, xv, p. 292. 1890.

'91 Faussek, V. Zur Embryologie von Phalangium. *Zool. Anz.*, xiv, p. 3. 1891.

'82 Faxon, W. Selections from Embryological Monographs. I. Crustacea. *Memoirs Mus. Comp. Zoöl.*, ix. 1882.

'58 Gegenbaur, C. Anatomische Untersuchungen eines Limulus. *Abh. Naturf. Gesellsch. Halle*, iv. 1858.

'79 Grobben, C. Die Entwickelungsgeschichte des Moina. *Arb. zool. Inst. Wien*, ii. 1879.

'81 Grobben, C. Die Entwickelungsgeschichte von Cetochilus. *Arb. zool. Inst. Wien*, iii. 1881.

'86 Heathcote, F. G. The Early Development of Julus terrestris. *Quart. Jour. M. S.*, xxvi. 1886.

'86 Henking, H. Untersuchungen über die Entwicklung der Phalangiden. *Zeit. wiss. Zool.*, xlv. 1886.

'89 Heidlr, Karl. Die Embryonalentwicklung von Hydrophilus piceus. Jena, 1889.

'85 Howell, W. H. Observations upon the Chemical Composition and Coagulation of the Blood of Limulus polyphemus, Callinectes hastatus, and Cucumaria sp. *Johns Hopkins Circ.*, v, p. 4. 1885.

'84 KINGSLEY, J. S. The Development of Limulus. *Science Record*, ii, p. 249. 1884.

'85 KINGSLEY, J. S. Notes on the Embryology of Limulus. *Quar. Jour. Mic. Sci.*, xxv. 1885.

'86 KINGSLEY, J. S. The Development of Crangon vulgaris. *Bulletin Essex Inst.*, xviii. 1886.

'90 KINGSLEY, J. S. The Ontogeny of Limulus. *Amer. Nat.*, xxiv, p. 678. 1890.—*Zool. Anz.*, xiii, p. 536. 1890.

'90 KISHINOUYE, K. On the Development of the Araneina. *Jour. Coll. Sci. Imp. Univ. Japan*, iv. 1890.

'86 KOWALEVSKY, A. and SCHULGIN, M. Zur Entwicklungsgeschichte des Scorpions. *Biol. Centralbl.* vi. 1886.

'78 LANKESTER, E. R. Motility of Spermatozoids of Limulus. *Quar. Jour. Mic. Sci.*, xviii. 1878.

'90 LAURIE, M. The Embryology of a Scorpion (Euscorpius italicus). *Qr. J. M. S.*, xxxi. 1890.

'70 LOCKWOOD, S. The Horse-foot Crab. *Am. Nat.*, iv. 1870.

'86 LOCY, W. A. Observations on the Development of Agelena nævia. *Bull. M. C. Z.*, xii. 1886.

'75 LUDWIG, H. Ueber Eibildung im Thierreiche. *Arb. z. z. Inst. Würzburg*, i. 1875.

'77 MAYER, P. Zur Entwicklungsgeschichte der Decapoden. *Jena. Zeit.*, xi. 1877.

'82 MERESCHKOWSKI, C. V. Eine neue Art von Blastodermbildung bei den Decapoden. *Zool. Anz.*, v. 1882.

'66 METSCHNIKOFF, E, Embryologische Studien an Insecten. *Zeit. w. Zool.*, xvi. 1866.

'68 METSCHNIKOFF, E. Istoria Razvitia Nebalia. *Zap. Imp. Acad. St. Peterb.*, xiii. 1868.

'70 METSCHNIKOFF, E. Entwicklungsgeschichte des Chelifer. *Z. w. Z.*, xxi. 1870.

'71 METSCHNIKOFF, E. Embryologie des Scorpions. *Z. w. Z.*, xxi. 1871.

'38 MILNE-EDWARDS, H. Recherches Relatives au Dévelopement des Limulus. *Ext. Proc. Verb. Soc. Philomath. Paris.* 1838. (Teste van der Hoeven.)

'39 MILNE-EDWARDS, H. In Regne Animal de Cuvier, edition illustré. Crustacés, Pl. 76, Figs. 2 l 2 i. "1839."

'40 MILNE-EDWARDS, H. Histoire Naturelle des Crustacés, tom iii, pp. 538–551. Paris, 1840.

'91 MORGAN, T. H. A Contribution to the Embryology and Phylogeny of the Pycnogonids. *Studies Biol. Lab. J. H. Univ.*, v. 1891.

'87 MORIN, I. Zur Entwicklungsgeschichte der Spinnen. *Biol. Cbl.*, vi. 1887.

'85 OSBORN, H. L. The Metamorphosis of Limulus polyphemus. *Johns Hopkins Circ.*, v. 1885.

'72 OWEN, R. On the Anatomy of the American King Crab. *Trans. Linn. Soc., Zool.* xxviii. 1872.

'70ª PACKARD, A. S. The Embryology of Limulus polyphemus. *Am. Nat.*, iv, p. 498. 1870.

'70ᵇ PACKARD, A. S. Morphology and Ancestry of the King Crab. *Am. Nat.*, iv, p. 754. 1870.

'70ᶜ PACKARD, A. S. An Account of the Development of Limulus polyphemus. *Proc. Bost. Soc. Nat. Hist.*, xiv. 1870.

'71 PACKARD, A. S. On the Embryology of Limulus polyphemus. *Proc. Am. Assoc. Adv. Sci.*, xix. 1871. — *Quar. Jour. Mic. Sci.*, xi. 1871.

'72 PACKARD, A. S. The Development of Limulus polyphemus. *Mem. Bost. Soc. N. H.*, ii. 1872.

'73 PACKARD, A. S. Farther Observations on the Embryology of Limulus, with Notes on its Affinities. *Am. Nat.*, vii, p. 675. 1873.

'75 PACKARD, A. S. On the Development of the Nervous System of Limulus. *Am. Nat.*, ix, p. 422. 1875.

'80 PACKARD, A. S. The Anatomy, Histology, and Embryology of Limulus polyphemus. *Anniv. Mem. Bost. Soc. N. H.*, 1880.

'85 On the Embryology of Limulus polyphemus. III. *Proc. Am. Phil. Soc.*, xxii. 1885. — *Am. Nat.*, xix, p. 722. 1885.

'60–'61 PAGENSTECHER, H. A. Beiträge zur Anatomie der Milben. Leipzig, 1860–61.

'84 PATTEN, W. The Development of Phryganids, with a preliminary note on the development of Blatta germanica. *Q. J. M. S.*, xxiv, 1884.

'89 PATTEN, W. The Segmental Sense Organs of Arthropods. *Jour. Morph.*, ii. 1889.

'90 PATTEN, W. On the Origin of Vertebrates from Arachnids. *Q. J. M. S.*, xxxi. 1890.

'86 REICHENBACH, H. Studien zur Entwicklungsgeschichte des Flusskrebses. *Abh. Senckenb. Nat. Gesell.*, xiv. 1886.

'87 REINHARD, W. Zur Ontogenie des Porcellio scaber. *Zool. Anz.*, x, p. 9. 1887.

'87 SCHIMKEWITSCH, W. Étude sur le Développement des Araignées. *Arch. de Biol.*, vi. 1887.

'86 STUHLMANN, F. Die Reifung des Arthropodeneies nach Beobachtungen an Insekten, Spinnen, Myriapoden, und Peripatu. *Ber. Naturf. Gesell. z. Freiburg i. B.*, i. 1886.

'81 ULIANIN, B. Zur Entwicklungsgeschichte der Amphipoden. *Z. w. Z.*, xxxv. 1881.

'84 URBANOWICZ, F. Zur Entwicklungsgeschichte der Cyclopiden. *Zool. Anz.*, vii. 1884.

'51 VAN BENEDEN, P. Développement de l'Atax ypsilophora. *Mem. Acad. Roy. Belg.*, xxiv. 1851.

'69 VAN BENEDEN, E. Recherches sur l'Embryologie des Crustacés. II. Développement des Mysis. *Bull. Acad. Belg.*, II, xxix. 1869.

'38 VAN DER HOEVEN, J. Recherches sur l'Histoire Naturelle et l'Anatomie des Limulus. Leyde, 1838.

'89 VOELTZKOW, A. Entwicklung im Ei von Muscav omitoria. *Arb. z. z. Inst. Würzburg*, ix. 1889.

'89 WATASE, S. On the Structure and Development of the Eyes of Limulus. *Johns Hopkins Circ.*, viii, p. 34. 1889.

'90^a WATASE, S. On the Morphology of the Compound Eyes of Arthropods. *Studies Biol. Lab. Johns Hopkins*, iv. 1890.

'90^b WATASE, S. On the Migration of the Retinal Area and its Relation to the Morphology of the simple (Ocelli) and compound Eyes of Arthropods. *Johns Hopkins Circ.*, x. 1890.

'63 WEISMANN, A. Die Entwicklung der Dipteren im Ei. *Z. w. Z.*, xiii. 1863.

'84 WITLACZIL, E. Entwicklungsgeschichte der Aphiden. *Z. w. Z.*, xl. 1884.

'78 WHITMAN, C. O. The Embryology of Clepsine. *Q. J. M. S.*, xviii. 1878.

EXPLANATION OF THE FIGURES.

Reference Letters.

ar.	Artery.
bl.	Blastema.
bs.	Blood sinus.
c.	Cerebrum.
ec.	Ectoderm.
f.	Flabellum.
g.	Gill-bearing appendage.
I.	Appendage I.
l.	Liver tubule.
me.	Mesoderm.
mo.	Mouth.
n.	Neuromeres.
o.	Ovum.
op.	Operculum.
ov. e.	Ovarian epithelium.
pc.	Primitive cumulus.
pg.	Polar globule ?
pgr.	Primitive groove.
po.	Primordial ovum.
pr.	Protoplasmic processes.
ss.	Segmental structures (glands or sense organs?).
x.	Cell in process of delamination.
y.	Yolk.
z.	Junction of ectoderm and mesoderm at the margin of the germinal disc.

DESCRIPTION OF PLATE V.

FIGS. 1, 2. Sections (longitudinal and transverse) through a portion of the liver and ovary of a Limulus four inches in length, showing the formation of the primordial ova and the intrusion of older ova between the ovarian epithelium and tunica propria.

FIG. 3. Section of an egg one hour after impregnation, showing a possible polar globule.

FIGS. 4, 5, 6. Surface views of eggs four hours after impregnation, showing the peculiar segmentation of the surface previous to true segmentation. Fig. 6 is a polar view of the egg shown in Fig. 4.

FIG. 7. Section through an egg of four hours, showing the peripheral columns, distinctly cut off in most regions from the central yolk.

FIG. 8. A portion of the egg in Fig. 7, more enlarged.

FIG. 9. Projection of an egg with eight nuclei.

FIGS. 10–14. Surface views of successive stages of surface division.

FIG. 15. Section of an egg in early segmentation showing cleavage planes at one pole of the egg.

FIG. 16. Projection of an egg with twenty-six nuclei.

FIG. 17. Enlarged view of a superficial cell in early segmentation showing the peripheral protoplasm (blastema) and protoplasmic processes extending down between the blastomeres.

FIG. 18. Egg at the close of early segmentation, before the differentiation of ecto-mesoderm.

FIG. 19. Section of an egg during the process of delamination.

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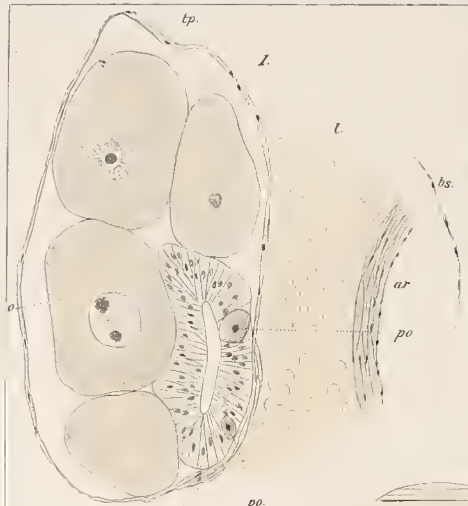

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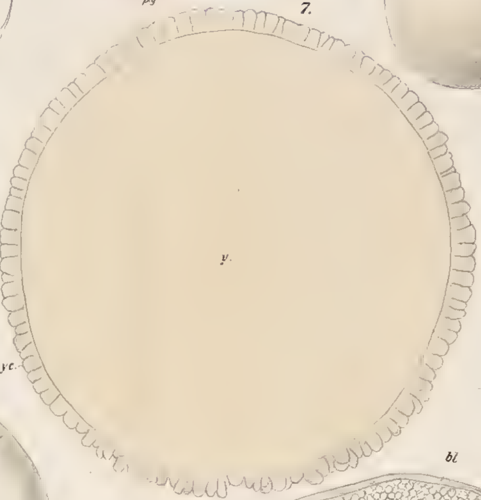

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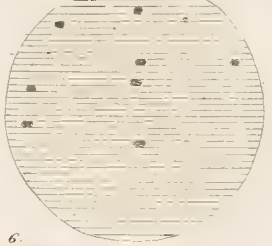

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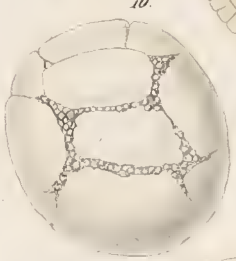

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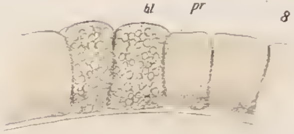

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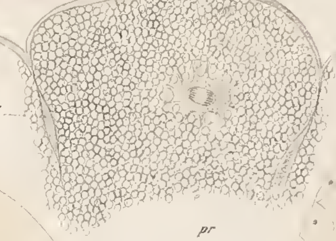

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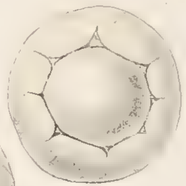

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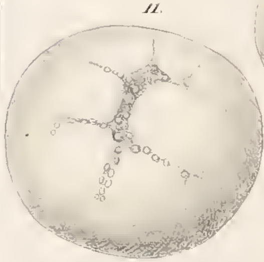

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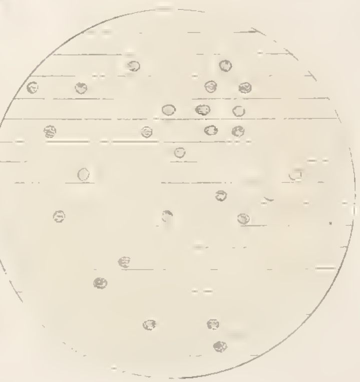

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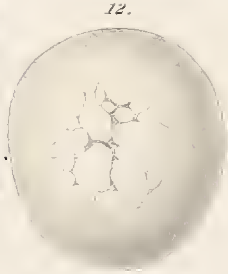

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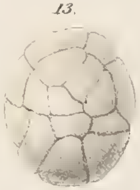

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DESCRIPTION OF PLATE VI.

FIG. 20. A part of Fig. 19 more enlarged, showing the process of delamination.

FIGS. 21–26. Successive stages of the germinal area previous to the formation of the appendages. See the text.

FIG. 27. Budding of the legs.

FIG. 28. An unusual form of embryo, appendage I. not yet formed.

FIG. 29. The germ viewed as a transparent object. Appendages I.-VI. present. The nervous system is covered by circularly arranged nuclei, the centres of rapid cell proliferation. Outside the germinal area are seen (*ss*) segmentally arranged structures of possibly glandular or sensory functions.

FIGS. 30, 31. Two surface views illustrating the transfer of the mouth backwards, accompanied by the formation of the stomodæum.

FIG. 32. Appearance of the embryo before the distinction of cephalothorax and abdomen is prominent.

FIG. 33. Side view of a late embryo, the abdomen differentiated.

FIGS. 34, 35. Dorsal and ventral views of the last larval stage before the appearance of the telson. R. Takano, del.

FIG. 36. Longitudinal section of a stage about like Fig. 21, showing the primitive cumulus and its central spot.

FIG. 37. Early stage of mesoderm formation.

FIG. 38. Late stage of same, showing primitive groove and lateral connection of mesoderm and ectoderm.

FIG. 39. More enlarged view of primitive groove.

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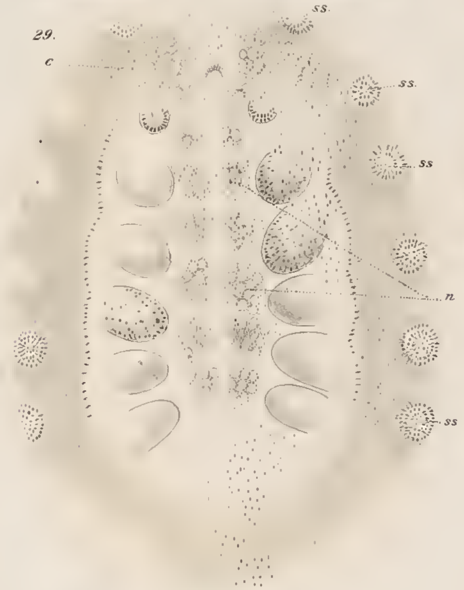

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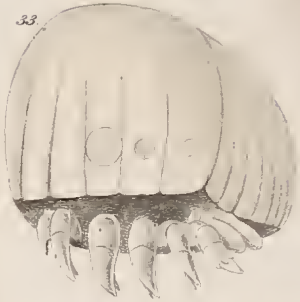

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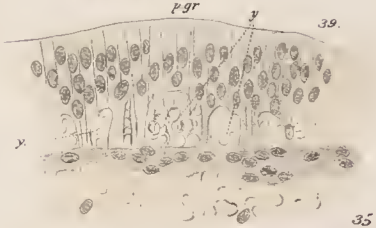

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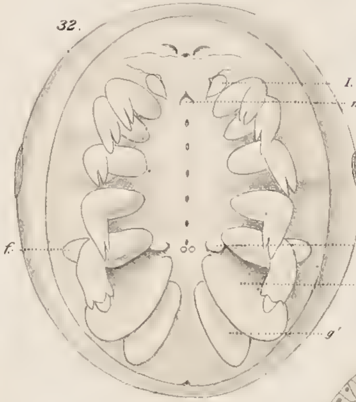

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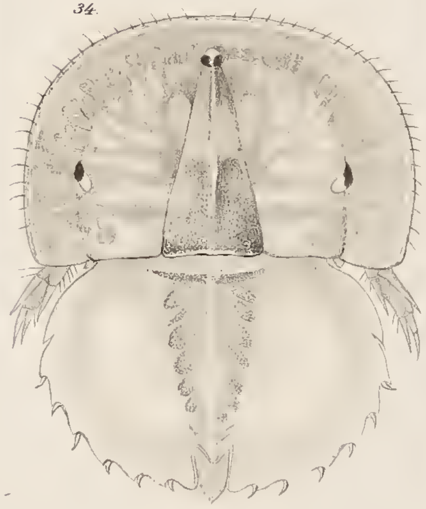

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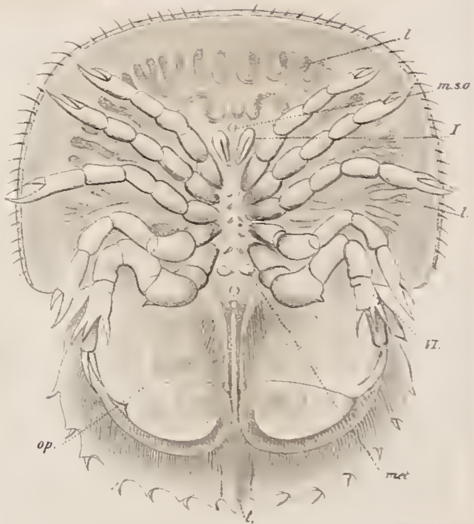

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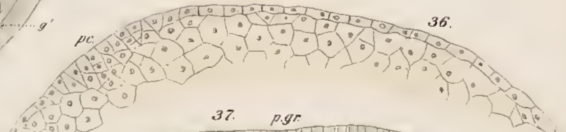

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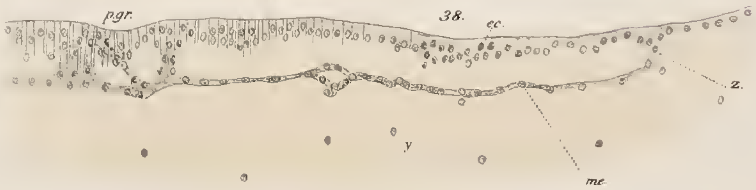

THE
EMBRYOLOGY OF LIMULUS

(PART II.)

BY

J. S. KINGSLEY

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THE EMBRYOLOGY OF LIMULUS.—PART II.

J. S. KINGSLEY.

CONTENTS.

INTRODUCTION.

THE preceding portion of this paper (this Journal, Vol. VII, p. 33) dealt with the habits, ovigenesis, the origin of the germ layers, and the development of the external form of *Limulus polyphemus*, together with some more general questions connected with the matters under discussion. In the present part the development of some of the organs is followed out, and in conclusion I have considered the bearings of the facts upon the systematic affinities of the Xiphosura and upon the classification of the Arthropods.

I would, before beginning, call attention to the fact that, disregarding the neuromeres, I have numbered the somites and the appendages, beginning with the first appendage. This may account for some apparent discrepancies later, and it also brings my article into harmony with those of other writers. At present we are in a transition condition, and no other course seems advisable. The matter of the neuromeres will be discussed in its proper place.

THE MESODERM AND ITS DERIVATIVES.

As previously described the mesoderm arises by cell proliferation from a median longitudinal line on what will eventually form the ventral surface of the embryo. For this line of mesodermal formation the name primitive streak, borrowed from vertebrate embryology, seems especially appropriate. From this streak (*cf.* Figs. 42, 43) the middle layer grows outward on either side between ectoderm and entoderm (yolk), the process of differentiation beginning in front and gradually extending backwards, where the process continues for sometime after it has ceased anteriorly and after the cœlomic pouches have formed in the first somites of the body. This fact gives confirmation of the correctness of interpretation of anterior and posterior in the earliest embryos (*vide* '92, p. 47), a point upon which absolute certainty was impossible, since the features there described only become visible upon the employment of methods which coagulate the albumen and consequently kill the egg.

At first the mesoderm forms a continuous sheet across the egg, but one or two cells in thickness, and united to the ectoderm in the line of the primitive streak (Figs. 42, 43); and frequently there is also apparently a marginal connection between the two layers, the line of junction being indicated by a groove[1] (Figs. 42, 44). This line of union is apparently secondary, and I interpret it as a precocious differentiation of dorsal and ventral surfaces. I have seen no evidence of an augmentation of mesoderm by cell proliferation in this region.

With the appearance of metamerism the connection between mesoderm and ectoderm is lost, except in the stomodæal region (Fig. 43) and in the abdominal portion of the embryo where new cells continue to be added to the mesoderm for some little time. At first, after the separation of the two layers (Fig. 44), the mesoderm extends as an unbroken sheet, one or two cells in thickness, across the germinal area, the ectoderm outside this area losing its columnar character and becoming more flattened. As yet there is no appearance of cœlomic cavities.

So far as my observations show metamerism obtains its first expression in the ectoderm. Thus Fig. 40 represents a longitudinal section to one side of the median line (where the cœlom first appears) of an embryo, which in surface view showed differentiated cephalic and caudal areas, separated by a single somite. The boundaries of these regions are recognizable in the ectoderm of the section marked by arrows, while the mesoderm shows no corresponding metamerism.

Cœlom. — Owing to difficulties of manipulation I have not been able to correlate surface views and sections, and so cannot say exactly how many somites are outlined when the cœlom first appears. It is, however, preceded by a splitting of the mesodermal sheet into right and left halves,[2] a condition which is maintained (*cf.* Fig. 48) until after the appearance of the limbs. By this splitting are produced two mesodermal bands, the inner margins of which are undulating. As shown

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[1] This has already been noticed and figured by Patten ('90, p. 375) who suggests a comparison with similar appearances in vertebrates.

[2] Except in oral and caudal regions.

by Fig. 45, which is a sagittal section through an embryo with seven differentiated somites, the mesoderm extends farther toward the middle line in a segmental than in an intersegmental area. Had the section passed further from the middle line the mesoderm would have formed a continuous sheet from head to caudal region.

The cœlom arises (Fig. 43) by a splitting of the lateral halves of the mesoderm, a pair of cavities being thus formed for each somite. These cœlomic cavities long remain distinct from each other, and the dissepimental walls persist until a later stage of development. The later history of the cœlom is, however, very difficult to follow on account of the subsequent appearance of numerous lacunæ in the mesoderm, which, so far as my observations go, have no connection with the primitive cavities which I would homologize with the cœlom of other forms. The cœlomic pouches appear in the six thoracic segments before they do in those of the abdomen (Fig. 46). An especially interesting fact is that there is no preoral cœlomic pouch, but the cavities of the first postoral somite send prolongations (Fig. 47) into the region in front of the mouth.

The walls of the cœlom differ in thickness. The somatoplure is usually several cells thick, while the splanchnoplure is only one cell in thickness and rapidly takes the form of a thin layer of pavement epithelium closely applied to the underlying yolk. A partial exception to this general statement occurs in the abdominal region where (Fig. 49) the somatoplure at first may also be a single cell thick. With the appearance of the limbs, as I pointed out in my earlier paper ('85, p. 532), the cœlom extends into these members, but it is soon excluded by the rapid growth of mesoderm in their interior. Of the fates of the cœlomic pouches I cannot speak with absolute certainty. The following is what appears to me the probable history. In all of the thoracic segments a portion (if not all) of the cœlom is gradually carried, with the advancing mesoderm, from the ventral on to the dorsal surface of the embryo. That a portion is thus carried is certain; but the rapid formation of lacunar spaces in the somatoplure renders it impossible to say whether a portion is left in the ventral region of each segment. That a portion does so persist in the fifth segment will appear later.

Until after the splitting of the chorion only eight pairs of schizocœlia are produced, there being a pair for each[1] (Fig. 46) cephalothoracic and for the two anterior abdominal somites. At first these cavities are flat, and broader than long; the first pair, however, rapidly elongates and sends a diverticulum forward beneath the brain on either side of the œsophagus, into the preoral region. At first all of the cavities are distinct, and their walls epithelial in character, but soon it becomes difficult to follow their fate with certainty since a secondary splitting of the mesoderm soon produces a large number of anastomosing lacunar cavities (*e.g.* Figs. 53 *bs.*, 59 *lac.*, etc.) connected later with the vascular system and developing into the so-called "body-cavity" of the Arthropod, the existence of which much confuses the sections.

With the growth at first laterally, then dorsally and medially, of the two halves of the mesoderm, a portion (if not all) of the cœlom in somites II, III, IV, VI and VII, and a part of that in somite V, is carried towards the dorsal median line of the embryo, where, in the latest stages I have studied, the cavities, now run together, persist as a longitudinal tube (Figs. 63–67) beneath the pericardial sinus, on either side of the heart and its anterior arterial prolongation. Posteriorly this paired cavity does not at any time extend further back than somite VIII or IX. Whether in any of the somites all of the cœlom is thus carried to the dorsal surface I am unable to say, while I have not followed the fate of the cœlom of somite I. According to Kishinouye the anterior cœlomic pouches are pushed inward with the advancing stomodæum, and hence give rise to the splanchnoplure of the œsophagus and proventriculus. In somites I–IV, and also in somite VI, I am unable to recognize any ventral cavity as distinctively cœlom much later than the time when motion is seen in the appendages. In the posterior abdominal somites the cœlom persists

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[1] According to Kishinouye there is no cœlom in somites II, III, IV of the Japanese Limulus.

on the ventral side until a later date, and is then apparently obliterated by a flattening of the cavities and a growing together of their walls. In the fifth somite, however, I can speak with more confidence,—for here the cœlomic cavities divide into two moieties, a dorsal and a ventral, and the latter remains upon the ventral surface and gives rise, in a way soon to be described, to the nephridia.

Concerning the fate of the dorsal portion of the cœlom I am uncertain. It persists, as has been said, as a perfectly distinct cavity with epithelial walls on either side of the central circulatory organ in the latest stages which I have studied. From its position and from its posterior termination I am inclined to think that this portion of the cœlomic epithelium is finally converted into the reproductive organs. In young Limuli an inch and a half in length I have found no traces of the cavity except as it might be represented in the gonads. I regret also that I have not been successful in tracing the history of the reproductive ducts. There are, however, so many lacunæ developed in the genital somite that I have not been able to follow the fate of the lower portion of the cœlom in that somite.

From this point the subsequent history of the mesoderm is best followed under the headings of the different organs, but before taking them up it is well to consider the facts already described.

Comparisons. — The only previous papers[1] dealing with the mesoderm of Limulus are those by Patten ('90), Kishinouye ('91, '92) and myself ('85), and Patten's remarks are only incidental to the discussion of an entirely different question. According to him there is a short slit-like invagination at the posterior end of the embryo, and from the walls of this inpushing much of the entoderm and mesoderm is produced, essentially as described above for mesoderm alone. Again

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[1] Possibly an exception should be made made in favor of Dr. Packard's last paper, where ('85, p. 269) a few statements are made concerning this layer. He recognizes (Fig. 3) two cœlomic pouches in the region in front of the first pair of appendages; but his figures clearly show that he has not seen the true cœlom; the cavities described being either lacunar or artifacts. The cœlom does not exist in the plane of his section in the stage he has studied.

Patten describes an immigration of ectoderm cells from different portions of the germinal area ; and lastly, the middle layer receives further accessions from the marginal groove already referred to above. The cells of this marginal area are described as containing an extremely long, coiled, brilliantly refractile filament ; and some of these cells become elongated to form the dorsal muscles, the filament forming the longitudinal striation.

I have not seen, either in surface views or in sections, the slit-like invaginations described by Professor Patten ; I have seen no additions to the mesoderm from various points of the blastoderm, outside of the limits of the primitive streak ; I have not seen any cells, much less great masses of them, separate from the primitive streak and wander into and become scattered through the yolk ; and I have yet to see the peculiar origin of the dorsal muscle-cells which he describes. He figures (p. 374 Fig. 18 D, *pstr.*) a cylindrical rod of invaginative tissue, an appearance lacking in my sections, and refers to masses of entoderm cells at the inner end of the œsophagus which are quickly absorbed and which I am confident do not exist.

Kishinouye ('92) has the mesoderm in *Limulus longispina* arising from three sources :— from the cells forming the lower part of the blastoderm thickening ; from the primitive streak ; and from the yolk cells. The first portion forms the mesoderm of the cephalothorax ; the second the mesoderm of the abdomen ; the last probably the blood corpuscles. I must be permitted to express my scepticism upon this account of the origin and fate of the different portions of the middle layer. In the subsequent history however we are in close accord and only the points of difference need be noted. The order of the appearance of the mesoderm somites is the same and in them the cœlom appears as schizocœlia. According to Kishinouye no cœlomic cavities appear in somites II, III, or IV, and in the others they do not extend into the appendages. In both points the Atlantic Limulus differs ; cavities occurring in every postoral somite (Fig. 46) and at first extending into the limbs. In both species the cœlom (or at least a part of each cavity) migrates to the dorsal surface where it comes to lie at either side of the central circulatory organ. Kishinouye says it disappears before hatching. I do not find that it does so but find it persisting (*cf.* Fig. 87) after the assumption of the adult characters, for a portion of the length of the body. My belief that it gives rise to the gonads was referred to above.

Our knowledge of mesoderm formation in the Arachnida is deficient, but as far as it goes it agrees well with that of Limulus. Thus all accounts agree in the following : The mesoderm arises by a proliferation from a median ventral primitive streak, the proliferation continuing later in the posterior region than in front ; next the mesoderm (+ entoderm in Euscorpius) separates from the ectoderm and forms at first a broad sheet across the ventral surface of the embryo ; and, next, this sheet becomes divided into right and left bands connected behind ; and into distinct somites in either half of the body. Later in each half of each somite a cœlomic cavity is formed by splitting and these cavities extend temporarily into the corresponding cephalothoracic appendages. This will apply equally well to Limulus, but farther, differences in details are to be noted. Thus Balfour ('80, p. 174, Pl. XX, Fig. 13) describes cells from the yolk migrating into and adding to the mesoderm, while in Euscorpius (Laurie '90) the mes-entoderm is first differentiated from the ectoderm and then later it is divided into mesoderm and entoderm. From what we now know of Arachnid development I think it safe to regard the view of Balfour that the mesoderm was increased by migrations from the yolk as erroneous, certainly his figure ('80, Pl. XX, Fig. 13) does not require such interpretation, while the differences in scorpions is readily understood in connection with the peculiar features of the formation of the entoderm already discussed (Part I, p. 53 ff.)

Both Laurie (Scorpion) and Balfour (Agalæna) describe a prestomial cœlom but without stating whether it actually belongs to the prestomial area or migrates to that region as in Limulus. Kowalevsky and Schulgin, on the other hand ('86) describe in the scorpion a preoral somite with a distinct cavity. Laurie has also studied the genital duct which according to him develops from the cœlom of somite VII. Owing, however, to its late appearance he is not certain as to its nephridial nature.

Nephridia (so-called *Coxal Glands*). — As has been described above, a portion of the cœlom of the fifth somite remains upon the ventral side of that somite, while the other cœlomic cavities are migrating toward the dorsal surface (Fig. 52). For a considerable time this cavity shows no changes worthy of remark, and first in about Stage G, (Fig. 32) is any modification noticeable. The cavity now begins to elongate and to become bent upon itself like the letter U, the rounded portion being directed anteriorly. The U now grows in length and, the posterior end being fixed, soon extends into somite IV. With this change in shape a differentiation in the epithelial cells becomes noticeable, most of them becoming cubical or columnar, while those upon the inner side of the inner end of the U retain their pavement character.

These changes, just before Stage H, produce the following results (Figs. 56–59): The cœlom (of somite V) is now divided into two portions, (1) a true cœlomic portion (the "end sac" of authors, Fig. 58 *nst.*) bounded by pavement epithelium on its inner side, and passing directly into the nephrostomial portion with columnar cells ; and (2) the nephridial duct which passes forward (Fig. 57), as the proximal limb of the organ, to the loop (Fig. 56) and then backward, as the other limb (Figs. 57, 58, 59 *nd.*), to the posterior limits of somite V. As yet it has no connection with the exterior, but in the last section (Fig. 59) can be seen an inpushing of ectoderm (*no.*), which is to form its external aperture. In the various sections in the neighborhood of the coxal gland at this stage may be seen numerous lacunæ (*lac.*) in the mesoderm, which is rapidly assuming the trabecular condition characteristic of the later stages. I have never been able to certainly trace any connection between these lacunæ and the cœlomic cavity and am strongly of the opinion that none exists.

In Stage H (Fig. 54 *a–i ;* Fig. 55, reconstruction) the same conditions are seen, except that the duct now opens to the exterior. We have here the end sac (*c* 5) which passes directly into the nephrostome without any sharp line of demarcation (except that of change in the character of the cells) and this in turn into the two limbs of the duct. In this series of sections a peculiarity is seen, which in most cases does not make an appearance until a much later stage, *viz.* the formation of trabeculæ of mesodermal tissue which invade the cavity, and passing from wall to wall of the proximal portion of the organ tend to subdivide it and give it an anastomosing character.

The changes which have occurred up to the Stage I are represented in the horizontal sections (Figs. 61 *a–e*) and the sagittal section (Fig. 62). Figs. 61 *f* and *g* are reconstructions by projection of the whole series of which a few sections are represented in 61 *a–e*. The tube has now become more elongate, extending in front nearly to the anterior limits of somite IV, while the two limbs are relatively much more closely applied to each other than before. With this growth the regions are much more differentiated. The end sac (Fig. 61 *d*) is separated from the, now numerous, lacunæ of the mesoderm by a layer of pavement epithelium which in my series nowhere shows a break.[1] This cœlomic sac passes directly, as before, into the nephrostome (*nst.*) and this again into the duct, which shows no change, except increase in length, until in the distal limb, when about at the level of the end sac it becomes enlarged into an excretory vesicle or bladder, *ev.* (Figs. 60 and 61 *f*, *g*).

Later than Stage I, I have comparatively few notes which add to the information contained in my earlier paper ('85) and in the simultaneous one by Mr. Gulland ('85). One reconstruction, however, demands attention; that represented in Fig. 62. This is the nephridium in Stage K just before the molt in which the telson appears in the adult form. One error however is noticeable in it; the lateral amplification is too great and consequently the diameter of the tubes and the extent of the outgrowths are exaggerated. In this the same parts are recognizable as before but they have undergone some modifications. Thus in the region of the end sac a fenestration is

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[1] In my earlier paper I was in doubt upon this point and thought that possibly ('85, p. 535) I had found such an opening, which led to the reconstruction of the tube with an internal funnel. Still I was not positive. I now feel confident that the opening of that paper was an artifact.

observable, the beginning of the anastomosing condition of the adult (*cf.* Fig. 55); while the proximal (internal) limb is thrown into a series of four, outwardly directed diverticula which are segmentally arranged and which occupy somites two to five. The external (distal) limb shows fewer modifications, the chief being that the excretory vescicle is relatively smaller than before; the external opening still persists and I have not found out when it closes. This figure corresponds quite closely to Gulland's ('85) Fig. 3, except that in his reconstruction the outgrowths from the proximal limb are represented as taking a sagittal direction and the anastomosing character of the inner end is carried still farther, a condition doubtless due to the older stage with which he worked.

Although I have not followed it out the appearance at this stage gives countenance to the view that the whole organ of the adult is derived from the cœlom of somite V and that the apparently metameric lobes figured by Packard ('80, Pl. III, Fig. 7, copied by Lankester '84 p. 153 Fig. 3) are not the remnants of the nephridia of the corresponding somites but are rather the derivatives of the diverticula shown in my reconstruction. Besides an increase in the size of the lobes all that is necessary to convert my reconstruction into the "coxal gland" of the adult are closure of the external opening, more or less complete fusion of the two limbs of the duct, accompanied by an increase in the anastomoses, the result being to convert cœlom and duct into the spongy tissue of the adult, the whole organ being a series of anastomosing tubes, the "cæca" of Lankester. This view of the morphology of the organ receives confirmation from the fact that I have seen no fusion of cœlomic spaces two to five while Kishinouye, as already stated, finds no cœlom at all, in the anterior somites which are later invaded by the coxal gland.

A word as to the external opening of the nephridium. Gulland ('85, p. 513) states that it is "at the base of the coxa of the fifth limb on the side next the fourth appendage and on the dorsal surface." I find upon repeated examination that it is rather upon the posterior side of the coxa of the fifth pair of legs, as I stated it in my earlier paper ('85).

Comparisons. — The foregoing account differs in some points from that which I gave in 1885. I then failed to recognize the genetic connection between the nephridium and the cœlom and also failed to recognize the closed condition of these organs. The history of our knowledge of the nephridia in Limulus can be briefly summarized.

These organs were first noticed by Packard ('75[a]) who from their histology and by exclusion, concluded that they were renal in function and homologous with the green gland of Crustacea. Five years later ('80) he redescribed and figured their adult structure and suggested a comparison in their position with the shell gland of the Entomostraca. Lankester in 1882 described these organs and compared them with the coxal glands of the scorpion and later ('84) gave the histology with some detail. In both papers he was inclined to compare them with the green gland of the Crustacea but still admitted the possibility or even probability of their being ectodermal or entodermal with a frame work of "skeletotrophic tissue." In the next year Gulland ('85) described the organ in young specimens while Kingsley at the same time gave an account of the early history of the organ, comparing it exactly with the shell gland of the Entomostraca and claimed that it and the genital ducts of both Crustacea and Arachnida should be regarded as Nephridia. In 1890 Kingsley stated that the coxal gland of Limulus was derived from the cœlom of somite V, that it terminated cæcally and gave in outline the above account of the origin of the segmentally arranged lobes. Kishinouye ('91[a]) stated that in *Limulus longispinus* the coxal gland is formed from the ventral part of the cœlom of somite V and later ('91[b]) describes the method more at length. His account agrees well with the foregoing excepting that the outgrowths of the metameric lobes occur at an earlier stage and the end sac (his "funnel") is in the mesoblastic dissepiment between the fifth and sixth appendage bearing segments.

All others who have had occasion to refer to the nephridia of Limulus have used the material included in the papers enumerated above. This is true of Eisig ('88) Loman ('88) and Sturanay ('91).

Of the coxal glands of the Arachnids we know considerable concerning the adult structure and little about the development. They have been found in Scorpions, Phalangids, Solpugids, Acarina and Araneina. They occur in either somite III or V or they may co-exist in the same individual in two somites at the same time. Usually the external duct becomes closed, as in Limulus, at an early date but in Phalangids (Loman '88) it remains open through life.

Laurie ('90) describes the development of the coxal gland in *Euscorpius italicus*. In the youngest stage studied it is a simple straight tube opening distally to the exterior and proximally by a funnel to the cœlom of somite V, which is a much larger space than in Limulus.[1] In the next stage the duct becomes bent on itself so that it appears in sections cut in three places. Its connection with the cœlom is still evident. Later it becomes more complicated and the whole gland becomes enveloped in a thin capsule of mesoderm cells, but the process is not further described. The external opening persists until after hatching.

Kishinouye ('90) has studied the development of the gland in Agalæna, Lycosa, and other spiders. In these it occurs in somite III and is described as consisting of a duct of ectodermal origin which breaks through to the cœlom. The schematic figures do not prove this origin of the duct.

Lebedinsky's account ('92) of the development in Phalangids is most complete. The first appearance of the nephridium is a weak outgrowth of the wall of the cœlom of somite III. The cells of this outgrowth become columnar while its external end grows into connection with the ectoderm of the first ambulatory appendage. This thickened portion, which is to form the duct of the organ, now grows inward, carrying the wall of the cœlom with it, so that its internal end is surrounded by a ridge. This inner ingrowth forms the nephrostome. The ectoderm is resorbed later, giving an opening to the exterior, and the tube becomes convoluted.

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[1] Kowalevsky and Schulgin ('86) saw the organ when it was but little complicated; they describe its duct as ectodermal.

That these organs in Limulus and Arachnids are homologous admits of little doubt. It is scarcely more doubtful that they belong to the same category as the antennal glands and shell glands of the Crustacea. The correspondence, as I earlier pointed out, is exact between the coxal gland of Limulus and the shell gland of the Entomostraca. Their closure in Limulus and certain arachnids is paralleled for instance in the case of Argulus (teste Leydig, '89), where the shell gland is functional only in early life. On the other hand, as stated above, the coxal gland in Phalangids is functional in the adult.

In the light of recent investigations these organs must be regarded as nephridia, and the arguments to the contrary advanced by Eisig ('88) are without foundation. Two recent studies are of interest here: That of Sedgwick on the development of the nephridia in Peripatus, and those of Weldon ('89 and '91) on the relations of the antennal gland to the cœlom in the Decapods. In Peripatus the development is strikingly like that in Limulus, except there are numerous pairs of nephridia in the former. In both there is the formation of small cœlomatic spaces; in both (*cf.* Kishinouye, '91^b) a division of the cœlom into dorsal and ventral portions, and in both the conversion of the ventral cœlom into end sac, nephrostome, duct, and bladder. It is interesting in this connection to note that according to Loman ('87) in Phalangium, where the nephridial opening does not close and the organ remains functional through life the Malpighian tubes — the other urinary organs — are lacking.

I am inclined to believe that the genital ducts of Limulus are also to be regarded as nephridia, but I have searched in vain for any trace of their development. Laurie's account of the origin of the ducts in the scorpion is, as he says, intelligible upon the ground that they are nephridia; their somewhat tardy appearance and lateness in opening to the exterior not seriously militating against such a view.

Muscles. — I have not attempted to trace the history of the muscles except to a slight extent. The muscles, which move the feet and which extend from the dorsal surface of the body down to the appendages, are developed along the intersegmental lines. The tissue from which they arise is the boundaries of the somites which extend inward toward the median line and which by their encroachment into the yolk outline the liver lobes. The early history of this portion is traced in connection with the alimentary canal. In the abdominal region the differentiation of the muscles of the gill appendages is accomplished in the same way, and it is interesting to note (see Fig. 79) that the anterior wall of the somite develops the extensor and the posterior the flexor of the corresponding appendage.

ENTOSTERNITE. — Passing between the alimentary canal and the nervous system in the cephalothoracic region, and serving at the same time to connect the pedal muscles of the right and left sides is a layer of tissue which serves as a tendon, or rather as a series of tendons, and which by its later chondrification or chitinization (vide Lankester, **'84**, p. 133) gives rise to the entosternite. It is to be noticed that in its development the entosternite (Figs. 74, 84, 86, 87 *es*) is always fibrous and it arises from the fibrous tissue of the region. The other "cartilages" occurring as axial tendons in the gills and operculum (Fig. 79) present in their early stages a distinctly chondroid appearance.

ORGANS OF CIRCULATION. — The early history of the central circulatory organ — the heart — of Limulus was outlined in my paper of 1885. Later, Kishinouye has added to the account given there and has corrected some points in my description. So this early history need not be detailed here. The heart arises as a result of the extension of the mesoderm over the yolk towards the dorsal median line. Its walls are formed by the edges of the advancing tissue, and, according to Kishinouye, as the walls of the tube thus formed are interrupted in the intersomitic region, a series of segmentally arranged openings into the cavity — the ostia — are produced. The differentiation of the heart begins at first behind and gradually extends forward. In its early formation the heart of Limulus affords support to the theory of Bütschli (**'82**) in regard to the relations of the circulatory system to the segmentation cavity.

My present description begins with Stage H (Fig. 64). In this the heart may be seen with walls in which no definite arrangement of cells is visible and with two blood corpuscles in its interior. It is connected in this section with the dorsal ectoderm by a cord of cells, while on either side are two cavities, a dorsal and a ventral. The ventral is clearly the cœlom of the somite, and its walls, somatoplure and splanchnoplure, are perfectly distinct. The upper cavity, the pericardium, is plainly lacunar, and is produced by a splitting of the mesoderm, and at this early stage is limited distally by the trabecular tissue so characteristic of the embryo of Limulus. Farther forward (Fig. 66) the heart is larger, and the cells of its walls are arranged in a single layer.

In the next stage (I, Fig. 66) the somatopluric mesoderm has given rise to the alary muscles which are best developed in the anterior portion. In the abdominal region (Fig. 67), the heart is larger, but in all parts it as yet consists of the single layer of cells which were found in the preceding stage. Fig. 67, which passes through the plane of the genital operculum, shows on either side the posterior extension of the dorsal cœlom. A few sections further back (Fig. 68) this cavity disappears from the sections. In longitudinal section (Fig. 82) the heart is seen to extend back to about the middle of the abdomen and forward to the anterior end of the yolk, following this down toward its junction with the stomodæum. At its anterior end the heart divides into two aortic arches (the "crosses aortiques" of Alph. Milne Edwards, '73) which I have called the sternal arteries. These arteries (Fig. 76) pass down one on either side of the stomodæum to dispose themselves at first as two tubes upon the upper surface of the ventral nerve chain. I have not satisfied myself of the way in which these sternal arteries arise but the observations which I have made are not incompatible with the view that dorsally at least they are interseptal. This point is however difficult to settle on account of the numerous lacunae, which, as already mentioned, early appear in the mesoderm and confuse the observer. At this stage (I) no other arteries arise from the heart.

In Stage K the conditions are much the same, the relations of the anterior end of the heart and the sternal arteries being shown in Fig. 77, drawn from a wax reconstruction.

In Stage L, the heart (Figs. 72, 73, 82) has nearly attained its adult condition so far as segmentation into chambers is concerned. In Fig. 73 — representing a horizontal section — the anterior end of the heart is shown, enclosed in the pericardial space and supported by the alary muscles. In front, on either side are the roots of the sternal arteries but I have not seen at this or any earlier stage the frontal arteries of Milne Edwards. Fig. 72, taken at a lower level, shows the section of the sternal arteries on either side of the narrow duct connecting the proventriculus with the mesenteron.

It is not until late Stage H that the sternal arteries reach the nervous system. At first they extend themselves as two separate tubes along the dorsal surface of the nervous cords and extend backwards but a slight distance upon them forming the rudiments of the neural artery. There is at this time no trace of any tube beneath the nerves. It is especially interesting that this condition which is transitory in Limulus should be permanent in the Scorpion.

In Stage I the neural artery extends back behind the middle of the cephalothorax but its termination is indistinct. In somite VII (Fig. 67) no traces of it are to be found. The partition between the two arteries still persists (Figs. 70–71) but on either side the artery is extending itself around the nervous system and appearing beneath it, thus giving rise to the peculiar condition so well known as characteristic of the adult horseshoe crab. This condition is brought about, at least in part, by outgrowths from the dorsal tubes but whether there be cavities formed independently beneath the cord which are later taken into the neural artery I cannot say. Most of it is accomplished by the downward growth and the wrapping of these portions around the cord, there being as Milne Edwards has suggested a soldering of the two edges of the vessel and a subsequent resorption of the resulting lamella. As will be seen, by this process of formation the nerve does not float freely in the blood but is surrounded by a neurilemma which is part of the arterial wall. In other words the artery is not morphologically inside the artery.

In Stage K, as shown by the reconstruction Fig. 77, this process has been completed at the anterior end of the ventral cord. Below, this figure shows the neural artery (*av.*) represented as filled with a solid mass, while the omission of the nerve cord leaves a central cavity from which proceed the openings for the nerves on the sides. In front (to the right) below, the forwardly directed process shows the nature of the outgrowths by which the ventral artery is extending itself beneath the brain.

In Stage L the dorsal portion of the neural artery has reached the abdomen, while in the somite of the fifth appendage the conditions are advanced as far as shown in Fig. 74. In the oldest embryos I have sectioned the arteries surrounding the nerves have extended themselves into the appendages (Fig. 89).

I have not attempted to follow the development of the blood sinuses, *etc.* They occur most abundantly in the abdominal region (Figs. 65, 68, 73, *etc.*) and that they are produced by a splitting of the mesoderm is easily seen in the development of the gills. The pericardial sinus belongs to the category of these blood spaces, the cœlom taking no part in its formation.

Comparisons.—I have above referred to Kishinouye's account of the formation of the heart in Limulus with which my recent observations are in fair accord. In my first account I described the heart as arising from a solid cord of cells but this was a mistake. A re-examination of the slide showed that at the stage described the heart was already formed and its cavity was filled with blood corpuscles.

In the Arachnida most observers have described the heart as arising from the coalescing edges of the somites, meeting in the dorsal median line, there being slight differences in details between the Scorpions (Kowalevsky and Schulgin, Laurie) and the Araneina (Schimkewitsch, Locy, Morin, Kishinouye). In the other groups, as far as I am aware, no detailed observations have been made.

The pericardium of the spiders, according to Schimkewitsch ('87) arises as a layer of mesoderm split off from the splanchnoplure, while the somatoplure gives rise to the alary muscles. If this be so it is an important point of difference between Limulus and the Arachnids. Schimkewitsch further describes the pulmonary veins arising as outgrowths from the pericardium, the lateral arteries as outgrowths (Ausstülpulgen) from the heart itself.

ALIMENTARY TRACT.

The alimentary tract of Limulus, like that of all Arthropods, consists of three divisions ; stomodæum and proctodæum, of ectodermal origin, and mesenteron (including the "intestine" and "liver"), derived from the entoderm. These parts are easiest considered in connection with each other.

MESENTERON. — The separation of the entoderm from the ecto-mesoderm by delamination was described (p. 46) in the first part of the present article. As will be remembered, I regard the whole of the nucleated yolk after that separation as the true entoderm. From the time of differentiation of this layer until the first molt there is but slight histological change in the region of the midgut and its diverticula aside from a slight increase in number and consequent decrease in size of the yolk (= entoderm) cells. There is, however, a very considerable change in the shape of the entoderm which may be summarized as follows : —

When the entoderm is first separated from the rest of the egg, it is, like the egg, spherical in outline. It then becomes gradually flattened (*cf.* Fig. 82) and more and more ovoid in outline, viewed from above, corresponding in this with the changes in shape of the embryo. As a result there may soon be distinguished a large semicircular mass of entoderm in the cephalothorax and a smaller, more cylindrical portion in the abdomen. Coincidently with this change in outline the beginning of the differentiation of midgut and "liver" occurs. As the mesoderm extends itself peripherally from the median ventral line of the embryo, it gives rise to slight intersegmental ridges, the septa of Balfour. Until this centrifugal growth reaches its extreme these septa are slight in extent, but as it attains the margin of the carapax and, turning on to the dorsal surface, begins to grow back to the dorsal median line, there begins a rapid centripetal growth of these septa, resulting in broad sheets of tissue which divide the peripheral portion of the yolk into a corresponding number of lobes, those of the first division being of course segmentally arranged. Thus there are in the cephalothoracic region six pairs of these lobes, while in the abdomen they are less distinct and less extensive and are only temporary, disappearing totally at an early stage. The fact of their temporary appearance in this region is, however, of considerable interest.

A similar process of lobulation of the yolk has been described by several authors for various Arachnids, and it may be regarded as characteristic of the large-yolked eggs of the group. It however occurs to a greater or less extent in other forms. Thus, in the Crustacea the lobulation of the midgut gland ("liver") is of the same character, while in the leeches, as described by Dr. Whitman ('78), the differentiation of the intestine and its diverticula is exactly the same. Were this process of differentiation of liver, lobes and intestine to go on regularly, it would result in the production of a Limulus with a paired liver in each somite, each half emptying by its own duct directly into the intestine. This, however, does not occur. With the development of the extensive muscular system of the gill-bearing appendages and the large blood sinuses in that region the abdominal midgut diverticula disappear. In the cephalothorax the primitive regularity shows the following modifications. The septa do not all grow at the same rate, and (Fig. 83) some are interrupted at points in their growth, so that two or more lobes remain in direct connection with each other. This occurs between lobes 1, 2 and 3, and also between lobes 4, 5 and 6. At the same time the inner ends of the septa become expanded by the development of the muscles of the feet so that they in places run together, cutting off lobes 1 and 2, and 5 and 6 from direct connection with the central mass. In this way the six primary liver lobes and the two hepatic ducts (*hep.*,^{1} *hep.*^{2}) of either side of the adult are differentiated. A later peripheral ingrowth of mesoderm still farther divides up the primary lobes into lobules (Figs. 34, 35) resulting in the adult condition.

At the anterior end of the body an ingrowth[1] similar to the septa carries back the anterior end of the intestine, and intervenes to separate the first pair of lobes from each other. With this ingrowth this pair of lobes, which at first were at right angles, come to lie parallel to the principal axis of the body.

The central unsegmented part of the yolk which remains after the differentiation of the "liver" forms the "intestine" of the adult. It extends from the point of the first appearance of the stomodæum back to the posterior end of the body.

Until after the first molt after hatching the entoderm retains the same histological characters which it had at its first differentiation. It is a mass of yolk without lumen and is divided into a number of polygonal cells with clearly marked cell walls and central nuclei.[2] Excepting in a slight difference in size, it is impossible to distinguish histologically between the entoderm cells of Stages C and I. That some change does occur in the interval, of a chemical rather than of a histological character, is shown by the fact that while in the earlier stages the yolk is very difficult to section, in the later it cuts as readily as any other tissue of the body.

After the molt which produces the adult form (Stage L) the histiogenesis of the epithelium of the midgut and its diverticula begins. It appears first in the intestine and later in the liver; and in the intestine it is first seen at the anterior end (Fig. 81). From the study of numerous sections (*cf.* Figs. 81, 85, 88) the process is clearly seen to be a direct conversion of the yolk-cells into the epithelial lining of the mesènteron. In Fig. 85 — a sagittal section through the junction of stomodæum and mesenteron at early stage L — the entoderm cells, *en,* near the

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[1] For clearness this and the lateral septa are considered as ingrowths, but they are to a large extent outgrowths as well, since the margin of the carapax is farther removed from the median line in the later than in the earlier stages, and it is coincidently with this change in the relative position of the margin of the body that the septa are developed. This is even more marked in front than at the sides of the body.

[2] In my figures the yolk is represented as solid, neither cell walls or nuclei being shown. They are, however, very distinct in all of my preparations.

middle line, are seen to have assumed a columnar character and to be nearly free from yolk, while on either side they pass into a tissue crowded with yolk spherules (*ys.*) in which the cell boundaries cannot be followed and in which the nuclei are irregularly arranged. In Fig. 84 — a transverse section of a slightly older embryo — the same conditions are shown upon a smaller scale. On the upper left side of the intestine (*mes.*) the cells have a well-marked epithelial character, while on either hand they pass directly into the normal yolk cells of the earlier condition. In a slightly older individual (Fig. 81) the whole anterior end of the intestine is free from yolk, and its lining cells (represented diagrammatically) have the character of a columnar epithelium, while at the posterior end they pass directly into the yolk cells which still fill the whole cavity in this region.

This rearrangement of the epithelium is well advanced in the intestine before it begins in the liver, and it advances more rapidly in the central than in the peripheral parts of the latter. It thus forms first the epithelium of the hepatic ducts (Figs. 72, 86) and then the secretory epithelium. In the latter I have failed to recognize an early differentiation of purely epithelial and excretory cells such as has been described in some spiders.

As will be seen, I regard the yolk in Limulus from the time of its delamination as true entoderm. I fail to recognize, at least here, the existence of "vitellophags" whose purpose is merely the metabolization of the yolk and which then degenerate. I look upon the yolk cells from the beginning as morphologically a true epithelium, the cells of which, being gorged with yolk, are crowded from their proper position, thus obliterating the lumen and obscuring their true nature. In the later stages, when there is a rapid development of tissues, there is a corresponding call upon the entodermal structures for nourishment. Then it is that the yolk cells act temporarily as "vitellophags" and, metabolizing the yolk, pass the products on to the other tissues. It is only then that, the yolk being out of the way, they are able to rearrange themselves as a true epithelium.

While this view is in full accord with the observations of most students of Arachnid development, it is at variance with some of the commonly received ideas of Arthropod embryology, which are to the effect that the yolk cells are "vitellophags," degenerating and not contributing to the formation of the entodermal epithelium which arises from cells derived from some other source. I feel confident that this is not the case in Limulus. I have yet to see any evidence of degeneration of the yolk cells, and further, I have seen no cells other than those of the yolk which could supply the epithelium of intestine and liver. From the very time when the yolk is first included in a mesodermal envelope this layer is to be clearly traced (*sp.*) as a splanchnoplure closely enveloping the yolk, and in the later stages the same layer is seen (Figs. 84, 85) in exactly the same place and presenting the same conditions. In some sections which I have made of Hexapod eggs I have seen appearances which lead me to think that possibly in these forms the entoderm of authors is in reality splanchnoplure. The fact that most observers have closed their investigations before the development of a well-differentiated entodermal epithelium leaves a gap which renders their interpretations not conclusive on this point.

STOMODÆUM. — As already described (Vol. VII. p. 52) the anterior end of the primitive streak is marked by a spot where the cells are deeper and more columnar (Figs. 43, 45, *mo.*) than elsewhere in the median line, and this spot is usually, in Arthropods, regarded as marking the position of the future mouth, and all discussions of the transfer of the mouth from a preappendicular position to one behind the first pair of appendages are concerned with the connection of this spot with the mouth of the adult. In reality this spot marks the junction of stomodæum and mesenteron and forms the inner end of the foregut. Hence to call it the mouth is to introduce an element of confusion.

At the time of the first outlining of the limbs the invagination of the stomodæum begins, and the process is one which finds its closest parallel in the invagination of the neural canal in the vertebrates.[1] At first it is a shallow pit with small

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[1] It is needless to say that this affords no foundation for the curious vagaries of Gaskell, as to the origin of the vertebrate nervous system from the alimentary tract of the Arthropod.

lumen and with an external opening pear-shaped in outline, narrower in front and wider behind. It is in fact enclosed by two ridges, one on either side, while posteriorly it is without distinct boundaries and passes directly into the ventral ectoderm. The lateral walls gradually unite in front (*cf.* Vol. VII, Figs. 30, 31), and are at the same time added to behind. It is by the continuation of this process that the stomodæum is invaginated and the mouth comes to occupy a position behind the first pair of appendages. Thus it will readily be seen that with regard to Limulus, at least, Claus is wrong when he says ('87, p. 129) that the preoral condition of the appendages is "nicht ein Lagenwechsel des Mundes . . . sondern eine im Laufe der Entwicklung vollzogene Aufwärtsbewegung der Gliedmassen mit entsprechenden Verschiebung der Ursprungsstelle des zugehörigen Nerven." It would seem probable that the same conditions obtain in the Crustacea, but detailed observations are as yet lacking.

At first the cells of the stomodæum invaginated in this manner form a low cubical epithelium, but they soon elongate and assume the columnar character which is found in this region in all the later stages. At an early date they also begin the secretion of the chitinous cuticle. At the outset all of the stomodæum is apparently formed by this invagination, and the tube is straight between mouth and the inner end. Later it begins to elongate by interstitial growth, and in this way a flexure in the sagittal plane is produced (*cf.* Figs. 81, 82). This flexure is also increased by the flattering of the embryo.

With the introduction of the flexure there begins a differentiation of the stomodæum, at first into an internal proventriculus (stomach of most authors) and an outer tube. Later, the latter in turn is subdivided into buccal cavity and œsophagus proper (Fig. 81) In the proventriculus there soon develop longitudinal folds, and before the connection of stomodæum with mesenteron is effected, the proventriculus has, except in size, the characters which it has in the adult.

After the epithelium of the midgut has been formed at the anterior end, the connection between fore- and midgut is effected by a breaking down of the wall between them. At first the proventriculus empties directly into the mesenteron, but later (Fig. 72) the inner end of the former becomes drawn out in a slender tube which projects slightly as the "cone" into the intestines. The limits of the two regions, ectodermal and entodermal, at this stage are clearly distinguished by the chitinous cuticle upon the former.

PROCTODÆUM.— In striking contrast to its development in the Crustacea the proctodæum in Limulus is late in its appearance and small in extent. As late as Stage I (Fig. 82) it appears merely as a slight inpushing of the ectoderm upon the ventral surface. In Stage L it is wider but scarcely deeper than before (Fig. 81). In still older specimens (Fig. 88) the boundary between mesenteron and proctodæum has broken through and the now more elongate proctodæum has become thrown into inner folds. At the point of juncture between ectoderm and entoderm there appears, above and below in the section, an enlargement of the lumen of the tube and a second similar enlargement occurs within the entodermal portion of this tract. As to the meanings of these enlargements I have nothing to offer aside from the fact that in connection with them the Malpighian tubules of the Hexapods and the analogous structures of the Arachnids naturally suggest themselves.

Comparisons.—Almost nothing was previously known of the development of the alimentary tract of Limulus. In 1885 I gave essentially the same account of the formation of the stomodæum and the differentiation of the liver-lobes, illustrating both with diagrammatic figures. In the same year Brooks and Bruce in their preliminary paper ('85) describe the entodermal epithelium as arising from the yolk cells in the same way as I have done and they further say, though without any details, that the stomodæum arises as an ingrowth which at first goes upward and forward and then bends upon itself. Though not specifically the same in words the account given by Kishinouye ('91) of the development of the stomodæum is easily brought into harmony with the foregoing, and especially interesting is his statement (pp. 79–80) that "As the upper lip grows posteriorly, the mouth opening which was at first pre-appendicular gradually shifts its position backward." Kishinouye has nothing to offer concerning mesenteron or proctodæum.

In the Arachnida almost all observers describe conditions closely similar to those obtaining in Limulus. Since the time of Balfour's paper ('80) the liver-lobes have been recognized as differentiated by the ingrowth of mesodermal septa into the yolk in the same manner as in Limulus, and the hepatic ducts (of course different in number) as formed in substantially the same way. Balfour, while thinking that certain observations possibly pointed to the origin of the hepatic epithelium from the cells of the thickened ends of the septa, still recognized the entoderm in the yolk. Balfour did not trace the formation of the entodermal epithelium but later authors agree that it arises in the spiders from the yolk cells, the differentiation beginning at first at the posterior end. So far as their observations go Locy, Morin (the text of his preliminary paper, the copies of the figures of his later article in Russian), and Schimkewitsch ('87) agree in the recognition of the yolk nuclei of spiders as the nuclei of the future entoderm. Later, Schimkewitsch ('90) changes his views ; he now recognizes as entoderm in the "Tracheates," the smaller cells which lie on the ventral surface of the yolk, while the mass of the yolk cells in the Arachnids are the Anlage of the blood corpuscles. Such a view is impossible with Limulus, since before the yolk cells undergo any change they are entirely enclosed in the splanchnopleural layer of the mesoderm, through which migration to the blood vessels is impossible.

Faussek, in his account of the development of the Phalangids ('91) says that at the close of the embryonic period the yolk cells (derived as in Limulus by delamination) divide rapidly, and, with a small amount of protoplasm, begin to throw themselves down upon the mesodermal envelope of the midgut and its diverticula. At first these patches of entodermal epithelium are irregularly scattered but they soon begin at the anterior end, to arrange themselves in the cylindrical epithelium of this region.

In the scorpions the conditions are quite different. As already pointed out (Vol. VII, pp. 55 ff.) Kowalevsky and

Schulgin ('86) and Laurie ('90) show that in the early stages the entoderm is a distinct differentiation from the germinal area; it remains for a long time as a solid mass at the posterior end of the embryo and only later spreads itself out as a definite layer enclosing the yolk and forming the epithelium of the midgut and its diverticula. Of the details of the formation of the liver-lobes but little is said, but apparently it occurs through the ingrowth of the mesodermal septa as in Araneina and in Limulus. The different type of formation of the entoderm in the scorpions and Limulus is possibly the strongest objection which can be raised to the close association of the two forms, for while the two types can be reconciled, it implies an extremely long separation of the forms. Still it must be borne in mind that if this be advanced as an objection it must be equally valid in proving that the Araneina and the scorpions are but remotely connected, a thesis which I hardly care to defend, while on the other hand it would show closer relationship between Limulus and the spiders than between the former and the scorpions, a view which is negatived by numerous other facts of structure and ontogeny.

Limulus also agrees with the Arachnida in the early appearance and elongation of the stomodæum and the shortness and lateness of appearance of the proctodæum. As yet, no observations are recorded as to the manner of invagination of the stomodæum, but as figured by Morin (in Korschelt and Heider '92) and Locy ('86) it bears close resemblance to that of Limulus in its bending and in the early differentiation of a terminal pouch clearly comparable to the proventriculus of Limulus. In the only sagittal section given by Laurie of the later stage of the stomodæum in the scorpion ('90, Pl. XVII, Fig. 48) the proventricular enlargement is not very apparent but the buccal cavity is well marked. Concerning the proctodeal region the comparisons reveal little of importance. In the spiders we have in this region the formation of the stercoral pocket[1] which is without parallel in Limulus (*vide*, however, *supra* p. 219 and Fig. 88).

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[1] Kishinouye's observation ('90, p. 68) that the stercoral pocket is developed from the unpaired cœlom of the caudal region certainly needs confirmation.

NERVOUS SYSTEM.

I leave all questions concerning the nervous system and sense organs untouched, except in so far as is necessary to explain some points which will appear later. I do this the more willingly since my friend, Dr. Wm. Patten, has for several years been devoting especial attention to this system. I find in Limulus that at an early stage the nervous system, viewed from the surface, presents the appearance of numerous circular pits (Fig. 29). These, which are shown in section in Figs. 49 and 65, I suppose to be what Patten ('89 p. 602) refers to in his statement that "the central cord and brain of Arthropods, is at first composed entirely of minute sense organs, which in the scorpion have the same structure as the segmental ones at the base of the legs." Kishinouye has also seen the same structures and compares them to the ommatidia of the eye. There is, however, no such differentiation of the nuclei as are shown in the figures of the latter. Unlike Patten, I interpret these inpushings of the nuclei as centres for the rapid proliferation of nerve cells, and not as sense organs. I also am inclined to withdraw my original account of the formation of segmental sense organs ('90), as I am now inclined to believe that the structures which I described as sensory in structure (various figures "*ss*") are more probably glandular. The brain arises from three pairs of ganglia in front of the pair which innervates the first pair of appendages. I believe these three ganglia to represent: the first, the primitively preoral nerve centre, the homologue of the "brain" of the annelids; the other two to belong, like the deuto- and tritocerebrum of the Hexapod, to ganglia which have left the postoral and have wandered into the preoral region. Upon the real state of affairs I have, however, almost no actual observations, and base my opinions largely upon the conditions in other groups.

RESPIRATORY ORGANS.

As is well known the respiratory organs of Limulus are borne upon five pairs of appendages situated on somites VIII–

XII. Each of these appendages has upon its posterior surface a large number of rounded quadrilateral lamellæ (the number varying with age), the "gill-leaves," and the whole organ is known as the "gill-book." The first of these appendages to appear is the most anterior one (VIII). It grows out from the body, not as a cylindrical process like appendages I–VI, but as a broad lobe with an oblique insertion upon the ventral surface of the body (Figs. 28, 32 *g*). At first this lobe consists merely of a fold of ectoderm (Fig. 78) marked off from the ventral surface by an impushing behind, and containing in its interior scattered branching mesoderm cells between which are numerous large lacunæ. At stage H this appendage shows the first appearance of the gill lamellæ in the form of a single fold of the ectoderm of the posterior surface at about midway of the length of the member. Very soon a second and smaller outgrowth appears between the first leaf and the body, and so on in regular succession (Fig. 79) the new leaves continuing to be added at the base of the appendage, the outer leaves being the larger and older.

When the first gill-leaf appears on appendage VIII, appendage IX is budded, and on this the first gill-leaf appears (Fig. 79) when on appendage VIII there are four or five lamellæ. The subsequent growth of these appendages and the new gill-leaves is but a repetition of that already given. At the molt with which the telson appears and with which my studies end, appendage X has appeared, but is as yet without lamellæ, while appendages VII and IX are well provided in this respect (Fig. 80).

At stage I (Fig. 79) the gills and gill appendages present the following appearances in their finer structure. The ectoderm has become columnar and has secreted on its free surface a thin cuticula. In the gill-leaves the two walls are united here and there by fine mesodermal filaments which extend between the two walls like the tie rods of an architectural structure. Between these trabeculæ are lacunæ without definite walls, and in these, scattered blood corpuscles are to be seen, showing that these spaces are in connection with the general circulatory system. These lamellæ are shown in cross section in Fig. 68, where also may be seen, at either side of the gill-leaf larger lacunæ, forming the afferent and efferent blood channels of the lamella.

In the gill appendage as in the operculum (appendage VII) is a central rod of compact tissue somewhat resembling cartilage, but whose fate I have not traced. In my former paper ('**85**, Pl. XXXIX, Fig. 38) the line from the abbreviation for muscle, was by mistake of the lithographer, run to this structure. On either side of this rod are developed the muscles of the appendages. They have their origin in a narrow line on either side of the back (Fig. 67) and are inserted in the wall of the appendage at the lower end of the rod just referred to. In transverse section these muscles (Fig. 67) are seen to be fan-shaped, the line of insertion embracing nearly the entire width of the appendage. From its origin and insertion the muscle in front of the rod is seen to be antagonistic to that behind and we may consider the two as respectively flexor and extensor in function.[1] The flexors of one somite and the extensors of the next have their origins closely approximate, and their traction soon results in the drawing inwards a small patch of the dorsal ectoderm, thus producing in the adult the line of depressions on either side of the middle of the tack, and the corresponding chitinous ingrowths in the interior of the same region. One of these ingrowths of chitin secreting ectoderm is cut across in Fig. 68 *ent.*

In the last stage studied (Fig. 80) the conditions are essentially the same as before, except that the gill-leaves are larger and more numerous. The section, however, does not pass in the right plane to show the muscles and internal rod. For a description of this section I cannot refrain from quoting MacLeod's ('**87**, p. 4) description of the lung-book of a scorpion:— "Nous trouvons en [la figure] la coupe d'un certain nombre de fines lamelles, les lamelles pulmonaires, placées horizontalement, libres à leur extrémité postérieure ou caudale, c'est-à-dire la plus rapprochée de l'extrémité caudal de l'animal, vers la droite

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[1] I have been unable to identify with certainty these muscles with those of the adult as described by Benham ('**83**). At this early age they are not differentiated as they are later.

de la figure, et attachées en avant. Entre ces lamelles se trouvent des cavités en forme de fentes qui communiquent en arrière avec une cavité générale laquelle débouche à son tour à l'extérieure par une fente stigmatique."

Comparisons. — The only previous accounts of the gill development are by myself ('**85**) and Kishinouye ('**91**, p. 72), and the foregoing differs from them in being somewhat fuller in some details (Kishinouye calls the metastoma an appendage[1] hence his appendage IX is my VIII, etc.). The process is extremely simple — the outgrowth of lamellate processes from the posterior surfaces of the corresponding appendages, the newer lamellæ being formed proximally — and yet my early account does not seem to have satisfied Laurie, who says ('**91**, p. 137) "a detailed account of the development of these appendages Limulus may throw more light on the matter" of the homologies of the respiratory organs of the scorpion and the king crab. Had not Laurie been confused by some strange[2] ideas of the homologies I think that my previous account would have proved detailed enough for his purposes, for the two organs, — the gill of Limulus and the lung of Scorpio, — can be compared in detail in the simplest manner, without the invocation of any inversion, of any "parabranchial stigmata," of any conversion of air space into blood space, or the like.

Several workers have described the development of the respiratory organs of the Arachnida, and from the papers of Metschnikoff ('**71**), Kowalevsky and Schulgin ('**86**), Locy ('**86**), Bruce ('**87**), Kishinouye ('**90**), and Laurie ('**90** and '**92**), we may gain the following summary of the development of the lung books in these forms.

In these forms the lungs develop in connection with the abdominal appendages. These appendages grow out for a short

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[1] See upon this Kingsley ('**85**, p. 541, and '**92**, p. 60).

[2] Thus Laurie says (*l.c.* p. 136): "The additional appendages of Limulus are directed towards the tail as one would expect abdominal appendages to be. Now if the appendage had sunk without invagination, one would expect it to be still directed towards the tail, unless there were some very good reason for its having changed its direction. If, on the contrary, it had become invaginated it would naturally be directed in the opposite direction towards the head, and this is what we find in the scorpion. The inpushing is from the beginning towards the head, and the aperture opens toward the tail."

distance and then an inpushing takes place just behind the appendage, the opening of the invagination, according to Kishinouye being away from the median line. This sac, the future pulmonary cavity, continues to increase in size, while the appendage proper soon becomes obsolete. In this way the pulmonary sac, with its external opening or stigma, is developed. After the pulmonary sac is formed there begins on its anterior wall, — *i.e.* on the continuation of the posterior wall of the appendage, — a series of foldings of the ectoderm, the lung-leaves. As the animal increases in size, new lung-leaves are added at the inner or proximal end. In short, as the adjacent diagrams show, the homologies between the two types of organs are perfect.

In *I* we have a condition which will apply equally well to the young of either Limulus or Scorpio. At the right side the appendage is just budded out, and on the left the sinking

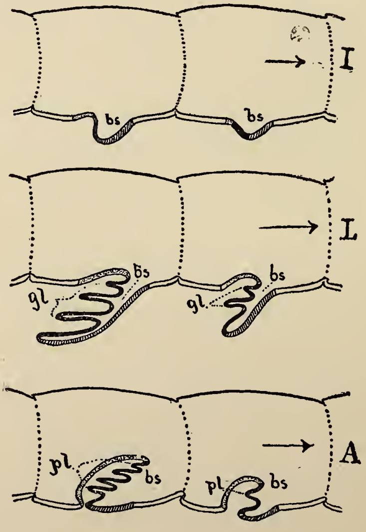

Diagram of the respiratory organs in (*A*) an Arachnid; (*L*) in Limulus, and (*I*) in an intermediate condition. The arrows point toward the head, the cross-lined portion is the anterior, the black, the posterior surface of the appendage, the dotted surface that part of the ventral surface of the somite, which is invaginated to form the posterior wall and roof of the pulmonary sac. *bs*, blood space; *gl*, gill-leaves; *pl*, pulmonary leaves.

in, behind it, has begun. In *L* we have the modifications of *I*, which result in the formation of the gill-book. On the posterior face of the appendage the gill-leaves are budding out. In *A* we have the Arachnid modifications of *I*. On the right side the post appendicular insinking has resulted in the formation of the pulmonary sac from the anterior wall of which,— and which is plainly the posterior surface of the appendage — the pulmonary leaves are being produced (cf. Laurie, '90, pl. XVII, Fig. 47). At the left side of the figure the same conditions are carried further, and the opening of the pulmonary sac is now reduced to the narrow spiracle. In all the figures the anterior surface of the appendage is crossed-lined, the posterior is black, the invaginated portion of the ventral surface dotted, the rest of the ventral surface is white. The arrow points towards the anterior end of the animal.

When the comparison is made in this way the similarities, as to appendages and lamellæ, are seen to be very close. When viewed from the histological standpoint the resemblances are so exact that the description of the pulmonary organ of the spider or of the scorpion will apply almost, word for word, as shown above, to the gill book of Limulus. This, taken in connection with the fact that the very appendages which in the scorpion (IX–XII) are converted into the lung-books, are in the Limulus the bearers of gill-books, and that appendages VIII of the scorpion (the pectines) have a structure also easily reducible to the gill-book of the corresponding somite of the horse-shoe crab, place the homologies of the organs in such a light that few identities of structure and of phylogeny are more certain.

The consideration of the relations existing between the lungs and the tracheæ of the Arachnids will be taken up later.

The Relationships of Limulus.

It would seem hardly necessary to review in detail the discussion of the systematic position of Limulus since it has been done by almost every author who has treated of its anatomy or ontogeny or who has studied the spiders. Yet some space must be devoted to it because of the new facts brought out by the present investigations and especially because some of the arguments advanced by the advocates of the arachnidan affinities of the horse-shoe crab do not seem to be understood by several recent writers.

Notwithstanding the early suggestion of Strauss-Durckheim (*teste* Lankester) and the later one by the younger Van Beneden (**'71**) there was no serious question of the relationship supposed to exist between Limulus and the Crustacea until the publication of Lankester's paper (**'81**) "Limulus an Arachnid." Previous to that date there was a general agreement that the Arthropods were divisible into two great classes: — Tracheata and Branchiata — the division being based primarily upon the method of respiration; and this view was greatly strengthened by Moseley's discovery (**'74**) of tracheæ in Peripatus, thus apparently providing for a line of descent for the Tracheates without the necessity of any close association between these and the Crustacea. The Arachnids were of course included in the Tracheata for in most of the group were found tracheæ, apparently built upon the same plan as those of the Hexapods, while Leuckart had shown long ago (**'49**) that the pulmonary sacs of the spiders and scorpions were clearly homologous with the tracheæ of the other Arachnids.

Although not primarily based upon the respiratory system Lankester's conclusions were in substance that the lungs of the Arachnids were homologous with the gills of Limulus; and the deduction necessarily followed that all Tracheates must have come from a Limuloid ancestor or that the group "Tracheata" must be polyphyletic in origin and that the similarities of the tracheæ in Hexapods and Arachnida must be due to homoplassy rather than to community of descent.

Lankester's paper produced no little discussion and the points presented by the numerous papers upon the subject as well as those based upon the present investigations may be presented in categorical order as follows :—

I. Limulus agrees with the Crustacea and differs from the Arachnida in :—

1. A branchial respiration.
2. The possession of biramous appendages.

3. The absence of Malpighian tubules.

4. The absence of salivary glands.

5. The absence of embryonic envelopes.

6. The presence of compound eyes.

II. Limulus and the Arachnids agree in, and both differ from the other "Tracheates" (Hexapoda and Myriapoda) in :—

7. The primitively postoral condition of appendage I and its later transfer to a prestomial position.

8. The six-jointed appendages II–V.

9. The existence of a metastoma (chilaria) upon the sixth somite.

10. A regional division of the body behind somite VI.

11. The openings of the genital ducts upon appendage VII.

12. The subservience of appendages IX to XII (Limulus VIII–XII) to respiration.

13. The possession of a post-anal spine.

14. The formation of deutova.

15. The formation of the entoderm by delamination.

16. The early appearance of metamerism in the body.

17. The occasional later appearance of appendage I and its somite.

18. The existence of a well-marked cœlom (schizocœle) extending at first into the appendages.

19. The extension of the cœlom of somite I into the preoral region.

20. The presence of a chitinous entosternite.

21. The presence of a posterior artery from the heart.

22. The possession of a pair of sternal arteries passing, one on either side of the œsophagus, to unite below in —

23. A longitudinal arterial canal upon or surrounding the nervous system.

24. The possession of blood colored blue by hæmocyanin.

25. In the possession of reticulate genital ducts.

26. In the method of oviginesis.

27. In the possession of nephridia in somite V.

28. In the pitted origin of the nervous system.

29. In the concentration of the postoral ganglia in a circumœsophageal nerve ring.

30. The invaginate character of the median eyes.

31. The long stomodæum.

32. The large mesenteron.

33. The large midgut glands (hepatopancreas) emptying by metameric ducts.

34. The short proctodæum.

III. Limulus and the Arachnids agree with the Crustacea, and differ from the "Tracheates" in points 14, 21, 27, 31, and also in:

35. The absence of any differentiated head.

36. The position of the genital ducts in the appendages near the middle of the body.

37. The development of the respiratory organs in connection with the appendages.

38. The paired sexual openings.

Several of the foregoing points need but little discussion since they have already been considered both by Prof. Lankester ('81) and by myself. It is, however, to be noted that this enumeration of resemblances and differences omits all reference to characters which are common to all great groups of Arthropods, and also to those which are peculiar to any one group, except so far as they are, apparently, based upon misconceptions. It must also be mentioned that Peripatus is omitted from the discussion, since, notwithstanding the recent researches of von Kennel, Sedgwick, Sclater and Miss Sheldon, its position in the Arthropod phylum is not beyond question. So too with the chilognathous Myriapods, since for reasons which will appear later, their relations to the chilopods are exceedingly doubtful.

I have already discussed in the previous part of this paper the evidence presented by the ovigenesis, in which there is a close parallel between the Arachnids and Limulus, the egg in both passing into a follicle formed by the separation of the *tunica propria* from the germinal epithelium. I have also considered the matter of the origin of the entoderm in both Limulus and the Arachnids (and Pycnogonids) by delamination, and the early segmentation of the body, closely parallel in both groups, before the appearance of the legs. A farther point of similarity is in the tendency toward a late appearance of appendage I in both groups, it having been noticed by both Metschnikoff and Laurie in the scorpion and by Birula ('**92**) in Galeodes. This, however, has less weight than it otherwise would have were it confined to these forms alone, Grobben having noticed ('**79**) a similar delay in the appearance of the antennulæ in Moina.

To several other points exceptions may be adduced. Thus a chitinous entosternite has been noticed in several Crustacea, *e.g.* in Apus and by Claus ('**92**) in Ostracodes. Deutova[1] occur in both Arachnids and Limulus but as Zaddach described long ago ('**41**) they are found in Apus as well. In the American Limulus, as in the Arachnids, the cœlom at first extends into the appendages (Kishinouye says it does not in the Japanese species) but similar conditions have lately been shown to occur in the Hexapods. Reticulate genital ducts occur in the Phyllopods. I cannot agree with Kishinouye that the metastoma of Limulus possesses a separate somite, and as I have already pointed out ('**92**, p. 60) his figures can receive another interpretation. There is no somite and no neuromere for the metastoma, and as it occurs upon somite VI which is already provided with appendages, its appendicular nature is not apparent. Metastomal structures occur in other Arthropods; the exact serial similarity between that of Limulus and that of the Arachnids is the important point.

The possession of a post-anal moveable spine (telson in Limulus, sting in the scorpions, multiarticulate whip in Thelyphonus) is not paralleled outside of these forms. It is to be regarded not as a somite or a series of somites — the position of the anus settles that — but as an articulated outgrowth of the supra-anal region of the terminal somite of the body.

The foregoing disposes of points 9, 13, 14, 15, 16, 17, 20, 25 and 26, while no discussion need here be given to items 8, 24,

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[1] I have used this term, introduced by Claparède, for those molted cuticula or "Blastodermhauten" which serve as protective envelopes — Packard's "vicarious chorion" — after the splitting of the chorion, and before the young is turned free to shift for itself. Henking has called ('**82**) the same structures in the Arachnida "apoderma."

29 and 30, as they have either been treated of sufficiently in previous papers or they are based upon conditions not described in the present series. For the discussion of a large number of the remaining points it becomes necessary first to review briefly our knowledge of the homologies between the somites in the principal groups of Arthropods.

Until we have more evidence than we now possess of the total disappearance of a somite from the anterior portion of the body of any arthropod it will be necessary in making our comparisons between the regions in the different groups to proceed upon the assumption that the metamerically repeated portions are, somite for somite, the same in the whole phylum, and are to be compared throughout upon the serial basis, the first being equivalent throughout, and so with the second, and so on, the comparison ceasing only with the hinder region of the body, where the budding zone occurs and behind which is the terminal or caudal lobe. Upon no other basis can any comparison be made.

The great difficulty with this is in the recognition of the metameres in the anterior end of the body for there we find a tendency toward the obliteration of parts and the obsolescence of those features by which the existence of the somite is made most apparent. The nervous system seems, at present, to afford us the most certain means of recognition of the somites and upon this we must place the most dependence, since in some cases the cœlom of the somite may disappear, its mesoderm becoming fused with that of its neighbors while the appendages may totally fail to develop. In the Hexapods various authors have expressed the idea that the so-called brain was a compound structure, and of these the later writers — Tichomiroff (*teste* Cholodkowsky) Patten ('**88**) and Cholodkowsky ('**91**) represent it as composed of three neuromeres, and Carriere (in Chalicoderma) has recognized still another in the cephalic region. Of these the most anterior, the protocerebrum, is apparently prestomial and hence is to be regarded as homologous with the annelid cerebrum, and the descendant of the "Scheitelplatte." All recent observers — Patten, Heider, Wheeler, Graber, Carriere, Cholodkowsky *et. als.* — have amply confirmed the early observation of Weismann ('63) that the Hexapod antennæ are postoral, and have shown that they are innervated from the second or deutocerebral neuromere. Between this and the mandibular ganglion is the third component of the brain, the tritocerebrum, and in a few forms this has been shown to have a small embryonic appendage which apparently becomes obsolete in the later stages. This has been observed by Tichomiroff (*teste* Cholodkowsky[1]) in the silk-worm; by Carriere ('90) in the bee Chalicoderma[2] while in a note Dr. Wheeler sends me an account and a drawing of the embryo of the Collembolan, *Anurida maritima*, in which the appendage between the antenna and the mandible, the tritocerebral appendage, is well marked. Apparently Wheeler had seen traces of the same in Doryphora ('89, p. 337 Fig. 44). Regarding these neuromeres and appendages the conclusion is inevitable that they belong to the primitively postoral series. They arise in the same line and agree in all respects with those further back. The only other supposition would be that they are preoral and temporarily wander backwards to be immediately returned to their proper position, a supposition of very doubtful value. In the light of these observations we must regard the Hexapod head as composed of at least six elements, the procephalic lobes and five postoral somites, each of the latter having appendages.

In the Arachnida our evidence is much less abundant and much less detailed. Schimkewitsch ('89) describes in the spiders ocular and rostral ganglia (Pl. XXI, Fig. 3) in advance of the ganglion of the cheliceræ, while in the schematic Fig. 5 of his Pl. XXIII he represents the cerebral ganglion (in front of the rostral ganglion) as three-lobed. Patten ('90) describes the brain of the scorpion as composed of three pairs of ganglia,[3] while Jawonowsky ('92) figures four postoral somites in front of the cheliceral somite, the posterior of which bears a pair of

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[1] In his preliminary paper Tichomiroff merely says "Es existirt bei dem Seidewurm eine echte untere Lippe . . . und die als der allbekannten Oberlippe der Insecten homolog betrachtet werden darf." His later paper is unfortunately buried in an outlandish tongue.

[2] Carriere recognizes *four* cerebral somites and finds a preantennal appendage.

[3] See also Metschnikoff ('70), Pl. XV, Fig. 14.

appendages, possibly the same as that of Croneberg (**'80**) in Dendryphantes. No preoral ganglion is indicated in his extremely unsatisfactory figures, while his evident desire to find the Hexapod antennæ in the Arachnids has possibly influenced his observations.[1] Locy has also figured (**'86**, Pl. XI, Fig. 70) a distinctly three-lobed brain in Agelena. I regret that I have not been able to consult the original plates of Morin's account of the development of the spiders, but as copied by Korshelt and Heider (**'92**, Fig. 383B) the brain of Theridium consists of four lobes, the posterior of which is apparently the cheliceral ganglion. Kishinouye (**'90**) also describes the brain of Agelæna as three-segmented.

In Limulus both Patten and myself have recognized a three-ganglioned cerebrum in front of the ganglia of the cheliceræ. None of these cerebral ganglia have been seen by me in a postoral position, but their relation to the ventral chain is such as to justify the supposition that here, as in the Hexapod, there is a very early shifting.

In the Crustacea I know of no observations of evanescent appendages or neuromeres, unless, possibly in the case of the metastoma. So far as observations go the series is, apparently: first, the procephalic lobes ; second, a pair of ganglia in front of the antennulæ, figured by Bumpus (**'91**, Pl. XVII, Fig. 1) then, antennulæ, antennæ, etc. As to just where the line between preoral and postoral is to be drawn is uncertain. That the antennulæ of the Crustacea are to be classed in the primitively postoral series is evidenced by several facts. In the first place, they are placed by all observers at first in a paraoral if not a postoral position, and in a direct continuation of the postoral appendages. Secondly, the evidence presented by Apus is clearly understood upon the basis of a complete transfer of the ganglia and appendages to a preoral position. In the adult the ganglia of the antennulæ (*cf.* Pelseneer, **'85**) are fused with the cerebrum, while the course of the nerves (see Zaddach, **'41**, Pl. III, Figs. 1 and 5) shows distinctly a transfer of the structures

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[1] In the light of the observations of Carriere and Wheeler his discovery does not help matters, for there is still a somite lacking, to make the parallel exact from his standpoint.

at either end of the cord. I do not quote my own observations upon the postoral position of the antennulæ of Crangon because their accuracy has lately been denied by Weldon[1] ('**92**) and by Herrick ('**92**), and hence they need confirmation.

It is evident, I think, from the foregoing *résumé* that we cannot with much confidence compare, somite for somite, the bodies of even the most studied Arthropods, but we may present the following tentative statement, merely remarking that as far as Arachnid and Limulus are concerned, the correctness of our assumption receives confirmation from other sources discussed in this essay.

	HEXAPOD.	ARACHNID.	LIMULUS.	CRUSTACEA.
Neuromere I	No Appendage	No Appendage	No Appendage	No Appendage
" II	Antennæ	No Appendage	No Appendage	No Appendage
" III	Appendage	No Appendage	No Appendage	Antennula
" IV	Mandible	Chelicera	1st Leg	Antenna
" V	Maxilla	Pedipalpus	2d Leg	Mandible
" VI	Labium	1st Leg	3d Leg	Maxilla 1
" VII	1st Leg	2d Leg	4th Leg	Maxilla 2
" VIII	2d Leg	3d Leg	5th Leg	Maxilliped 1
" IX	3d Leg	4th Leg	6th Leg	Maxilliped 2

It will be noted that this comparison brings the end of the Hexapod thorax, and the hinder margin of the cephalothorax of both the Arachnids and Xiphosures into correspondence. Further, if we insert into the Crustacean line a segment for

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[1] Professor Weldon and myself are apparently at variance upon several points with regard to the embryology of Crangon, but the points in dispute cannot be settled except by renewed observation. I would, however, point out that in several places he has attributed to me views which I do not hold and which he would not have obtained had he read my papers carefully or had he availed himself of his opportunity to talk over the points of difference while his paper was in press. Thus he says (*l. c.* p. 349) that I claim that the blastopore closes completely. I have ('**89**, p. 6) repudiated this view. He refers to my "remarkable Fig. 32 . . . . in which a black dot placed between the optic lobes is called the mouth" as representing my evidence as to the postoral nature of the antennulæ. The figure is distinctly stated to be a diagram to illustrate the plane of the sections; Fig. 11 is the one to which he should have referred. I have no desire for controversy, but would respectfully suggest that possibly Weldon's figure (7),

the metastoma (which numerous authors have regarded as an appendage homodynamous with the others) the result will be to bring the third thoracic foot of the Hexapod into homology with the first rather than the second maxilliped of the Crustacea, and there is no little evidence to show that here, if anywhere, the line between head and thorax in the Crustacea is to be drawn. We are, however, more concerned at present with the serial comparison between Limulus and the Arachnids, and the studies of the nervous system warrant the comparisons made above.

Although we are fully justified in the recognition of somites in both Limulus and Arachnids in front of the segment of the first appendage, I have, from convenience, followed the old nomenclature in the following discussion, and have numbered the somites according to the appendages, somite I being that of the first appendage. From the foregoing it will be seen that point 7, the transfer of appendage I from a postoral to a prestomial position has but little value in deciding the affinities of Limulus, while, if our comparisons be correct, point 10, the existence of a regional division of the body behind appendage VI occurs in the Hexapods and possibly in the Crustacea as well. Point 35 — the absence of any differentiated head — is closely allied to this last. In the Arthropods the terms "head" and "thorax" must be used with physiological rather than morphological values. The cephalothorax of Limulus, as well as that of the Arachnids, is co-extensive, so far as our present knowledge goes, with both head and thorax

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upon which he relies to support his statement that "the first antennæ are evidently preoral from the very earliest period at which the mouth is visible," represents not the first antennæ, but the optic lobes alone. Herrick says ('**92**, p. 442) that he cannot agree with me in saying that Reichenbach "has all the appendages at first distinctly postoral." Reichenbach figures (Fig. 7*a*) the condition to which I referred. A leader (*Ib.*) goes to the "labrum," a thickening of cells some distance in front of his antennulæ ($E.^{ii}$). His sections show that there is behind this but (if I read his description aright) still in front of the atennulæ, a mass of cells, his "Vorderdarmkeim." If this be so I am certainly justified in my reference to Reichenbach as showing the mouth in front of the first pair of appendages. There is as yet no functional mouth found, but the collection of cells indicated by Reichenbach marks the point of the later stomodæal invagination.

of the Hexapod, and — if we be permitted to recognize a metastomal somite in the Crustacea — with the "head" of the Tetradecapods and also of that of the Decapods as limited by Milne Edwards, but not with the Decapod head as understood by Huxley. The argument which Huxley draws for placing the division between head and thorax in the Crustacea between appendages V and VI, is largely based upon his views of the cervical suture of the crayfish which Dana long before (**'51**) showed to be untenable and which Ayers (**'85**) has more lately reviewed.

Upon the standpoint we have taken the cephalothorax of the Arachnids and Limulus must be regarded as equivalent to the combined head and thorax of the Hexapod. In the forms first mentioned we find no tendency towards a differentiation of this region except in the case of the Solpugids, a knowledge of whose embryology would prove so interesting. As the Solpugids are not primitive forms, and as no such regional divisions occur in the more ancestral types, we would rather suspect that the apparent existence of the Hexapod thorax in the group was secondary and adaptional rather than derived from a common ancestor. Thorell's view that the Solpugids are Hexapods is not tenable.

In this connection the multiarticulate character of the anterior appendages of both Limulus and the Arachnids is interesting. In the Hexapods and Myriapods the mandibles are at no time of either embryonic or adult life multiarticulate, a fact which would apparently indicate that this appendage had obtained its present form and function at an early period. It is, as Lang has suggested, hardly to be supposed that the well segmented corresponding appendage of the Arachnids has been derived from the specialized mandible of the Hexapods. The modification of the basal joints (coxa) of several appendages in both Limulus and scorpions for manducatory purposes should be alluded to here as well as the persistence of the same number — six — of articles in the legs of these animals.

It would hardly seem necessary to review in detail the arguments for the homology of the respiratory organs of

Limulus and the Arachnids were it not that the question is frequently misunderstood. The difficulty, at least in some instances, seems to lie in the failure to recognize the possibility of the tracheæ of the Hexapods and those of the Arachnids being homoplastic rather than homologous organs. Thus to these persons the attempt to derive the tracheæ of the Arachnid from the gill of some branchiate form seems to imply the promotion of the Arachnids to the position of the "Stammform" of the Tracheata, a conclusion which no one would care to defend at the present day.

There exists at present no question of the accuracy of the view of Leuckart ('49) that the lungs of the scorpions and spiders on the one hand and the tracheæ of the Araneina and other Arachnids are homologous, but these organs differ in one important respect from the tracheæ of the Hexapods which would prevent their close comparison. In the Hexapods (as also in the Chilopodous Myriapoda) the stigmata are placed outside or dorsal to the appendages and they never develop in connection with the legs. The observations of Chun ('75) followed by those of later writers would tend to show that the Hexapod tracheæ were derived from dermal[1] glands. In the Arachnids, observations are as yet lacking as to the ontogeny of the tracheæ, but several students have described the development of their homologues, the pulmonary organs.

The lungs of scorpions — Metschnikoff, ('71); Kowalevsky and Schulgin ('86) Laurie ('90) — and those of spiders — Bruce ('87); Locy ('86) — develop in connection with the abdominal feet in the embryo. The lung-leaves arise as outgrowths upon the posterior faces of these appendages, concomitantly with the formation of a pit behind the appendage and the sinking of the appendage itself. In this it is, making allowance for the position of the organ — freely projecting in the one, sunken in the other — closely comparable to the gills of Limulus, and in the later stages, the resemblance extends to the minute histological details.

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[1] The recent speculations of Bernard ('92, '93) in which the endeavor is made to trace all tracheæ — Hexapod and Arachnid — to the setiparous glands of the Chætopods should possibly be referred to here.

Between the lungs of the scorpion and the gills of Limulus the resemblances are closest. In Limulus the gills are borne on appendages VIII–XII, in the scorpion upon appendages IX–XII and in no Arachnid do tracheæ occur behind this point.[1] Farther, appendage VIII in the scorpion — the pecten — shows plainly its homologies with its homologue in Limulus, the teeth of the comb being the gill-leaves. This is exactly what we should expect upon our hypothesis, for the scorpions, where the resemblances are closest, are admitted by all to be the most primitive of the Arachnids and which naturally should possess the most ancestral type of respiratory organs. The other view, that the lungs are modified tracheæ,[2] leads into considerable difficulties for we then find the oldest stock, — the Stammform of the Arachnida — possessing the most highly differentiated organs of breathing, while in the most aberrant groups the tracheæ have been retained in an unmodified condition. Again the Arachnida as a class, according to the observations of Plateau (**'86**) and Berteaux (**'90**), show an entire absence of those visible respiratory movements of the body wall which are so characteristic of Hexapods and Chilopods, a fact in full accordance with the thesis here maintained but not easily explained upon the standpoint of a common origin of all Arthropod tracheæ.

Farther, the conversion of the gills directly into tracheal tubes is at present going on in the case of the Oniscid Crustacea where we have tubes lined with a chitinous intima penetrating to the interior of the organ and conveying air to the blood.

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[1] Bernard claims (**'93**) to have found traces of stigmata in the Pseudoscorpions behind this point, but apparently his discovery is not a new one for von Siebold pointed out, over forty years ago (**'53**, p. 370) that Bernard's predecessors had also mistaken the cutaneous insertion of muscles for stigmata.

[2] This view is held by Sinclair (**'92**) who seems to ignore the possibility of there being two kinds of tracheæ; and, influenced by his observations upon the peculiar dorsal tracheæ of Scutigera, states his opinion "that we have a series from the simple tracheæ found in Peripatus up to the complete lungs of spiders which is incapable of explanation in the present state of our knowledge, except as representing the stages of development of tracheæ into the pulmonary organ of spiders." A few lines lower he seems to think that the derivation of the lungs of scorpions from gills implies a difference between spiders and scorpions greater than has been supposed.

Cases like this clearly show us that tracheæ may arise in different ways from different sources.

The presence of the so-called spiral thread in the tracheæ of both Arachnids and Hexapods has been adduced as an argument in favor of the homology of the organs in both groups. As in both cases the tracheæ are formed as invaginations of the external integument it is natural that they should consist of tubules of ectoderm lined with a chitinous intima, and the thinner this intima the easier the transfer of gases through it. But if it become too thin the tube is liable to total collapse by the pressure of the various viscera upon it and so the chitinous layer is developed into folds or corrugations, which when regularly arranged form the spiral "threads." In many spiders they are not regular and show clearly their origin in response to the mechanical conditions presented.

The greatest difficulty in connection with this view of the origin of tracheæ from gills through the lungs is that presented by the Solpugids and certain Acarina where tracheal stigmata occur in the cephalothoracic region, where they should not occur according to our thesis. Yet until we know more of the structure and ontogeny of these organs the full weight of this objection cannot be properly estimated. A full history of Solpuga would settle many questions of arthropod morphology.

To summarize: The lungs of the scorpion arise in the same way and on the same somites as the gills of Limulus. In the one they sink into a pit, in the other they remain free. The homologies between the lungs and tracheæ of Arachnida were demonstrated by Leuckart. Hence the lungs, the fan tracheæ of authors, are to be regarded as the primitive, the bush-like the derived form, and these tracheæ have no relation to those of Hexapods.

The comparisons between the nephridia of Limulus and those of the Arachnida have been made upon a previous page. The observations made by Laurie, Kishinouye, and myself have clearly shown that we have to deal here with structures homologous with the nephridia of the worms, although but a single pair may persist in its unmodified condition. We find, however, nephridia occurring either in the young or the adult of other Arthropods, and hence a more accurate review of our knowledge becomes necessary. In Peripatus the investigations of von Kennell ('84), and especially of Sedgwick ('88), have shown that in each somite, except the posterior one, the cœlom on either side divides into dorsal, lateral and ventral moities; the dorsal becomes converted into the gonad, while the ventral portion becomes converted one part into the nephridium and the lateral into the funnel and end sac. The connection between the dorsal and ventral portions of the cœlom persists in the posterior somite, and from the cavity thus formed the genital ducts are developed, in other words, the posterior nephridia of Peripatus become modified for reproductive ducts. In the Hexapods Heymons ('90), Graber and Cholodkowsky ('91)[1] have described a similar division of the cœlom into three portions, the gonad developing in connection with the dorsal portion; the formation of genital ducts, much as in Peripatus; and the development of the third division into a temporary structure to be regarded as the homologue of the nephridium of Peripatus, and which later disappears. In the Crustacea nephridial structures also occur. Our knowledge of them and of their relations to the cœlom are most detailed in Decapod. Here Weldon ('89, '91) has described a large cœlomic dorsal sac, extending back to the heart and the gonads and connected ventrally with the green (antennal) gland, the character of which as a nephridium is thus placed beyond question.[2] The position of the so-called "shell gland" is less certain, though all evidence goes to show that this is also to be regarded nephridial. As I pointed out several years ago this organ, opening in the Crustacea at the base of the second maxilla is apparently exactly homologous with the coxal gland of Limulus. Although recent researches (*vide supra*) have changed our views

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[1] There is not full agreement between these authors as to the details of the process.

[2] Both Grobben ('79) and myself ('89) have shown that the green gland of the decapod is mesodermal. Richenbach in his first paper upon Astacus ('77) stated that it was derived from the ectoderm. Although he was corrected in this by Grobben he reiterates his account in his later paper on the crayfish ('86) and ignores Grobben's correction.

of the somites of the Arthropods, still if the metastoma be admitted as an appendage in the Crustacea, the correspondence between the opening of the duct of their shell gland and that of the coxal gland is exact. Another fact which goes to show that the shell gland is nephridial is, that it and the antennæ gland but rarely coexist in the same individual (Nebalia, Claus).

From the evidence presented by the nephridia therefore, we are justified in the close association of the Arachnids and the Xiphosures. We are also apparently led to associate these two groups more closely with the Crustacea than with the Hexapods.

The correspondence between the genital ducts of Limulus and those of the Scorpion is as close as that of the respiratory organs. In Limulus the genital ducts in both sexes open upon the posterior surface of appendage VII. In the scorpions Narayanan ('89) has shown that the genital operculum is a paired organ in both sexes and that the genital ducts open up on what is morphologically its posterior surface. Farther, Laurie's observations upon the development of the ducts show beyond a question that they belong to somite VII. In Limulus I have failed to see the development of the duct, it being apparently delayed even longer than in the scorpion.

There is to-day little doubt that the genital ducts of all Arthropods are to be regarded as modified nephridia. I have alluded, just above to the method of development of these structures in the Hexapods and in Peripatus. In the scorpion Laurie's account of their development would indicate that here, too, they are to be classed in the same category, the later appearance of their external opening being the greatest objection to such a view.

In the Crustacea we have, so far as I am aware, no direct observations upon the ontogeny of the ducts, but the facts of comparative anatomy are all but conclusive. Thus the relations of the gonads to the persistent cœlom are such as would be required were the ducts segmental organs, while the varying position of the ducts themselves in the two sexes of the same species and the fact that in abnormal instances two pairs of ducts may occur in the same individual, show that they must have been derived from some metameric structure connecting the cœlom with the exterior, and the nephridia of the annelids are the most probable if not the only ducts which answer the conditions.

Limulus, the Arachnids, the Crustacea and the Chilognaths agree in having the genital ducts some little distance in advance of the posterior end of the body while in the Hexapods and Chilopods they are sub-terminal, but how much weight is to be given this point is not yet apparent.

The reticulate and anastomosing character of the genital ducts in Limulus and the Arachnids has been commented upon by Lankester. Such conditions are not paralled in the Arthropods except in certain Phyllopods. Again the existence of motile spermatozoa in both Limulus and Arachnids and their absence from all Crustacea except the Cirripedia has a certain value as cumulative evidence.

The correspondences between the circulatory systems of Limulus and the scorpions are remarkably close. In both there is the same median anterior aorta which divides and passes downward, as a pair of sternal arteries — one passing on either side of the œsophagus — which unite below in a ventral vessel in close connection with the ventral nerve chain. In the scorpions this ventral vessel consists of an artery[1] lying *upon* the nervous system, and following not only the ventral cord but the various metameric nerves which arise from it. This condition, which is characteristic of the adult scorpion is found in the earlier stages of Limulus. Later the neural artery completely envelopes the ventral cord and its nerves in the manner first pointed out by Owen ('55, p. 310) and later so elaborately described by the younger Milne-Edwards ('72).

This relation between the neural artery and the ventral nerve chain is not confined to the Arachnids and Limulus; a large supra-neural vessel occurs in the Isopods and a smaller one in the Amphipods, each connected with the dorsal vessel

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[1] Houssay ('87) claims that this vessel in the scorpion is lacunar rather than arterial, a view which is negatived by its well-marked walls and its lack of connection with the other extra-vascular spaces of the body.

by similar paired sternal arteries. A similar supra-neural vessel was described long ago by Newport (**'43**) in several Myriapods. The supra-neural vessel of the Chætopods will naturally suggest itself in this connection. In the Hexapods, on the other hand, the sternal arteries and the neural artery have disappeared, possibly as a result of their richly developed tracheal system. In Peripatus also no supra-neural vessel is found, the ventral vessel first described by Balfour (**'83**) lying in the body wall and the "blood spaces" shown in Sedgwick's monograph lying near the ventral cord, are lacunar rather than arterial.

The alimentary canal of Limulus and the Arachnids agrees in the fact that nearly the whole tract is composed of stomodæum and mesenteron while the late appearing proctodæum is short. They also agree in the metameric nature of the lobulation of the hepatopancreas, the lobes being at first outlined by the ingrowth of the mesodermic septa into the yolk. In the Hexapods on the other hand the proctodæum appears much earlier and is comparatively long, at least equalling the stomodæum in this respect. In the Crustacea on the other hand the mesenteron plays but an inconspicuous part in the formation of the digestive tube, it being mostly restricted to the so-called liver.

The possession of an entosternite which characterizes both Limulus and the Arachnids, the structure and relationships of which has already been discussed by Lankester (**'84**) is only paralleled outside these forms in a few Crustacea (certain Ostracodes, Claus, **'92**).

The argument for the association of Limulus with the Crustacea and its separation from the Arachnids, based upon the possession of biramous appendages, has been accorded more weight than seems justifiable. At no stage of development do we find a biramous condition in the cephalothoracic appendages of Limulus, while that of the abdominal appendages may prove to be far different from that of the Crustacea. It appears much later than in the Crustacea, is characterized by a hypertrophy of the exopodite, and lacks the evident segmentation found in most Crustacea.

On the other hand, we must not lose sight of the fact that numerous observers have recorded a biramous condition in the appendages of various "Tracheates." Among others we would mention the biramous pedipalps in Dendryphantes recorded by Croneberg ('80), the biflagellate antenna of an Indian Lepisma, and of an embryo *Blatta javanica* by Wood Mason ('79), the bifid condition of the antenna of Blatta by Wheeler ('89), while Patten ('84), in the same form describes the maxillæ and labium as "formed respectively of two and three branches, the second maxillæ thus attaining the typical trichotomous structure of the Crustacean appendages." Neither must we forget the peculiar antennæ of the Pauropida in this connection.

The so-called Malpighian tubes (point 3.) have a far different bearing upon the classification of the Arthropods from that which they were supposed to have a few years ago. In fact, two entirely different structures have been included under the one name, and the existence of excretory tubules in both Hexapods and Arachnids, instead of proving the close relationship of the two groups, is, in view of our present knowledge, an argument against it. In the Hexapods these organs have been shown by numerous observers to be of proctodeal, and, therefore, of ectodermal origin. In the Arachnida the supposed homologous organs, to which the same name has been given, are, in all probability, outgrowths from the mesenteron, and hence entodermal. This has been shown by Loman ('86-7) for both the tetra- and the dipneumonous Araneina, and by Laurie ('90) for the scorpion.[1] Hence these organs, — ectodermal in the one group, entodermal in the other — instead of indicating community of descent for Arachnids and Hexapods, must rather be regarded as indicating that the group Tracheata as usually limited is polyphyletic in origin.

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[1] Kishenouye ('90) claims that in the Araneina both the Malpighian tubules and the stercoral pocket are derivatives of the mesoderm, the cavity of the latter being the cœlom of that region of the body. This is on its face improbable. It would seem that the failure of many investigators to recognize that these tubules are entodermal in origin was due to the fact that since they were known to be ectodermal in the Hexapods, they have been used as regional tests, the fact that they arose from a certain part of the alimentary canal being sufficient reason for regarding that portion as proctodeal. Beddard's view ('89) that the Malpighian tubes are derived from nephridia secures no support in the Arachnida.

Again, as I previously argued, the existence of similarly placed tubules in certain Amphipods can be advanced as an argument for the closer association of the Arachnids and the Crustacea. Still exact knowledge of these tubules in the Amphipoda is lacking. Nebeski ('80) regards them as diverticula of the hind-gut, while Spencer ('85), upon histological grounds, regards them as outgrowths of the mesenteron and hence, like those of the Arachnids, entodermal. It must be said, however, that this evidence is not conclusive, as the limits of the hind-gut are not clearly ascertained, and the assumption that these are entodermal is based upon the absence of a chitinous cuticule (Spencer, '85, Pl. XIII, Fig. 2) and by a break in the character of the epithelium in the alimentary canal at the point of origin of these tubes, the tubes themselves apparently belonging to the anterior portion.

All, then, that can be argued from the various structures known as Malpighian tubules is that homoplastic and analogous organs, rather than exact homologues, are included under this name ; that their existence in both Arachnids and Hexapods is an argument against the close association of these forms and that their absence in Limulus can only be used as a negative argument of little weight. In this connection the conditions figured on Pl. XIII, Fig. 88, deserve more detailed study in later stages.

The presence of salivary glands in the "Tracheates" and their absence from the "Branchiates" (Crustacea, Limulus) is possibly to be explained by the different method of life of the members of the two groups — aquatic in the latter, terrestrial in the former. It is, however, to be noted that salivary glands have been recognized in Astacus (Lang, '89, p. 344), while renewed studies must be made of the so-called salivary glands of the Arachnida before we are certain of their homology with those of the Hexapods. Several organs which have been called salivary glands among the spiders and their allies have been shown to be coxal glands (*i.e.* nephridia) or poison glands, and it is possible that all of these organs may have different homologies than those indicated by the name usually applied to them.

There is one point of resemblance between the Arachnids and the Hexapods which may have no inconsiderable weight. In the Scorpions as in the Hexapods, the embryo develops those as yet unexplained fœtal membranes which so closely simulate those of the higher vertebrates. It may be that here, as in other places, we have similar but not identical organs. The accounts of their development in the Arachnids by Metschnikoff, Kowalevsky and Schulgin, and Laurie differ considerably, and until we know something of the ancestry and real meaning of the structures which are united under this head we cannot be certain of the taxonomic value to be placed upon them. It may be noted here that the structures described by Bruce (**'87**) as occurring in the spiders are in all probability not amnion and serosa, but either the invaginations in connection with the brain or the inpushing to form the median eye.

THE CLASSIFICATION OF THE ARTHROPODA.

As a result of my studies it would seem as if the Arthropoda must be divided in some such manner as that here given :—

Phylum Arthropoda.
  Sub-Phylum Branchiata.
    Class Crustacea.
    Class Acerata.
      Sub-Class Gigantostraca.
      Sub-Class Arachnida.[1]
  Sub-Phylum Insecta.
    Class Hexapoda.
    Class Chilopoda.
  Sub-Phylum Diplopoda (Chilognatha).

Incertæ Sedes.

Pauropoda.
Pycnogonida.
Trilobitæ.
Tardigrada.
Malacopoda.

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[1] The attempt by Haller (**'81**) to separate the Acarina as a distinct class hardly seems warranted.

While the present is not the proper opportunity to support the above classification in detail, a slight amount of explanation seems necessary with regard to some of the novelties introduced above.

It has been shown, I think conclusively, that the relationship existing between the Arachnida and the Xiphosures is very close ; that they have more affinities with each other than, on the one side, the Arachnida have with the other "Tracheates," or than Limulus has, on the other hand, to the Crustacea. For the class formed by the union of these forms I proposed, eight years ago, the name Acerata,[1] a modification of the term Acera applied by Latreille to the Arachnida alone. For the sub-class containing the Xiphosures and the Eurypterina I have followed Dohrn in modifying and adopting the term Gigantostraca of Haeckel. For essentially the same group Packard has proposed at different times the names Palæocarida and Podostomata, while Steinmann and Döderlein (Elemente der Paläontologie) have applied to the same association of forms the term Palæostraca.

The resemblances between the Acerata and the Crustacea are much closer than those between either and any of the other groups of Arthropods, and from the fact that in each respiration is effected by gills or by their homologues, developed in all cases as membranous expansions of the limbs, the older term Branchiata, used with enlarged scope, seems most applicable to the group or sub-phylum formed by their union.

The so-called Myriapoda seems to be a heterogeneous association of forms, polyphyletic in origin, and only associated together through the possession of many locomotor appendages. On the other hand, the resemblances between the Chilopods and the Hexapods are far more numerous and of far more sig-

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[1] Since this use of the term Acerata Lankester has employed it ('90) as equivalent to the term Branchiata as limited in this article. Cholodkowsky ('91) objects to my group Acerata apparently more upon the inapplicability of the term than from any objection to the association of the Arachnids with the Xiphosures. As I think I have strengthened the ground for such union in the present article a name for the group becomes necessary, and as in both the Xiphosures and the Arachnids functional (if not morphological) antennæ are entirely lacking, I may be permitted to continue the use of the term.

nificance than those between Chilopods and Diplopods (Chilognaths). This was pointed out some years ago by Mr. Pocock (**'87**), of the British Museum, while I, independently (**'88**), stated similar conclusions.

Until we know more of both the structure and the ontogeny of the Myriapod forms the correctness of this view cannot be regarded as settled, but in the present state of our knowledge the following facts seem important:

The Diplopod head bears, besides the antennæ, but two pairs of appendages, — a pair of mandibles and a lower lip, composed of a pair of coalesced maxillæ.[1] In the Chilopod the conditions are as in the Hexapod, two pairs of maxillæ being present.

In the Chilopods as in the Hexapods, each somite bears a single pair of appendages, while in the Diplopods the majority of the segments bear two pairs of appendages, and the researches of Heathcote show that each segment is in reality composed of two coalesced somites, a condition without parallel elsewhere in the Arthropoda. In the Chilopods there is a wide sternum separating the coxæ of the ambulatory appendages ; in the Diplopods the coxæ are approximate, and the sternum is exceedingly narrow, or even entirely absent.

In the Chilopods the stigmata, a pair to a somite, are lateral (dorsal in Scutigera), and are placed above and outside the insertion of the limbs, exactly as in the Hexapods. The tracheæ which arise from them are branched, and the intima is thrown into a well developed spiral thickening as in the six-footed insects. In the Diplopoda, on the other hand, the stigmata are beneath or even in the coxæ, while the tracheæ (except in the Glomeridæ) are tufted and unbranched, and the thickening of the intima is poorly developed.

In the Diplopods there are well developed foramina repugnatoria upon the sides of each somite of the body. Such

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[1] The attempt made to show that this lower lip is a "gnathochilarium" composed of the two coalesced lower jaws, or first and second maxillæ of the Chilognaths receives no support from the embryology of Julus (Heathcote **'88**), where there is but a single somite when the hypothesis calls for two. Further the innervation of the sense organs of the lower lip (*cf.* vom Rath. **'86**, Pl. XX, Fig. 1) shows that but a single pair of appendages is concerned in the part.

structures are absent from the Chilopods (as from the Hexapods), except in a few Geophilidæ, where repugnatorial glands occur, opening by foramina in the mid-ventral line.

In the Chilopods the reproductive organs consist of paired[1] gonads situated above the alimentary canal and opening to the exterior by ducts which are at first paired, but which later unite into a common tube which leads to a single external opening situated in the penultimate segment of the body. In the Hexapods the conditions are almost exactly the same; the gonads are dorsal, the genital ducts unite (except in Ephemeridæ), and there is a single external opening, always at the posterior end of the abdomen. In both Hexapods and Chilopods the spermatozoa are motile. In the Diplopods there is a single unpaired gonad situated beneath the alimentary canal, and the genital duct, passing forward, divides into two, each of which has its own opening at the bases of the legs of the second post cephalic segment. The spermatozoa are quiescent.

We know so little of the embryology of the Myriapods that the aid of development can be had to only a slight extent in our comparisons, but the facts which it affords seem important. In the Chilopods the embryo escapes from the egg with numerous ambulatory appendages, a pair to each somite. The same is true of the typical Hexapods, all later observers agreeing that a polypod precedes a hexapod condition. The young Diplopod escapes from the egg in a hexapod condition, and the presence of these six legs has been seized upon as a proof of the near association of these forms. An exact comparison, however, seems to show that the two are in reality very unlike as appears in the following table.[2]

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[1] Single in Scolopendra.

[2] As nothing is known of the existence of a tritocerebral segment in the Diplopods, the comparison can only be made upon the basis of the appendages of the adult. If the tritocerebral segment should prove lacking in the millepeds the contrast will prove stronger than it now is. The statement of the Diplopod appendages is based upon Heathcote (**'88**).

	Hexapod.		Diplopod.	
Appendage I	Antenna	Head	Antenna	Head
" II	Mandible		Mandible	
" III	Maxilla 1		Lower Lip	
" IV	Maxilla 2		Foot 1	
" V	Thoracic Foot 1	Thorax	Absent	
" VI	Thoracic Foot 2		Foot 2	
" VII	Thoracic Foot 3		Foot 3	
" VIII	Abdominal Foot 1		Absent	
" IX	Abdominal Foot 2		Absent	

The result of these comparisons is sufficient, I think, to justify the dismemberment of the old group Myriapoda and the association of the Chilopoda with the Hexapoda in a group to which the much abused term Insecta may be applied, while, until more definite knowledge be obtained, the Diplopoda must be allowed to stand alone. The position of the Pauropoda is as yet very uncertain as we are almost entirely ignorant of their internal structure. In the tendency towards a fusion of somites, in the lack of a second pair of maxillæ, and in the positions of the external paired openings of the genital ducts at the base of the second pair of ambulatory appendages they show undoubted affinities with the Diplopoda; but the peculiar triramous antennæ and especially the characters of the hexapod young (if Ryder's (**79**) figure of the young of Eurypauropus be correct) militate against this view.

The Malacopoda[1] (Peripatus) are also frequently placed in close association with the Myriapods, but it may be that their status as members of the Arthropod phylum is not beyond question. In the following points they differ from all "Tracheates" and also from all Arthropods, while in just these same points they show affinities with the Annelids: —

The presence of functional nephridia in each body segment; the presence of well developed coxal glands (*cf.* setiparous glands of Annelids); the existence of an outer circular muscular

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[1] Malacopoda, Blanchard 1847; Onychophora, Grube 1853; Protracheata, Moseley 1874.

layer in the body wall; the absence of striation from all muscles except those of the mouth parts; the presence of cilia in the alimentary canal and in the nephridia; the situation of the antennæ as outgrowths from the primitively preoral region (*cf. supra* p. 232); the muscular nature of the pharynx, unlike that of any Arthropod and strikingly like that of certain Chætopods. The eyes too are unlike the visual organs of any other Arthropod but as figured by Balfour they closely resemble these organs in Autolytus. It is noticeable that Balfour has described (**'83**) a pair of problematical organs upon the lower surface of the brain of *P. capensis* (the auditory organs of Grube, **'53**). Sedgwick has shown that these organs are developed by an invagination of the cerebral surface while the slight account given by Balfour of the adult structure at once suggests a degenerate eye formed upon the same plan as the functional one. In Autolytid worms a second pair of eyes occur at the same point.

On the other hand the Arthropod structures are not to be ignored; the tracheæ; the appendicular jaws; the setting aside of a pair of nephridia for genital ducts; the heart, with several paired ostia, enclosed in a pericardium; the lacunar circulation, and the reduced cœlom.

To the discussion of the position of the Pycnogonids and the Tardigrades I can add nothing. Morgan (**'90**) has, it seems, shown that the Pycnogonids present certain features both in ontogeny and in adult structure which can only be paralleled in the Arachnids, while the Tardigrades may have no other claim upon a position in the same group than that afforded by their eight ambulatory feet.

For many years the general consensus of opinion has been to the effect that the Trilobites are closely related to the Xiphosures. We unfortunately know but little regarding the structure of the Trilobites aside from the features presented by the dorsal surface. For our knowledge of the appendages we have to thank the papers of Billings (**'70**) and Walcott (**'81** and **'84**). From Billings' paper (and from electrotypes of his specimens which I have studied) we can learn but little except the presence of jointed appendages. Walcott's researches tell much more, but the facts which they have added all are opposed to the close association of the Trilobites with Limulus. The body of Limulus, it must be remembered, possesses an anterior cephalothorax bearing six pairs of circumoral chelate appendages without differentiation into exopodite and endopodite,[1] and with no trace of gills. In the Trilobite but *four* pairs of appendages occur in this region. Hence, if the "head" of the Trilobite is to be compared with the cephalothorax of Limulus we must assume — for which we have as yet no evidence — that two pairs of appendages have been lost from the Trilobite. The abdomen of Limulus bears six pairs of broad leaf-like appendages, the posterior five pairs having lamillate gill books upon the posterior surface. In the corresponding region of the Trilobite, the thorax, we have an indefinite number of somites, each of which bears the *typical Crustacean foot,* consisting of basiopodite, exopodite, and endopodite, and, outside the exopodite, occupying the same position as the gill in the Decapod, a straight or curiously coiled structure interpreted by Walcott as the gill. In the horseshoe crab the abdominal region extends to the anus, behind which comes the non-segmental tail. In the Trilobites the thorax is followed by a segmented pygidium on which the series of appendages[2] is continued to the end, and there is no evidence of a supra-anal telson.

The necessary conclusion is that *the appendages of the Trilobite vary in number and differ totally in structure from those of Limulus,* and the association of the Trilobites with the Xiphosura is not warranted by our present state of knowledge. The trilobites would appear to be true Crustacea, the sessile eyes and general shape of the body allying them to the Isopods,

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[1] The flabellum of the sixth appendage cannot be considered as a representative of the expodite since it develops later than the rest of the limb, develops independently of it and only in the later embryonic stages does the base of the leg enlarge so that it is included.

[2] Walcott continues the series of ambulatory appendages through this region, but Professor Mickleborough (**'83**), who found the specimen forming the basis of Walcott's second paper (**'84**), thinks that these pygidial appendages were lamellar. Henry Woodward (**'70**) describes what he considers as the jointed palpus of one of the "maxillæ" of Asaphus with seven articulations beyond the basal joint.

while the biramous appendage and the epipodial gills would rather indicate relationships between the Phyllopods and the lower Podophthalmia. It will prove a profitable field for some student of Arthropod morphology to repeat Walcott's earlier investigations. It will be noticed that I place the grounds for rejection of the association of Limulus and the Trilobites upon different grounds from those advanced by Owen (**'72**, pp. 491–493) and the older Milne Edwards (**'81**).

Tufts College, Mass.,
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BIBLIOGRAPHY.

'85 Ayers, H. On the carapax and sternum of Decapod Crustacea. *Bull. Essex Inst.*, xvii. 1885.

'80 Balfour, F. M. Notes on the development of the Araneina. *Quart. Jour. Micr. Sci.*, xx. 1880.

'83 Balfour, F. M. The anatomy and development of Peripatus capensis. *Quart. Jour. Micr. Sci.*, xxiii. 1883.

'71 Van Beneden, Edouard. [No title.] *Comptes Rendus Soc. Ent. Belg.*, p. ix. 1871.

'89 Beddard, F. E. On the possible origin of the Malpighian tubules in the Arthropods. *Annals and Mag. Nat. Hist.*, iv. 1889.

'83 Benham, W. B. S. Description of the muscular and endoskeletal systems of Limulus. *Trans. Linn. Socy.*, xi. 1883.

'92 Bernard, H. M. An endeavor to show that the tracheæ of the Arthropoda arose from setiparous sacs. *Zoolog. Jahrbücher, Abth. f. Anat.*, v. 1892.

'93 Bernard, H. M. Additional notes on the origin of tracheæ from setiparous glands. *Annals and Mag. Nat. Hist.*, xi. 1893.

'90 Berteaux, L. Le poumon des Arachnides. *La Cellule*, v. 1890.

'70 Billings, E. Notes on some specimens of lower Silurian Trilobites. *Quar. Jour. Geol. Socy.*, xxvi. 1870.

'92 Birula, A. Beiträge zur Kenntniss des anatomischen Baues der Geschlechtsorgane bei den Galeodiden. *Biol. Centralbl.*, xii. 1892.

'85 Brooks, W. K. and Bruce, A. T. Abstract of researches on the embryology of Limulus polyphemus. *Johns Hopkins Circ.*, v. 1885.

'87 Bruce, A. T. Observations on the embryology of Insects and Arachnids. Baltimore, 1887.

'91 Bumpus, H. C. The embryology of the American lobster. *Jour. of Morph.*, v. 1891.

'90 Carrière, J. Die Entwicklung der Mauerbiene (Chalicodoma muraria). *Arch. f. mikr. Anat.*, xxxv. 1890.

'75 Chun, C. Bau, Entwicklung und physiologische Bedeutung der Rectaldrüsen bei den Insekten. *Abh. Senkenb. Gesell. Frankfurt*, x. 1875.

'91 Cholodkowsky, N. Die Embryonalentwicklung von Phyllodromia (Blatta) germanica. *Mem. Acad. St. Petersburg*, VII, xxxviii. 1891.

'87 Claus, C. Prof. E. Ray Lankester's Artikel "Limulus an Arachnid" und die auf denselben gegründeten Prätensionen und Anschuldigungen. *Arb. zool. Inst. Wien*, vii. 1887.

'92 Claus, C. Beiträge zur Kenntniss der süsswasser Ostracoden. *Arb. zool. Inst. Wien*, x. 1892.

'80 Croneberg, A. Ueber die Mundtheile der Arachniden. *Arch. f. Naturgesch.*, xlvi. 1880.

'52 Dana, J. D. Crustacea of the U. S. Exploring Expedition, Part I. Philadelphia, 1852.

'87 Eisig, H. Die Capitelliden des Golfes von Neapel. *Fauna u. Fl. Golfes Neapel*, xiv. 1887.

'88 Faussek, V. Entwicklung der Geschlechtsorgane bei Phalangium. *Biol. Cblt.*, viii. 1888.

'91 Faussek, V. Zur Embryologie von Phalangium. *Zool. Anz.*, xiv. 1891.

'79 Grobben, C. Die Entwicklungsgeschichte der Moina. *Arb. zool. Inst., Wien*, ii. 1879.

'53 Grübe, E. Ueber den Bau von Peripatus edwardsii. *Müller's Archiv.* 1853.

'85 Gulland, G. L. Evidence in favor of the view that the coxal gland of Limulus and other Arachnids is a modified nephridium. *Quar. Jour. Micr. Sci.*, xxv. 1885.

'81 Haller, G. Die Mundtheile und systematische Stellung der Milben. *Zool. Anz.*, iv. 1881.

'88 Heathcote, F. G. The postembryonic development of Julus terrestris. *Phil. Trans.*, 179 B. 1888.

'89 Heider, K. Die Embryonalentwicklung von Hydrophilus. Jena. 1889.

'82 Henking, H. Beiträge zur Anatomie, Entwicklungsgeschichte und Biologie von Trombidium. *Zeitschr. f. wiss. zool.*, xxxvii. 1882.

'92 Herrick, F. H. Alpheus: a study in the development of Crustacea. *Memoirs National Acad. Sci.*, v. 1892.

'90 Heymons, R. Ueber die hermaphroditische Anlage der Sexualdrüsen beim Männchen von Phyllodromia (Blatta). *Zool. Anz.*, xiii. 1890.

'87 Houssay, F. Sur la lacune sanguine perinerveuse chez les scorpions. *C. R.*, civ. 1887.

'91 Jaworowski, A. Ueber die Extremitäten bei den Embryonen der Arachniden und Insecten. *Zool. Anz.*, xiv. 1891.

'92 Jaworowsky, A. Ueber die Extremitäten, deren Drüsen und Kopfsegmentierung bei Trochesa singoriensis. *Zool. Anz.*, xv. 1892.

'84 von Kennel, J. Entwicklungsgeschichte von Peripatus. *Arb. zool. zoot. Inst., Würzburg*, vii. 1884.

'85 Kingsley, J. S. Notes on the embryology of Limulus. *Quar. Jour. Micros. Sci.*, xxv. 1885.

'88 Kingsley, J. S. The classification of the Myriapods. *Am. Naturalist*, xxii. 1888.

'89 Kingsley, J. S. The development of Crangon vulgaris, III. *Bull. Essex. Inst.*, xxi. 1889.

'90 Kingsley, J. S. The ontogeny of Limulus. *Am. Naturalist*, xxiv and *Zool. Anz.*, xiii. 1890.

'92 Kingsley, J. S. The embryology of Limulus. *Jour. Morphol.*, vii. 1892.

'90 Kishinouye, K. On the development of the Araneina. *Jour. Coll. Science, Univ. of Japan*, iv. 1890.

'91 Kishinouye, K. On the development of Limulus longispina. *Jour. Coll. Sci., Univ. Japan*, v. 1891.

'86 Kowalevsky, A. and Schulgin, M. Zur Entwicklungsgeschichte des Skorpions. *Biol. Cblt.*, vi. 1886.

'92 Korschelt, E. and Heider, K. Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere. Zweites Heft. Jena. 1892.

'89 Lang, A. Lehrbuch der vergleichenden Anatomie. Zweite Abth. Jena, 1889.

'81 Lankester, E. R. Limulus an Arachnid. *Q. J. M. S.*, xxi. 1881.

'82 Lankester, E. R. On the coxal glands of Scorpio hitherto undescribed and corresponding to the brick-red glands of Limulus. *Proc. Royal Socy.*, xxiv. 1882.

'84 Lankester, E. R. On the skeleto-trophic tissues and coxal glands of Limulus, Scorpio and Mygale. *Q. J. M. S.*, xxiv. 1884.

'85 Lankester, E. R. A new hypothesis as to the relationship of the lung-book of Scorpio to the gill-book of Limulus. *Q. J. M. S.*, xxv. 1885.

'90 Lankester, E. R. Article "Zoology." Encyc. Brit., 9th edit., Vol. xxiv.

'90 Laurie, M. The embryology of a scorpion. *Q. J. M. S.*, xxxi. 1890.

'91 Laurie, M. Some points in the development of Scorpio fulvipes. *Q. J. M. S.*, xxxii. 1891.

'92 Laurie, M. On the development of the lung-books of Scorpio fulvipes. *Zool. Anz.*, xv. 1892.

'49 Leuckart, R. Ueber den Bau und die Bedeutung der sog. Lungen bei den Arachniden. *Zeitschr. f. wiss. Zool.* 1849.

'89 Leydig, F. Ueber Argulus foliaceus. *Arch. f. mikr. Anat.*, xxxiii. 1889.

'92 Lebedinsky, J. Die Entwicklung der Coxaldrüsen bei Phalangium. *Zool. Anz.*, xv. 1892.

'86 Locy, W. A. Observations on the development of Agelena nævia. *Bull. Mus. Comp. Zool.*, xii. 1886.

'87 Loman, J. C. C. Altes und Neues über das Nephridium (die Coxaldrüse) der Arachniden. *Bijdr. tot Dierkunde N. A. M.* 14. afl.

'86–'87 Loman, J. C. C. Ueber die morphologische Bedeutung der sog. malpighi'schen Gefässe der echten Spinnen. *Tijdsch. nederl. Dierk. Vereen*, II, i. 1886–1887.

'84 MacLeod, J. Recherches sur la structure et la signification de l'appareil respiratoire des Arachnides. *Arch. Biol.*, v. 1884.

'84a MacLeod, J. Sur l'existence d'une glande coxale chez les Phalangides. *Bull. Acad. Belg.*, III, viii. 1884.

'92 Marchel, Paul. The coxal gland of the scorpion and its morphological relations with the excretory organs of the Crustacea. *Ann. and Mag. Nat. Hist.*, x. 1892 from *C. R.*, cxv. 1892.

'71 METSCHNIKOFF, E. Embryologie des Scorpions. *Zeitschr. f. wiss. Zool.*, xxi. 1871.

'83 MICKLEBOROUGH, J. Locomotive appendages of Trilobites. *Am. Nat.*, xvii, 1883. From *Jour. Cincinnati N. H. Socy.*

'72 MILNE-EDWARDS, H. Recherches sur l'anatomie des Limulus. *Ann. Sci. Nat.*, V, xvii. 1872. Also Miss. Sci. Mex. 1873.

'81 MILNE-EDWARDS, H. Compte rendu des nouvelles recherches de M. Walcott relatives à la structure des Trilobites. *Ann. Sci. Nat.*, VI, xii. 1881.

'91 MORGAN, T. H. A Contribution to the embryology and phylogeny of the Pycnogonids. *Studies Biol. Lab. Johns Hopkins Univ.*, v. 1891.

'87 MORIN, I. Zur Entwicklungsgeschichte der Spinnen. *Biol. Cblt.*, vi. 1887.

'74 MOSELEY, H. N. On the structure and development of Peripatus capensis. *Phil. Trans.*, clxiv. 1874.

'89 NARAYANAN, M. Notes on the anatomy of scorpions. *Q. J. M. S.*, xxx. 1889.

'80 NEBESKI, O. Beiträge zur Kenntniss der Amphipoden der Adria. *Arb. Zool. Inst. Wien*, iii. 1880.

'43 NEWPORT, G. The nervous and circulatory systems in Myriapoda and in macrurous Arachnida. *Phil. Trans.* 1843.

'55 OWEN, R. Lectures on the Invertebrata. Second edition. London. 1855.

'72 OWEN, R. On the anatomy of the American king-crab. *Trans. Linn. Socy.*, xxviii. 1872.

'75 PACKARD, A. S. As an undescribed organ in Limulus, supposed to be renal in its nature. *Am. Nat.*, ix. 1873.

'80 PACKARD, A. S. The anatomy, histology, and embryology of Limulus polyphemus. *Anniv. Mem. Bost. Socy. N. H.* 1880.

'84 PATTEN, W. The development of Phryganids. *Q. J. M. S.*, xxiv. 1884.

'88 PATTEN, W. Studies on the eyes of Arthropods. II. The eyes of Acilius. *Jour. Morph.*, ii. 1888.

'89 PATTEN, W. Segmental sense-organs of Arthropods. *Jour. Morph.*, ii. 1889.

'90 PATTEN, W. On the origin of Vertebrates from Arachnids. *Q. J. M. S.*, xxxi. 1890.

'85 PELSENEER, P. Observations on the nervous system of Apus. *Q. J. M. S.*, xxv. 1885.

'86 PLATEAU, F. De l'absence de mouvements respiratoire perceptibles chez les Arachnides. *Arch. Biol.*, vii. 1886.

'87 POCOCK, R. I. On the classification of the Diplopoda. *Ann. and Mag. N. H.* 1887.

86 VOM RATH, O. Beiträge zur Kenntniss der Chilognathen. *Inaug. Diss.* Bonn. 1886.

'86a vom Rath, O. Die Sinnesorgane der Antennæ und der Unterlippe der Chilognathen. *Arch. f. Mikr. Anat.*, xxvii. 1886.

'77 Reichenbach, H. Die Embryonalanlage und erste Entwicklung des Flusskrebses. *Zeit. wiss. Zool.*, xxix. 1877.

'86 Reichenbach, H. Studien zur Entwicklungsgeschichte des Flusskrebses. *Abh. Senckenb. Gesell.*, xiv. 1886.

'79 Ryder, J. A. An account of a new genus of minute Pauropod Myriapods. *Am. Nat.*, xiii. 1879.

'87 Schimkewitsch, W. Étude sur le developpement des Araignées. *Arch. de Biol.*, vi. 1887.

'88 Sedgwick, A. A monograph of the development of Peripatus capensis. *Studies Morph. Lab. Cambridge*, iv. 1888. From *Q. J. M. S.*, 1885–88.

'53 Siebold, C. Th. von. Anatomy of the Invertebrata, translated by W. J. Burnett. Boston. 1853.

'92 Sinclair, F. G. A new mode of respiration in the Myriapods. *Phil. Trans.* 183 B. 1892.

'85 Spencer, W. B. The urinary organs of Amphipoda. *Q. J. M. S.*, xxv. 1885.

'91 Sturanay, R. Die Coxaldrüsen der Arachnoiden. *Arb. Zool. Inst. Wien.*, ix. 1891.

'79 Tichomiroff, A. Ueber die Entwicklungsgeschichte des Seidenwurms. *Zool. Anz.*, ii. 1879.

'81 Walcott, C. D. The Trilobite: new and old evidence as to its organization. *Bull. Mus. Comp. Zool.*, vii. 1881.

'84 Walcott, C. D. Appendages of the Trilobite. *Science.*, iii. 1884.

'63 Weismann, A. Die Entwickelung der Dipteren im Ei. *Zeitsch. f. wiss. Zool.*, xiii. 1863.

'89 Weldon, W. F. R. The cœlom and nephridia of Palæmon serratus. *Jour. Marine Biol. Assoc.*, *N. S.*, i. 1889.

91 Weldon, W. F. R. The renal organs of certain Decapod Crustacea. *Q. J. M. S.*, xxxii. 1891.

'92 Weldon, W. F. R. The formation of the germ layers in Crangon vulgaris. *Q. J. M. S.*, xxxiii. 1892.

'89 Wheeler, W. M. The embryology of Blatta germanica and Doryphora decemlineata. *Jour. Morph.*, iii. 1889.

'78 Whitman, C. O. The embryology of Clepsine. *Q. J. M. S.*, xviii. 1878.

'79 Wood-Mason, J. Morphological notes bearing on the origin of Insects. *Trans. Ent. Socy. London.* 1879.

'70 Woodward, H. Notes on the palpus and other appendages of Asaphus. *Quar. Jour. Geol. Socy.*, xxvi. 1870. See also *Geol. Mag.*, Feby. 1884.

'41 Zaddach, E. G. De Apodis cancriformis, Bonn. 1841.

EXPLANATION OF THE FIGURES.

Reference Letters.

a.	Anus.
an.	Neural artery.
ar.	Artery.
av.	Ventral (circumneural) artery.
bs.	Blood sinus.
c. 1–*c.* 9.	Cœlomic cavities.
ce.	Cerebrum.
ct.	Cuticula.
ec.	Ectoderm (in figures 50–52 edge of carapax).
en.	Entoderm.
ent.	Entapophysis.
es.	Entosternite.
ev.	Excretory vescicle of nephridium.
g.	Ganglion.
gl.	Gill-leaves.
h or ht.	Heart.
hep.	Hepatic duct.
i.	Intima of heart.
iv.	Invaginations of nuclei in neural anlage (*cf.* Fig. 29).
l.	Liver and liver lobes.
lac.	Lacunæ.
m or me.	Mesoderm.
mes.	Mesenteron and in later stages, intestine.
ml.	Middle line of section.
mg.	Marginal groove.
mo.	Mouth.
mt.	Metastoma.
mu.	Muscles.
n.′–n.^{8}	Segmental nerves.
nd.	Nephridial duct.
ne.	Nephridium.
n. a.	Neural anlage (in Fig. 54, the anterior loop of the nephridium).
no.	External opening of nephridium.
nst.	Nephrostome.
oc.	Ocellus.
œ.	Œsophagus.
œc.	Œsophageal commissure.
on.	Nerve to ocellus.
op.	Operculum.
pd.	Proctodæum.
pe.	Pavement epithelium of cœlom 5.
pr.	Proventriculus.
ps.	Pericardial sinus.
pst.	Primitive streak.
sg.	Sympathetic ganglion.
sn.	Sympathetic nerve.
sp.	Splanchnoplure.
ss.	Segmental sense (?) organs.
st.	Stomodæum.
so.	Somatoplure.
t.	Telson.
y.	Yolk-entoderm.
ys.	Yolk spherules.
yx.	Yolk cells.
I–X.	Somites and appendages.

EXPLANATION OF PLATE X.

FIG. 40. Longitudinal section of an embryo with cephalic and caudal areas and one intermediate somite developed. The arrows mark the limits of the somite.

FIG. 41. Through primitive streak in advance of mouth, Stage C, early.

FIG. 42. Transverse through the posterior primitive streak, Stage C, early.

FIG. 43. Transverse through the anterior end of the primitive streak ("mouth"), showing cœlom of somite I, Stage C, early.

FIG. 44. Through primitive streak and marginal groove, Stage C, early.

FIG. 45. Longitudinal section through an embryo of Stage C, late.

FIG. 46. Longitudinal section (a little oblique) through an embryo, with eight somites developed, showing a cœlomic cavity developed in each of the anterior seven somites.

FIG. 47. Obliquely transverse section, Stage C, showing the neural anlage, cœlom I, and the segmental structure (? gland) of somite II.

FIG. 48. Through somite V, Stage C, late. (Through a misunderstanding on the part of the lithographer this and Figs. 49 and 52, representing only one side of the body, are so turned upon the plate that the median plane is oblique.)

FIG. 49. Transverse through the abdomen, Stage C, late.

FIG. 50. Transverse through somite IV, showing the segmental structure (dorsal organ) of that somite, Stage D.

FIGS. 51, 52, 53. Transverse sections through somites V, VI, and VII, Stage E, showing the cœlomic cavities in each and the segmental structures (? glands) in V and VI.

FIG. 54 *a–i.* Modifications of the cœlom of somite V, Stage H, into the nephridium; Fig. 54 *i* is the most anterior. In this *n. a.* refers to the anterior bend of the nephridial tube.

Fig. 55. Reconstruction (by plotting) of the nephridium of Fig. 54.

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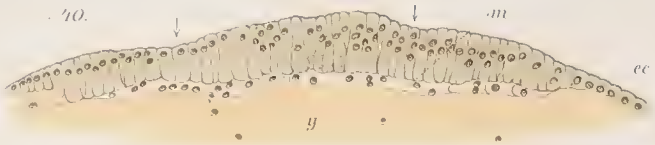

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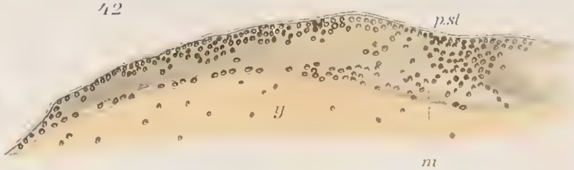

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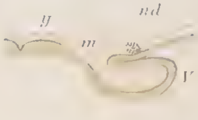

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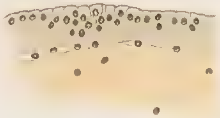

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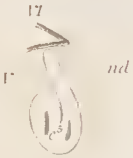

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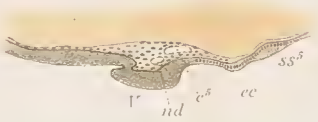

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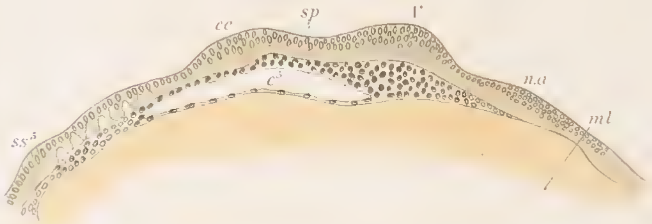

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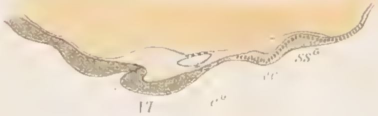

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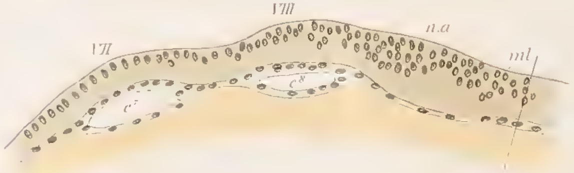

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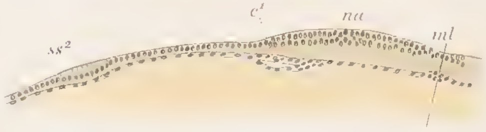

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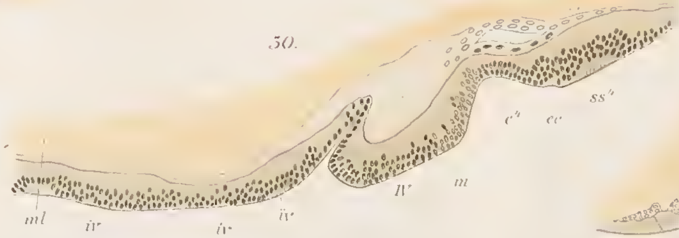

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EXPLANATION OF PLATE XI.

FIGS. 56, 57, 58, 59 transverse sections of the nephridium, about Stage H. Fig. 56, is most anterior.

FIG. 60. Longitudinal section of the nephridium after the duct is open to the exterior. The external opening is plainly on the posterior surface of the basal joint of the fifth appendage while the loop of the duct extends nearly to somite III.

FIG. 61 *a–e*. Horizontal sections through the nephridium, Stage I.

FIG. 61 *f* and *g*. Reconstructions (in wax) of the nephridium represented in Figs 61 *a–e*.

FIG. 62. Reconstruction (in wax) of the nephridium of Stage L. To be compared with Gulland's (**'85**) Fig. 2. (Is exaggerated in transverse diameter.)

FIG. 63. Longitudinal section of a portion of the abdomen showing the early appearance, by splitting, of somatoplure and splanchnoplure in that region. In the neural anlage (*n. a.*) can be seen the inpushing of nuclei for rapid cell proliferation producing the pitted appearance shown in Fig. 29.

Figs. 64 and 65. Transverse sections of the heart Stage H, Fig. 65, being the more anterior and the plane of section 64 passing through appendage V.

FIG. 66. Heart, transverse, Stage I.

FIG. 67. Transverse section through abdomen, the section passing through the operculum, Stage I.

FIG. 68. From the same series as Fig. 67, but more posterior.

FIG. 69. Transverse through œsophagus, œsophageal commissures and sternal artery, Stage I.

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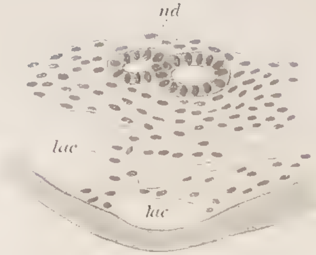

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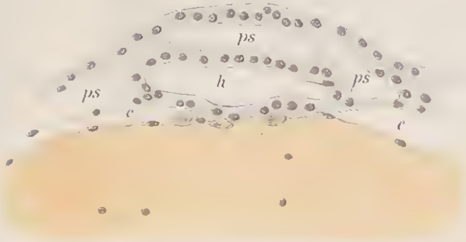

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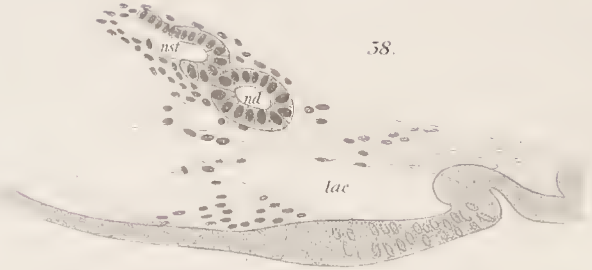

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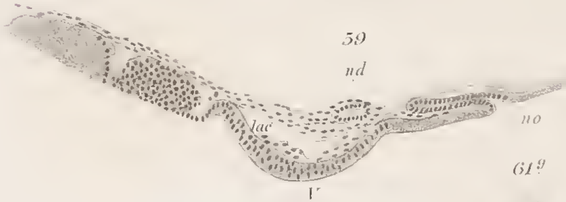

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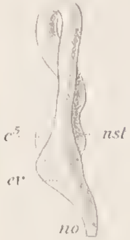

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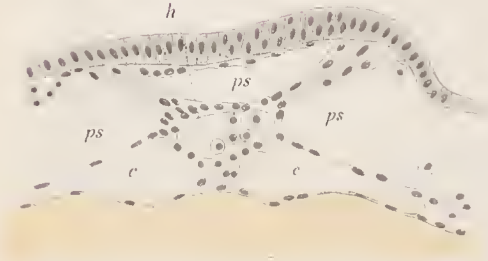

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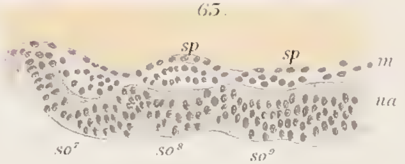

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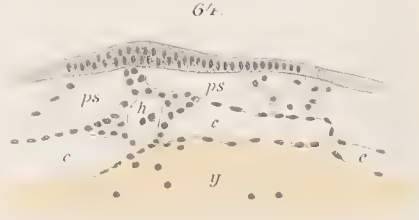

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EXPLANATION OF PLATE XII.

FIG. 70. Section posterior to that shown in Fig. 69. The sternal arteries have reached the nervous system and lie upon it. Beneath may be seen the anterior extension of the ventral part of the neural artery.

FIG. 71. More posterior, showing that the neural artery is paired above and below and also showing connection of dorsal and ventral parts of neural artery.

FIG. 72. Horizontal section, Stage L, through proventriculus, sternal arteries and anterior end of mesenteron with ducts of the hepato-pancreas.

FIG. 73. From the same series as 73, but passing through heart and showing the bifurcation for sternal arteries, *an.*

FIG. 74. Section from same series as Figs. 69–71, passing through fifth pair of legs.

FIG. 75. Through the abdomen, Stage L.

FIG. 76. From the same series as Fig. 74, showing the connection of sternal arteries with the heart and then splitting for the stomodæum.

FIG. 77. Reconstruction (wax) of the anterior end of the heart, sternal arteries and neural artery, Stage K. At the left is shown the cavity for the ventral cord; the dark spots mark the places for the exit of nerves.

FIG. 78. Long section through the abdomen, Stage G, showing the pit-like invaginations behind appendages VII and VIII.

FIG. 79. Operculum and anterior gill-bearing appendages, Stage I. (VII and VIII should read VIII and IX respectively.)

FIG. 80. First and second gill-bearing appendages, Stage L.

FIG. 81. Longitudinal median section, Stage L, in which the connection between the mesenteron and proctodæum is not yet made.

FIG. 82. Longitudinal section, Stage I.

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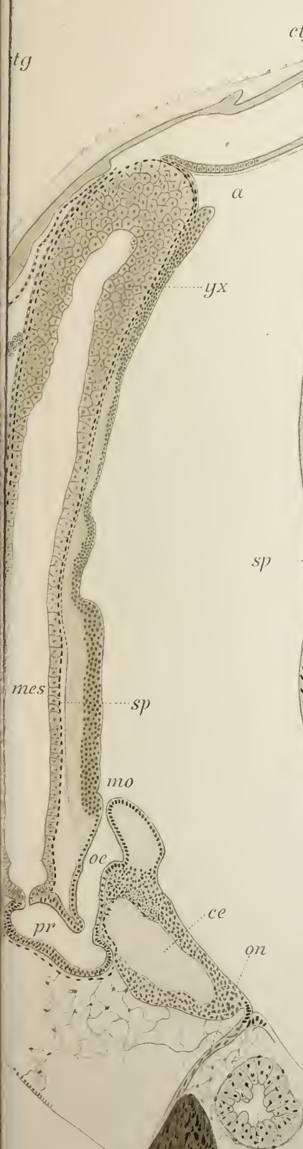

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Lith. Anst. v. Werner & Winter, Frankfurt M.

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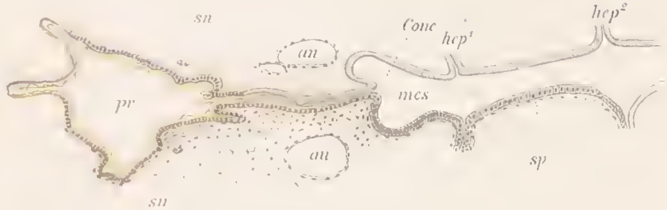

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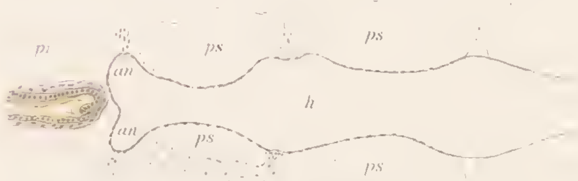

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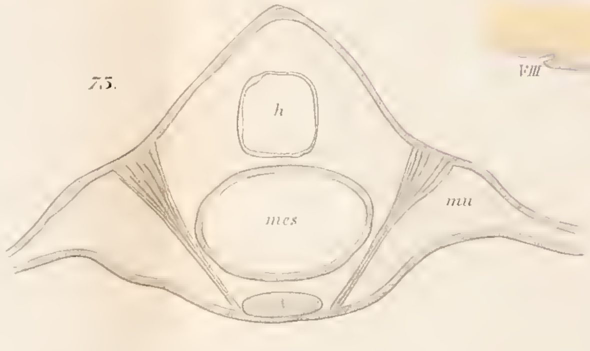

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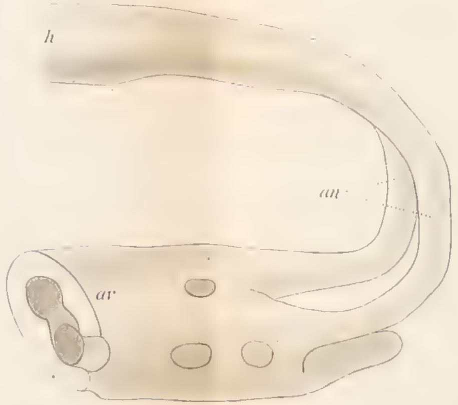

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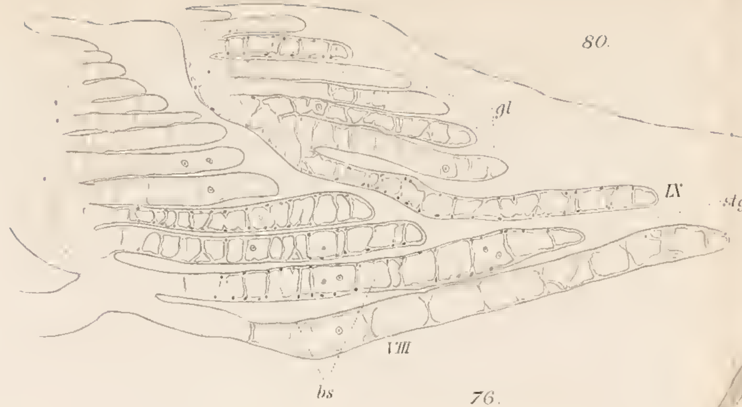

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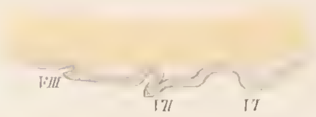

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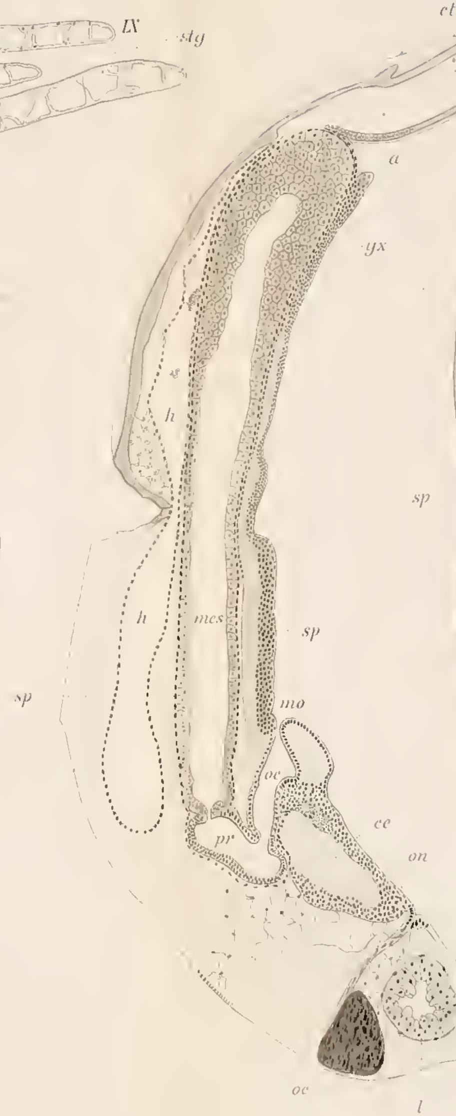

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EXPLANATION OF PLATE XIII.

Fig. 83. Horizontal section, Stage I, to show the relations of the mesenteron and lobes of the hepatopancreas.

Fig. 84. Transverse through an embryo of Stage L, to show the conversion of yolk cells into the epithelium of the alimentary canal.

Fig. 85. Longitudinal section through the junction of stomodæum and mesenteron, Stage L, before the connection of the lumens, to show the transformation of yolk cells into the columnar epithelium of the midgut.

Fig. 86. Late Stage L showing the first hepatopancreatic duct.

Fig. 87. Late Stage L through the third pair of appendages.

Fig. 88. Longitudinal section through the oldest larva studied, showing the junction of mesenteron and proctodæum. The section was not quite median and hence cuts off the folds in the proctodaeal region.

Fig. 89. Section of a leg, Stage L, to show the nerve surrounded by the artery.

EXPLANATION OF PLATE XIII.

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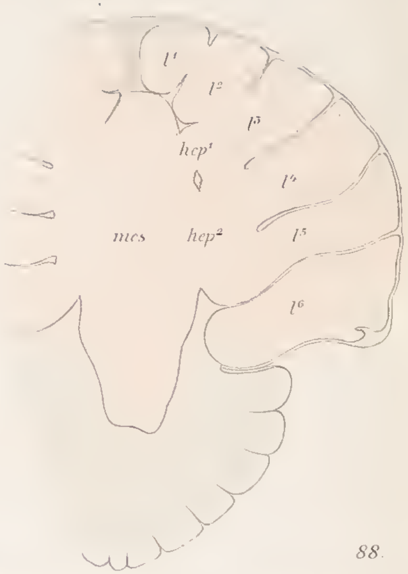
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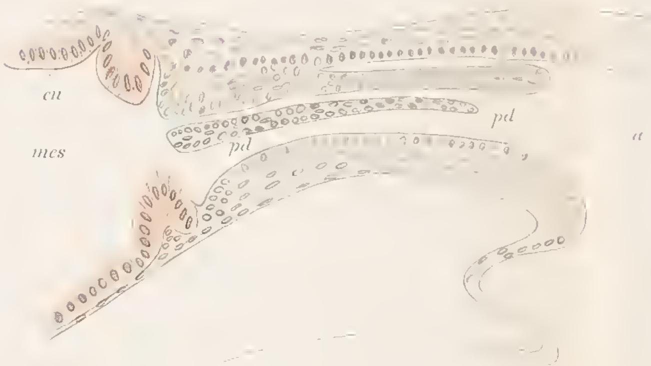
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