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NOTES

ON THE

EMBRYOLOGY OF LIMULUS.

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BY

J. S. KINGSLEY, D.Sc.
MALDEN, MASS., U.S.A.

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Notes on the Embryology of Limulus.

By

J. S. Kingsley, D.Sc.

Malden, Mass., U.S.A.

With Plates XXXVII, XXXVIII, XXXIX.

SEVERAL papers have been published upon the development of *Limulus polyphemus*, the titles of which will be found in the appended bibliography. Since Professor Ray Lankester has recently strongly advocated the Arachnid affinities of *Limulus* it has seemed especially desirable to study the embryology of this form by means of sections, a method scarcely touched by Dr. Packard, the most voluminous writer upon this subject.

I would here return my sincere thanks to my friend George H. Thompson for his assistance in obtaining material for my researches.

I have not witnessed the process of oviposition, which, however, has been described by Dr. Lockwood ('70),¹ but with some of his conclusions I would express dissent. The eggs are not all laid above high-water mark, for I have found them half way between tides, and have frequently taken the male and female coupled together, and buried in the mud below low-water mark.

All of my attempts at artificial impregnation have been unsuccessful, for animals kept in confinement, even when

¹ I have, in referring to the bibliography, adopted the admirable plan of Dr. E. L. Mark, by which the reference number gives the reader at once the approximate date of the article. A bibliography is appended.

caught in copulating, utterly refuse to lay their eggs. I obtained an abundance of good milt, and to all appearances the eggs were ripe. Again and again was fertilization tried, but although the eggs were kept for four weeks they showed no signs of change except those that might be the effect of decomposition (see *infra*). A further difficulty was found in manipulation of the early stages of the eggs obtained from the natural nests, and many experiments were tried to ascertain the best method of procedure. For surface views a slight staining with osmic acid proved best, while for sections hardening in successive grades of alcohol proved at least equal to chromic acid, Merkel's fluid, Perenyi's fluid, or corrosive sublimate. The coagulation of the albumen by heat, so advantageous in studying many Arthropods, was here worthless. The greatest difficulty with the earlier stages was found in the extremely refractory chorion, which did not separate at all readily from the egg proper. I had in most cases to cut it and the egg together, and the results were far from satisfactory.

The eggs were embedded in paraffin by chloroform, cut in ribbons, and fastened to the slide by the collodion method. They were then stained by eosin or hæmatoxylin. They did not readily take color, usually requiring ten minutes to stain with the former dye, which generally works much more quickly. My best results were with hæmatoxylin, overstaining, and then submersing in acid alcohol.

The eggs and embryos possess great vitality, living in confinement with only the slightest care; and, as I write, I have specimens living which I obtained five months ago: they have spent the last three in a common saucer, the only attention being to replace evaporation by ordinary hydrant water. The density of the water seems to have but little effect upon them, and I have had them live for several weeks in perfectly fresh water. This vitality, which is also characteristic of the adults, has an extremely interesting aspect when we consider the fact that Gigantostroma have an ancestry extending back to the Palæozoic rocks. Professor E. S. Morse has noticed a

similar correlation between the vitality of the individual and of the race in the case of the Brachiopods.

The eggs vary considerably in their characters. Some are spherical, others markedly oval. According to my measurements the average diameter is about two millimetres, varying between 1.75 mm. and 2.2 mm. Some are brown, some are ashy green, and others yellow or pink. Color seems unimportant, as I have had pink embryos hatch, the color persisting for some time after escape from the membranes. The egg is enveloped in a thick and dense chorion, which is apparently made up of layers, about twenty in number, the whole having a total thickness of about $\frac{1}{1000}$ th of an inch. In rupturing this chorion the line of tear usually goes straight across, and but rarely can traces of lamination be seen. Usually no traces of pores are visible, and I have sought in vain for a micropyle. Occasionally I have seen indistinctly what may be pores, and it is certain, for reasons which will appear anon, that there is some way in which water penetrates the chorion.

I greatly regret that I have nothing to offer regarding segmentation and the formation of the blastoderm, but my earliest embryos are already far along in their development. In the following pages I shall speak but briefly of the external development, except when my observations are at variance with the previously published accounts of Dohrn ('71) and Packard ('72). In studying the internal development I am unfortunate in having no predecessor, as I thus have nothing with which to check my results, and hence there is more chance for error to creep in. Even more unfortunate is the fact that I have no knowledge of the formation of the blastoderm wherewith to settle some features of the later stages which are uncertain.

EXTERNAL DEVELOPMENT.

The earliest egg seen was treated with osmic acid, and presented the appearance shown in fig. 4. Upon the surface is a longitudinal pyriform depression in the centre of a lighter field. This lighter area corresponds to the germinal area so frequently

described in Arthropod embryology, and the depression is the so-called germinal or ventral groove. In reality, at least in the case of *Limulus*, the lighter area marks the extension of the mesoblast (the epiblast extending entirely around the egg), and, in my opinion, the ventral groove is a modified blastopore. To this I will recur again.

LARVAL ENVELOPES.—In this stage sections show that the epiblast cells have begun the secretion of the first larval envelopes, which Dr. Packard has endeavoured to compare with the amnion of insects. This comparison is utterly without foundation, as this is a cuticular not a cellular structure, the polygonal cell-like markings with which the surface is ornamented being due to its mode of origin. Anticipating our account a little we will trace the history of what I would call the first larval cuticle throughout its history. In the stage 4, outside the mesoblastic area, the blastoderm consists of a single layer of large polygonal epiblast cells (fig. 39) resting directly upon the yolk. Each cell is covered with a thin cuticle which refuses to take any stain. This cuticle follows closely the contour of the surface of the epiblast, extending down between the various cells, thus giving rise to the polygonal markings which, in the later stages, are confined to the external surface, and which were so puzzling to Dohrn and Packard.

At the time of the appearance of the limbs this cuticle is nearly as thick as the epiblast, having increased by additions to the inner surface. The outer still retains its markings, but the inner is nearly smooth. As yet it is in close contact with the epiblast, the cells of which are still contributing to its increase (fig. 45). When the embryo arrives at stage 11 the cuticle separates from the epiblast, and the cells of its surface have an average diameter of mm. .0033. Of the explanation of the ensuing phenomena I am not certain, and the following is but tentative. It would seem that an osmotic action begins whereby water is taken in through the chorion and cuticle, thus creating a pressure which ruptures the

chorion. From the time of this rupture until the assumption of a free life this larval cuticle functions, as Dr. Packard has aptly expressed it, as a "vicarious chorion." As the embryo develops this cuticular envelope increases in size, always having a considerable space between it and the embryo (cf. Packard, '72, pls. iv, v, figs. 19, 24, *a*). This increase continues until at last the "vicarious chorion" has about twice the original diameter of the egg. This increase in size is not due to any growth, but only to elasticity. In the later stages the pseudocells are no longer visible, but long before the final hatching they have twice their original diameter.

A second cuticle is formed and molted before the embryo hatches. It makes its appearance at the stage 6, and in fig. 11 it is represented as lifted up on the extremities of the limbs. The active movements of the embryo soon tear this second cuticle off, and in the subsequent stages it is seen as a delicate membrane wadded up at one side of the chorion. Dr. Packard ('72, p. 165) describes this molt.

Between 4 and 5 a considerable gap occurs in my material, and I am not able to say whether here, as in scorpions (Metschnikoff, '71) and spiders (Balfour, '80, *b*), any metamerism appears before the appendages or not. In fig. 5 all the cephalothoracic appendages have appeared, and I have seen no evidence to support Dohrn's idea that the first pair appears later than the others. Occasionally it is invisible in the living egg, but osmic acid always renders it distinct. An important fact was pointed out by Packard that at this early stage all the appendages are post-oral, although long before hatching the first pair acquires a pre-oral position. These appendages are at first simple outgrowths from the surface. In the median line of the embryo can be seen mouth and anus, each having a slender pyriform outline, the narrow end being in front. On first seeing this in connection with fig. 4, I was forcibly reminded of Balfour's figures of *Peripatus* ('83, pl. xx, figs. 34 to 37), and, were the narrower end of the mouth turned in the opposite direction, the natural inference would be that

the blastopore had closed in the middle, leaving the mouth and anus at the ends. This, I believe, is the true explanation, allowances being made for the modified form of gastrulation (*vide infra*). The fact that the narrow extremity of the oral opening is turned forwards is due to its being in the act of transference from a position in front of the first pair of appendages to one behind it. Between the mouth and anus is apparently a shallow groove. In reality this is produced by the neurulation, and is internal. Sections show that the external surface is smooth (fig. 47), and that the blastopore has entirely disappeared, except as mouth and anus.

The first pair of abdominal appendages (opercula) are partially marked out, and it is to be noticed that these and the gill-bearing appendages develop in a slightly different manner from the true limbs, a fact which would not be inferred from Dr. Packard's drawings (e. g. '72, pl. iv, fig. 16). In reality they arise as broad plates, separated from the surrounding surface by a tucking in of the epiblast behind (cf. 'Formation of Lungs of Scorpion,' Metschnikoff, '71, p. 225, pl. xvi, fig. 12). Besides the opercula the abdomen as yet shows no trace of segmentation or appendages. The limit of the mesoblast is much more distinct than in the preceding stage. It extends slightly beyond the limbs, and has an elongate oval outline slightly narrower in front. Outside the limits of the mesoblast, on a line between the fourth and fifth pairs of appendages, are seen the rudiments of the compound eyes. They are not visible in the living egg, but stain readily and deeply with osmic acid.

Between this and the stage figured in 6 the changes are slight. This is slightly earlier than Dr. Packard's ('72) pl. iv, fig. 16. The mouth and anus still retain the same outlines as before, and the neural groove is still conspicuous. The limbs are now elevated above the surrounding surface and begin to show traces of flexure. In the abdominal region the opercula are better developed and the first pair of gill-bearing appendages have appeared. In this and earlier stages I have failed to find that segmentation outside the mesoblastic area

described and figured by Dr. Packard as existing outside the "germinal area," and am of the opinion that it does not exist, as usually metameric segmentation does not exhibit itself in epiblast alone, and the mesoblast has not yet extended itself so far.

As was noticed by Dr. Packard, between this and the next stage a second moult takes place, the cuticle being lifted up upon the feet as shown in fig. 11. Now motion begins, and the movement of the limbs, at first very slow, tears this second cuticle, the remains of which can be seen until the time of hatching inside the "vicarious chorion."

In the next stage necessary to be mentioned (fig. 12) a limuloid appearance is visible. The body is elongated and the abdomen is differentiated, and it and the cephalothorax are distinctly segmented, six somites being visible in the latter and eight in the abdomen, the ninth or telson not being separated from the preceding segment. The cephalothoracic limbs are jointed and the chelæ outlined, while the peculiar whorl of spines on the sixth pair is already formed. The flabelliform appendage on the outer side of the coxa of the same pair and the metastoma are also visible. In the abdomen the operculum and the first branchial appendages are well developed, and the gills upon it are beginning to be formed. The second branchial appendage is just appearing.

Fig. 14 corresponds so closely with Dr. Packard's ('72) fig. 24 that there is no necessity for describing it here. I would, however, state that his representation of the appendages (a matter of no great morphological importance) is extremely faulty, and in 24, *a*, the eye is much too remote from the margin. At this stage specimens just killed with alcohol show the posterior portion of the nervous system very plainly through the integument, but I have not been able by surface views to show exactly the innervation of the anterior pair of limbs. This, however, is to be the less regretted, as my sections settle this point. I would in passing state that Dr. Packard's ('80, *a*) pl. v, fig. 8, cannot be relied upon as proving that the first pair are post-oral; the stage is too late for that demonstration.

Figs. 16 and 17 correspond with Packard's ('72) figs. 25 and 25, *a*, reproduced here. They represent the young *Limulus* as it leaves the egg. It is 4 mm. long; the cephalo-

Limulus just hatched.

thorax has a semicircular outline, and the abdomen, though smaller, has a similar shape. The dorsal surface of the cephalothorax is without traces of segmentation except in the lines bounding the cardiac region, where the depression marking the attachment of the muscles of the limbs are visible. These are not shown in the adjacent woodcut taken from Dr. Packard's paper, which is otherwise good, except that the segmentation of the abdomen is much less distinct in nature. I may say here that the segmentation in *Limulus* nowhere affects the epiblast and its derivatives, and at no time in the development do we find the body divided into a series of somites moveable upon each other like those in the abdomen of a lobster; the only joints are those between the cephalothorax and abdomen, and between the latter and the caudal spine.

Dr. Packard's figure of the ventral surface at this stage is very inaccurate. A better illustration will be seen in fig. 17, from which it will be seen that the appendages are closely similar to those of the adult female.

A number of individuals which hatched on the same day were isolated and the first moult after hatching was watched for with considerable interest. Soon after hatching the young *Limuli* bury themselves in the sand as do the adults, and appa-

rently undergo exuviation while thus concealed. The carapax splits along the frontal margin as in the adult. The first specimen moulted in exactly five weeks after hatching, while the others struggled along at intervals of one or two days, the last one of the lot casting its skin in seventy-two days after leaving the "vicarious chorion." After the moult the animal is much larger, and the most important change is in the increased length of the caudal spine, the general appearance being shown in Packard's ('72) fig. 27 of plate v. For our purpose it is not necessary to carry the account of the external changes any further. Nowhere in the external development are there any startling metamorphoses, and nowhere, except in the closure of the blastopore and the post-oral position of the first pair of appendages, do we find facts which aid us in a discussion of the affinities or phylogeny of the Xiphosura; certainly nothing which would indicate Crustacean relationships.

INTERNAL DEVELOPMENT.

The earliest stage of which I possess sections is that of fig. 4, but from difficulties of manipulation these are not very satisfactory, though they show some important points. The egg was cut transversely to the rudimentary blastopore, and one section is shown in fig. 44. The epiblast, a single cell in thickness, envelops the whole egg. The groove, which I regard as blastopore, is as deep as the thickness of the epiblast. Beneath this groove and extending to a short distance either side is the mesoblast, the limits of which correspond to the lighter area in fig. 4. This mesoblast arises wholly from the bottom and edges of the groove, and in the sections a rapid cell-proliferation is visible here. Beneath these two layers (epiblast and mesoblast) is the yolk. I believe that not only this groove but the primitive streak of all tracheates, as suggested by Balfour, is the homologue of the blastopore and that the yolk is wholly hypoblast. Schimkewitch ('84) comes to the same conclusions from studies of the spiders. How this modification arose I am not now ready to discuss, but when we consider the recent researches of Balfour on *Peripatus*, Hatschek on *Amphioxus*, and

Bateson on *Balanoglossus*, and especially the Hertwigs' Cœlomtheorie and Sedgwick's essay on metameric segmentation, and the light they throw on the origin of the mesoblast, I think we are justified in reversing the course of reasoning and concluding that, on account of the origin of the mesoblast, the primitive groove is the homologue of the blastopore.

The hypoblast has recently been recognised in the yolk, though in a rather vague and indefinite manner. Only one recent author (Ayres, '84), so far as I am aware, has had other views. The indecision has doubtless been caused by the late appearance of the archenteric, or rather mesenteric lumen. To this we will recur again; but now I call attention to the fact that at the stages of figs. 4 and 5 the yolk is broken up into true cells, each with its nucleus and cell wall. I have yet to see any "free yolk-nuclei." In describing the development of spiders Balfour ('80^b) refers to and figures cells migrating from the yolk and taking part in the formation of the mesoblast, and says that the middle part of the dorsal mesoblast arises largely, if not wholly, in this manner. On the other hand Patten ('84), treating of the development of the Phryganids, reverses the operation, and claims a migration of mesoblast into the yolk. My observations do not allow me to decide which of the two is correct; indeed, I have seen but very slight indications of any migration, and those would, as I interpret them, tend to show that part of the mesoblast which forms the heart may arise in this manner. This view (a migration of yolk-cells into the mesoblast) does not conflict with the more recent ideas of the origin of the mesoblast in triploblastic animals nor with the nature of the yolk as above expressed, but merely shows that it is archenteric rather than strictly hypoblastic. Mr. Patten's views are rather difficult to reconcile with what we know of the origin of the mesenteric tissues in other Arthropods. It would seem to me that he has misinterpreted his facts.

Of the closure of the blastopore or neural groove I have nothing to say, as I have seen no eggs between figs. 4 and 5. Still, judging from the appearance of the two, I think the

inference justifiable that here, as in *Peripatus capensis*,¹ it closes in the middle, the extremities persisting as mouth and anus.

On a previous page I spoke of the shape of the oral opening, and said that it was due to the transference of the mouth. The mouth in fig. 5 is in front of the first pair of appendages, in the adult behind them. The process of this transference is interesting. After the disappearance of the primitive groove behind the mouth a depression gradually extends backwards, and at the same time at the front the edges rise up and finally unite to form a close tube, the stomodæum (figs. 40, 41, 42, 43), in almost exactly the same way that the neural canal is formed in the chick. This seems to me an important point, for it shows that the functional mouth is not a strictly homologous structure throughout the animal kingdom, but that in those forms with a stomodeum it has been considerably modified in position. Unfortunately we do not know if a similar modification exists in *Peripatus*. The anus (fig. 46) is a shallow pit, and at this stage shows no signs of forming a proctodæum.

From this point on it will prove the easiest and possibly the best to consider separately each of the tissues or organs without attempting to describe the embryo at each stage as a whole.

MESOBLAST.

In fig. 4 the mesoblast constitutes a broad sheet (fig. 44), but between this and fig. 5 a considerable gap occurs in my material. In this latter stage it has become separated into two broad bands, except at the extremities. It seems probable that this separation is effected partly by the rapid growth of the epiblast in the ventral region, and partly by a migratory movement of the cells. In the region of the mouth it is still

¹ Kennel's ('84) recent researches on two South American species of *Peripatus* do not prove Balfour wrong in his interpretation, and until further observations are published on *P. capensis*, I think that his observations, certified to by Moseley and Sedgwick, should be accepted. Nor do I think Kennel has proved Sedgwick's ideas "ungeheuerlich," for Lang on the Planarians and Wilson on the Alcyonaria come to the same general conclusions.

continuous and not differentiated from the epiblast, although it has become separated in the anal region (fig. 46). In the middle region the broad bands on either side extend into the legs (fig. 47), but no trace of a *cœlom* has yet appeared. On the neural side of the limbs it is a single cell thick, but in the region of the appendages it is much thicker. This thicker portion soon splits into somatoplure and splanchnoplure, and the resulting *cœlom* extends into the legs (fig. 30). It is to be noticed that the *cœlomic* cavities are separate, one being formed to each segment on each side, and further, that each metameric cavity forms at first as several parts which afterwards unite. In the stage of fig. 6 the mesoblast has extended itself to the edge of the carapax where it thins out, the *cœlom* not reaching quite so far. In a slightly later stage (fig. 34), but still not far enough advanced to be equal to fig. 11, longitudinal sections show larger *cœlomic* cavities, eight in number, one for each segment developed.

The mesoblast gradually extends itself upwards on either side until at the stage of fig. 12 (fig. 21) it meets as a single layer of cells in the dorsal region. On the dorso-lateral region it forms a longitudinal band-like thickening (fig. 21, *m*), the earliest appearance of the extensor muscles and the points of attachment of the muscles of the limbs. At the same time on the ventral surface of the body, either side of the median line, portions of the mesoblast grow up into the yolk, dividing it into segments (fig. 22, *mp.*). By this segmentation, as shown in the section just referred to, we have conclusive evidence that the metastoma (*chilaria*) is not to be regarded as a morphological appendage, since both it and the sixth pair of legs arise from the same segment. This was more than suspected by Professor Lankester, and is an important point in the series of homologies he has suggested between *Limulus* and the Scorpions. I might incidentally mention that embryology affords not the slightest evidence of the missing abdominal segments needed to render the correspondence between the two exact.

These septa not only furnish the boundaries between the segments, but they also give rise to the muscles of the appen-

dages, and eventually join the dorsal mesoblastic bands mentioned a few lines above. The septa are not wholly formed from these ventral ingrowths, but at the same time lateral inpushings are taking place as shown in fig. 13, the section being horizontal and passing above the level of the eyes, so that only a few of the abdominal segments are included. The result of this is that the yolk in the cephalothorax is broken up into a central mass and six pairs of lateral lobes, the history of which will be traced later.

It is not an easy task to trace the history of the coelom past the point where we left it, though some isolated features are readily seen. Thus it is seen that the mesoblast does not split in the dorsal region until after the formation of the heart as a tubular organ.

HEART.

Soon after the union of the two halves of the mesoblast in the dorsal region a longitudinal cord several cells in thickness is formed. How this thickening is produced I cannot say. In the yolk beneath it the nuclei are very numerous, and the cells are much smaller than in other parts, and it may be that some of these migrate into the mesoblastic tissues; but although I have examined many sections I have not yet seen any indisputable evidence of such migration.

Soon a lumen appears in this cord, and the size increases, at least to a considerable extent, through the budding of mesoblast cells into the tube, where they become transformed into blood-corpuscles. These processes are represented in figs. 31 to 33, which represent sections from the same individual, 31 being the most posterior. Two sections back of this is the end of the lumen. Between 31 and 32 intervenes a distance of 0.025 mm., and between 32 and 33 a distance of 0.2 mm. From this it appears that the heart is formed from in front backwards, and gradually the walls are reduced to a single cell in thickness. Not until after this stage is reached does the heart separate from either of the mesoblastic layers, and from these, first from the splanchnopleure (fig. 33). This single-celled

condition of the walls is found in all the embryonic stages, and the heart does not have epithelial and muscular layers until after hatching. This mode of the formation of the heart is paralleled in both Crustaceans and Spiders, and hence throws no light upon the affinities of *Limulus*.

At about the same time that the dorsal mesoblast begins to thicken for the heart a similar thickening is noticeable in the epiblast immediately above it (fig. 31). Reichenbach ('77) has noticed a similar thickening in the Decapods. Of the meaning I am uncertain; it may be that it is the remains of a degenerate "dorsal organ," but it seems more probable (at least in the case of *Limulus*) that it is the early stage of the median dorsal crest or ridge of the adult. In the latest stages which I have studied I have found no further change in it.

SEGMENTAL ORGANS (NEPHRIDIA).

Under this head I would place the brick-red glands first noticed by Dr. Packard ('75^a), and recently described in detail by Professor Lankester ('84). Concerning their earliest stages I am yet in doubt. The earliest trace of them which I have seen was in the shape of two patches of mesoblast, one on either side in the fifth segment of the body. With growth they increase in size, forming a well-defined tube, and join the epiblast by the posterior extremity. This junction takes place in the posterior coxo-sternal articulation of the fifth pair of legs, and soon after an opening appears enabling the organ to communicate with the exterior. I have not been able to follow exactly the way in which the complicated organ of the adult is developed from its comparatively simple beginning, as I have had to rely solely on sections. From these (figs. 23, 26, 27, and 30) and others I have constructed a diagrammatic figure of the shape of the organ at the time of communication with the exterior (figs. 9 and 10). From the opening a narrow tube lined with quadrate epithelial cells goes forward and upwards (fig. 23) a short distance and then widens out into a spacious sac, which narrows again before reaching the fourth segment of the body. The cells of this portion are more columnar, and

have the nuclei placed at the ends away from the lumen. From this point the tube bends back on itself, going back a short distance, and then turning again enters the fourth segment, where it turns again and comes back to its first turn, where it terminates. As to the character of the termination I am yet in doubt, although I have examined many sections, both transverse and longitudinal. In some it appears to communicate directly with the body cavity, the internal end being open (fig. 27, *fn.*). I have been unable to detect cilia in any part. In various parts of the tube the epithelium varies in character between columnar and quadrate cells. In all the cells the nuclei are very large, and are placed at times nearer the fore, at others to the deeper end of the cells. The general character of the quadrate cells is shown in fig. 28, which closely resembles Professor Lankester's delineations of these glands in the adult *Limulus*.

I see no reason why these glands in *Limulus* and the corresponding ones in the Scorpion, together with the so-called shell-glands of the Crustacea, should not be regarded as segmental organs. Later in this paper I will return to their discussion, but here I would call attention to the fact that at least in the later stages the inner end of the gland terminates cæcally as in the various Crustaceans. The closure of its efferent duct takes place later.

RESPIRATORY ORGANS.

On a previous page I have described the early stages of the abdominal appendages. They arise as broad lamellar outgrowths from the lower surface of the abdomen. At first, and in fact until the appearance of the gill books but two of these appendages are visible. These correspond to the operculum and first gill-bearing appendage of the adult. The others arise in regular sequence until the whole number (five) is reached. At first each of these appendages is simple, nothing that could be interpreted as a biramous condition appearing until the stage of fig. 12. One fact requires mention here: these appendages are from the beginning broad and leaflike, differing in

this respect from the corresponding embryonic limbs of Arachnids.

The operculum never develops gills, but in the adult bears the genital openings. In the others the leaflike respiratory organs first appear at the stage of fig. 14. The method is shown in figs. 37 and 38, and needs but little description. The leaves of the gill book arise as outgrowths from the posterior surface of the appendage, accompanied apparently by an intucking of the adjacent epiblast. This operation takes place first at the distal portion of the appendage, and new leaves are added at the base, the whole series overlapping each other like the shingles on a roof.

So far as I am aware, Professor Van Beneden was the first to suggest ('71) the homology between the branchiæ of *Limulus* and the pulmonary books of the Arachnids. This was further elaborated by Professor Lankester ('81). At first this resemblance seemed as far-fetched to me as it did to Dr. Packard ('82, p. 290), but subsequent studies seem to me to indicate its general validity, although I am not ready to follow all of Professor Lankester's intermediate steps, nor those of McLeod ('82).

Of the development of the pulmonary organs in the Arachnids the literature is extremely scanty, but with Lankester I am inclined to believe that when more is known of it, it will be found that the lamellæ arise in connection with the temporary abdominal appendages. On this point Metschnikoff, treating of the Scorpion, says ('71, p. 225): "The lungs also arise as invaginations of the epiblast (Hornblattes), which appear close under the segmental appendages of the four abdominal segments (Taf. xvi, fig. 12, *pn*).¹ They appear from the first as pocket-like sacs, which open by a broad mouth. With the further development of the lung sacs, which is accompanied by an atrophy of the abdominal segments [? appendages] (with the exception of the second pair of the same), they become more spacious and deeper. Only at the latest embryonic stage (Taf. xvi, fig. 14 from the ventral, fig. 15 from the dorsal, sur-

¹ Reproduced on Pl. XXXVII, fig. 15.

face) there grows from the dorsal wall of the lung a blind projection (Auslaufer), by which the leaf-formation of the interior of the pulmonary cavity is begun. The external opening is at this time evidently smaller. The walls of the embryonic lungs are lined with cylindrical epithelium, which secretes a thin cuticula. On the outer upper surface of the lung occur here and there some cell masses, which belong to the middle layer."

Bertkau ('72, pp. 211, 212), speaking of the increase in size of the lungs of *Lycosa*, says: "Mit dem Wachsthum der Spinne wächst auch der Luftsack und zwar stärker als das Stigma, so das seine Spitze bald weit von demselben entfernt ist. Der erste Anlage eines Fächers zeigt sich in Auftreibungen des Bodens des Luftsackes, von diesen die jedesmalig jüngste dicht neben der nächst älteren entsteht und durch Intussusception neuen Bildungsmaterials wächst."

Both of these accounts, as far as they go, agree with the development as it occurs in *Limulus*, and the addition of new lamellæ, as described and figured by Bertkau, is exactly paralleled by that occurring in *Limulus*, both in position and in manner, if we accept Lankester's views or those given below.

It, however, seems to me hardly necessary to invoke the aid of "parabranhial stigmata" in order to derive the internal organs of the Arachnids from the gills of *Limulus*. The change in the needs of the animal owing to its assumption of a terrestrial in place of an aquatic life would seem to be sufficient to account for a part. Such a change in habit would necessitate a protection for the respiratory organs, and this would be best secured by an outgrowth of the surrounding parts, so that finally appendages and gills would be enclosed in pits, the openings of which would then grow smaller. The greatest difficulty with this whole homology, as carried out by Lankester, is that this opening must become completely closed, and another one developed, that the side which at first was exposed to water and then to air should subsequently be bathed with blood, while the portion which originally contained the vascular fluid should finally become opened to the air. Although I believe that there is a genetic relationship between the respiratory

organs in the two groups this physiological change is too great to be readily accepted until we know more about the development of these organs in the Arachnids. Still, the description of Metschnikoff quoted above is, so far as it goes, not wholly incompatible with this view, that the primary stigma formed by the insinking of the respiratory book is not the functional one of the adult, since this author notices its decrease in size, while the mode of origin of the lamellæ from the dorsal surface of the cavity is still more in its favor. Emerton ('72, pl. 2, figs. 11, 13, 15) represents the abdominal appendages of the embryo *Pholcus* as broad and like those of *Limulus* at a corresponding stage, a fact opposed to their being merely modified ambulatory appendages, but in full accord with their homology with those of *Limulus*.

On the other hand, the derivation might be much more direct, and thus avoid the inversions and the functional changes. As I have mentioned above, the process of formation of the gill-leaves is largely by a process of outgrowth, but there is also a slight ingrowth, especially noticeable at the distal portion of the appendage. This, however, disappears with growth, but is very noticeable in all my sections. To transform the gill of *Limulus* into the lung of *Scorpio* it is only necessary that, together with the sinking of the whole organ, as described above, the inpushings of the integument to form the lamellæ should be exaggerated, and the outgrowths correspondingly decreased. On Plate XXXVII, figs. 18 to 20, I have diagrammatically illustrated the steps in the process, the gill-leaves being few in number to secure clearness. In 18 we have the typical condition found in *Limulus*, one appendage being shown half in section and half in perspective. In 19 we have an intermediate condition, when, as suggested above, the animal was leaving the water and seeking a terrestrial life. Here the gill-bearing appendage (*ga.*) is partially sunk in the surrounding tissues to secure protection. The same causes would also tend to produce a similar change in the gill-leaves (*gl.*), and they would also tend to be formed rather as ingrowths than as protruding processes. This change in structure would be the

more readily effected on account of a change of the medium of respiration. A gill needs either to project freely into the water, or to have some means of constantly changing the fluid which bathes it. An organ for aërial respiration, on the other hand, is not so restricted in its position, since the air is more fluid and more elastic, and hence more readily changed. Another advantage to the animal resulting from the change is that the oxygen is thus brought nearer to the tissues requiring it.

In fig. 20 we have a diagrammatic representation of the pulmonary sac of the Arachnids. The appendage (*ga.*) has now become sunk in the body and the hole through which it passed is the stigma (*stg.*) The gill lamellæ have entirely disappeared and the pulmonary ones (*pl.*) have taken their place. The process here described is different from that imagined by McLeod ('82). It accords more with the development of the gills in *Limulus*, and avoids the necessity of union of the gill-laminæ and the expansion of the sternum.

Having derived the lungs of the Scorpion in this manner, but little needs to be said concerning the origin of the tracheæ in the spiders. Many years ago Leuckart showed that the so-called lungs of the Arachnids were but modifications of the peculiar tracheæ of the same group. This conclusion holds good to-day, and I would accept it in an inverted condition: The tracheæ of the Arachnids are but modifications of the pulmonary organs existing in some of the group. To transform the lungs into the other type of organ but slight changes are necessary. A prolongation of one of the sac-like pulmonary lamellæ towards the thorax gives the condition found in *Argyroneta*; a slight amount of branching produces the tracheal system of *Zilla*, and so on through forms like *Thomisus* until the most complicated condition is reached. McLeod's observations are interesting in this connection.

The existence of the so-called spiral threads in the tracheæ of some of the Arachnids is to be explained on mechanical grounds. In some forms nothing of the sort is found and here the tracheæ are flattened tubes. To prevent them from being

completely closed by the pressure of the surrounding viscera and to enable them to open readily for the inspiration of air on the relaxation of the pressure some elastic element is needed. This is supplied at first by scattered chitinous rods or thickenings; next, these are arranged transversely to the tube, and, lastly, the rods become united to form the spiral. All of these stages can be seen in the adult *Araneinæ*. Leydig's observations ('78, p. 265) on the respiratory apparatus of the *Oniscidæ* are suggestive in connection with the origin of tracheæ. They will be referred to again.

NERVOUS SYSTEM.

Not until the mesoblast has become divided into the two bands mentioned above do we find any trace of the nervous system. Its first appearance is as two longitudinal epiblastic thickenings (fig. 47), one on either side of the median line. There is no external neural groove, but in its stead one on the inner surface of the cord. This of course is a variation from the normal of but minor importance, and doubtless arises from the fact that the egg fills its envelope so completely that an inward bending is impossible. In either band the arrangement of the cells show that a rapid proliferation is taking place, the result being a broad band on either side, the inner portions of which are to form the neural cord. At first, as is shown by longitudinal sections, this neurulation is continuous, there being no differentiation into commissures (connectives)¹ and ganglia until a later date.

The separation of the neural cords from the epiblast takes place at first in front and progresses more and more slowly posteriorly (fig. 29). The separation of the commissural portions is effected before that of the ganglionic areas, and in the latter the cleavage takes place first in the median line (fig. 25), even while in the lateral areas the epiblast is still

¹ I follow Professor Lankester and others in restricting the use of the term commissure to the cords which serve to unite the ganglia of the same pair, and employing for those which unite the ganglia of a side the term connective.

adding to the substance of the nervous system. I am not positive as to the origin of the commissures. From the figure last cited it would seem that here as in many other Arthropods they arose as epiblastic ingrowths. This at least is most reasonable. In the stage of fig. 12 (fig. 29) there are distinctly eight pairs of postoral ganglia and this number is not exceeded in embryonic life. Of these six correspond to the six pairs of ambulatory appendages, one to the operculum and one to the first pair of respiratory appendages. As will be seen, there is no ganglion for the metastoma (chilaria), another proof, if more were necessary, that they are not to be regarded as morphological equivalents of the limbs.

In the stage of fig. 14 several important features are introduced. Here begins that concentration of the anterior part of the nervous system which results in the nervous collar of the adult. I have found it difficult to trace the changes and have obtained my best results by external views of the whole animal treated in the following manner:—On removing the embryo from its envelope I placed it in a watch crystal on the stage of the microscope and then added some fifty per cent. alcohol. This, on penetrating the cuticle, first affected appreciably the protoplasm of the nervous centres rendering it alabaster white, and thus in most regions readily distinguishable against the darker background formed by the as yet indifferentiated food yolk. Soon, however, other parts were affected and their distinctness was lost. Fig. 14 was drawn from these specimens so treated, and as a camera was used it is correct in all respects except possibly the brain and the metastoma. These parts I was unable to see distinctly, and from my sections I am inclined to believe them incorrect. This figure shows posteriorly the nerves going from the respective ganglia to the sixth, fifth, and fourth pairs of legs. In the third and second pairs of nerves there seems to be a shifting forwards so that they do not arise exactly opposite to the centres of the ganglia but rather from their anterior margins. I have shown on a preceding page the manner of the shifting of the mouth, and this change in its position, and, consequently, in that of the limbs

accords well with the facts just noted. The anterior appendages were thus brought further from their nerve-centres and hence (if I may use the expression) they exert a tractive force first on the nerves which supply them and secondarily on the ganglia, for it is for the evident advantage of the animal to have the nerve-centres nearer the parts most used.

The foregoing account mentions five postoral and pregenital ganglia; the remaining one, the first of the series, has, as far as I can see, been merged in the œsophageal collar, and the corresponding pair of nerves (which supply the small first pair) appear to arise from the outer surface of the collar at about a level with the posterior margin of the brain. Of the exact position, however, I am not quite certain.

I have spoken above of the commissures, and while not sure of their origin, I am confident that the connectives do not arise as secondary epiblastic invaginations, but merely as differentiations of the primary neural ridges. With the specialization of the ganglia, which is brought about by a more rapid increase in size, the formation of the fibrous portion of the nervous system begins. In transverse section this has a granular appearance with scattered superficial nuclei, which may play a part in the formation of the neurilemma. The nerves to the appendages arise as outgrowths from the ganglia which extend themselves among the mesoblastic tissues (fig. 35). These outgrowths contain but few nuclei at any stage but are mostly fibrous, and are directly connected with the corresponding portion of the central nervous system.

One of the most marked peculiarities of the adult *Limulus* is the fact that the ventral nervous cord is ensheathed by the large sternal artery, a fact without parallel except in the Arachnids. The early stage of this artery is shown in fig. 36. At all times there is a considerable space between the mesoblast and the nervous system, and at this time processes begin to grow out above and below, on either side, from the mesoblast. These in the section figured partially embrace the cords; at a later stage the two halves unite and form the walls of the artery.

The description of the development of the brain, of the eyes, the midgut and its appendages, the genital organs and other mesoblastic structures, I leave for the second part of this paper where will be discussed their bearings. Still a few facts may be of interest here, without the details which will be given later.

The brain is at first separate from the rest of the nervous system. It arises as two halves and each lobe is divided in front as shown in fig. 11, presenting a marked similarity to that of the spiders. The mesenteron is formed from the central mass of yolk, the lumen appearing after the first moult after hatching. The diverticula of the liver arise from the lateral yolk masses, and the primary lobes of which it is composed are produced by the mesoblastic septa of the cephalothoracic region (fig. 13). After the stage where we left the œsophagus on a preceding page, it continues to elongate and joins the midgut soon after the lumen in the latter begins to appear. It is at all times much longer than the proctodæum. The outer layer of the cells of the mesenteron feed upon the central ones, absorbing and assimilating them, thus producing the lumen.

THE POSITION OF LIMULUS.

Professor Lankester has so recently discussed in an able manner the relationship of *Limulus* ('81) that all that I can add are the few facts gained from embryology. I must admit that at first I was strongly inclined to regard *Limulus* as a Crustacean, but a careful consideration of the subject leads me to believe in its being much more closely allied to the Spiders, and its being a representative in the seas of to-day of the stock from which the Scorpions sprang. On the other hand, its relationships to the Phyllopods are marked; in fact, it takes us back to a time when the distinctions between the Crustacea and the Arachnida were far less marked than they are to-day. The day of a belief in "types" is past, and yet some of the terminology once in vogue is convenient; in this way we may still call *Limulus* a synthetic type.

Since writing the earlier part of this paper I have learned that during the past summer Mr. H. L. Osborn attempted artificial fertilization of the eggs of *Limulus* at Beaufort, and that like myself he came to the conclusion that the operation was not a success and threw these eggs away. A few, however, were overlooked, and when found some time afterwards it was seen that they were really developing, and that the early changes were very slow. This fact recalled at once my observations on the eggs which I attempted to fertilize and the early changes that I witnessed in them, which I thought to be the indications of decomposition. At first the eggs were regularly granular, but half an hour after impregnation the surface inside the chorion became irregular and pitted with cavities varying greatly in size, each filled with a transparent fluid, which at the time I interpreted as caused by a migration of the protoplasm to the surface (fig. 1). These pits increased in size and number especially at one side of the egg, until they ran together leaving the surface ornamented by a number of hemispherical globules of yolk which twenty-one hours after impregnation presented the appearance shown in fig. 2. After this, though I kept the eggs for several weeks, I noticed no change except in those which were undoubtedly spoiled except in one instance. In that egg, twenty-nine hours after impregnation, a profile view showed two mushroom-shaped bodies (fig. 3) raised from the rest of the yolk, and suggesting polar globules but not very vividly. The meaning of these three observations is uncertain. If connected with the development of the egg the second would at once recall the peculiar segmentation occurring in some spiders. It is not certain that it was a normal condition, and any conclusions drawn from it are of no value until it is confirmed.

The first definite fact is the formation of a larval cuticle. This Dr. Packard regarded as cellular, but as he used no sections his mistake, as well as that of Dohrn in regard to the same envelope, is readily explained. Since the publication of my preliminary note Dr. Packard has re-examined the subject, and informs me that he agrees with my account of the nature

of this envelope. This early moulting of a cuticle seems to me to be of but little importance in ascertaining the relationships of *Limulus*, for it is paralleled more or less completely in both Crustacea and Arachnida. The cases which will at once suggest themselves are those of *Apus*, as described by Zaddach ('41), and *Atax*, by Claparède ('68). Indeed, it might be well to adopt the latter author's term *deutovum* for all such envelopes. Other cases, where the correspondence is not so exact (Asellus, &c.), will readily be recalled; but until a more definite knowledge is obtained of the exact origin of these *deutova* speculation as to their homology and meaning is useless. Kennel's speculations ('84) seem poorly founded.

The simultaneous appearance of the six pairs of ambulatory limbs seems equally unimportant, paralleled as it is with more or less exactness in either group. It merely indicates a concentration of development, and the fact that through abundant food supply the embryos or its nearer ancestors have not been compelled to begin free life at an early stage. The closest resemblance, however, exists in the scorpions and spiders, where, the first pair of appendages excepted, the corresponding parts appear. Were Dohrn's account true nothing more could be asked, but as I have had abundant material of earlier stages than any of his I believe that (as he suggests) he overlooked the first pair. I have not seen the slightest evidence in favour of his account. There is nothing in the development of *Limulus* that even suggests a Nauplius or a Zoea.

The position and early appearance of the compound eyes suggest some points of interest. Since in the Decapod and some other crustacea (*Squilla*, *Branchipus*, *Tanais*, &c.) the compound eyes are borne on stalks, which are articulated to the body, some morphologists have adopted the idea that these pedicles are homodynamous with the true limbs, and a few have even gone so far as to seek an "ocular segment" in the head of Hexapods. Without entering into a discussion of the many arguments against this view (which I believe totally erroneous even in the case of *Squilla*), I would say that I regard the eyes of all Arthropods merely as specialised portions

of the epiblast of the head,¹ and as having a common phylogenetic origin, namely, from an Annelid ancestor.

Such being the case, I regard the dorsal surface of the cephalothorax of *Limulus* as but the greatly expanded upper portion of the head, and believe that the segments indicated by the six pairs of appendages below are without proper terga. If we follow Packard and Lankester and recognise the dorsal surface of the shield as composed of six (or seven) coalesced terga, then the fact that the eyes are borne on the fifth or fourth and fifth² of these segments is difficult of explanation. This vagueness of expression as to the position of the eyes results from the fact that the dorsal epiblast of the cephalothorax never segments or shows any traces of division into somites, while in different specimens the boundary between the fourth and fifth mesoblastic somites is not constant in position as regards the eye, but at times it passes in front of the eye and at others beneath this organ, so that half of it is in one segment and half over the other. The ocelli are placed over the first of these segments. It seems to me that these facts can be explained only in the way indicated at the beginning of this paragraph.

A nearly parallel case is found in the carapax of the Decapod Crustacea. As usually described the carapax of the lobster or crayfish is regarded as composed of the coalesced terga of the segments visible below, and the obliquely transverse section which crosses it (the "cervical suture") is held to indicate the line of division between head and thorax. In the *Brachyura* the homologous suture is usually sought in the depressions surrounding the cardiac region of the carapax. The true explanations of these various structures was pointed out by Dana ('52, pp. 23—28) over thirty years ago, and their total neglect by all subsequent students is a partial excuse for their mention here. The carapax of the lobster is wholly composed

¹ The peculiar lateral eyes of *Euphausia* are not included.

² Dr. Packard, in his text ('72, p. 165), speaks of the compound eyes appearing "on the third segment of the cephalothorax," but his figures (pl. v, figs. 24, 24a) show them in their proper position.

of the coalesced terga of the second antennal and the mandibular segments, and the "cervical suture" indicates merely the line of their junction. In the crab the homologous suture is to be sought on the deflexed surface of the carapax below the lateral margin. The mandibular terga are comparatively small, and are the epimera of H. Milne Edwards.¹ It is needless to say that I do not accept the opinions of Young ('80) on this subject, nor his views of the supra-œsophageal ganglia.

This same view is perfectly applicable to the Arachnida, where otherwise we should have to regard the eyes as distributed on different segments in different species and even in the same species. A further confirmation is found in the fact that in the Scorpions (nor so far as I am aware in any Arachnid) the cephalothoracic tergum does not segment, or show any signs of the metamerism so evident on the ventral surface. This point seems to me an additional argument in favor of the union of *Limulus* with the Scorpions.

The post-oral nature of the first pair of appendages and the non-appendicular nature of the metastoma needed to render valid the comparisons of Professor Lankester have been previously suspected or proved, and my observations are only confirmative, though in the case of the metastoma conclusive proof was hitherto lacking.

Unfortunately Metschnikoff's account of the development of the mesoblast is very scanty owing to the fact that he did not employ sections, and so I can only refer to Balfour's account of the Arachnida. The process in *Limulus* and *Agalena* is closely similar and in its details considerably different from that found in Crustacea. In the latter group the mesoblast does not as a rule become divided into somites,² nor does the schizocœle extend into the legs at first. In both *Agalena* and *Limulus* it arises as a single broad sheet, which later divides into two bands which migrate to the region of the appendages. Then the cœlom is formed by splitting and

¹ 'Hist. Nat. Crust.,' pl. i, fig. 9, b.

² It does so in *Mysis* (Metschnikoff, teste Balfour) and in *Cyclops* (Urbanowicz in '84).

extends into the legs. The mesoblastic processes in both divide the yolk up into a series of lobes, but these partitions never reach clear across the body. A similarity is observable in the late appearance of the lumen of the alimentary tract *cf.* Isopods), and apparently in both (certainly in *Limulus*) the hepatic organs are formed from the lobes of yolk which extend between the mesoblastic partitions.

The yolk in *Limulus* never communicates with the *cœlom* as it does in many Hexapods and Crustaceans. Apparently the same is true with spiders.

The heart in *Limulus* arises by the hollowing out of a solid rod of mesoblast, its cells becoming transformed into blood-corpuscles. This is paralleled in spiders and in some Crustacea. Metschnikoff's account of the origin of the dorsal vessel in the scorpions is very improbable and needs confirmation before it can be accepted.

The close resemblances in the segmental organs of the adult scorpion and of *Limulus* have been pointed out by Lankester ('82 and '84), though in his later paper he does not refer to their possible homology with the segmental organs of worms, (suggested by Packard '75^a) as he was unable to find any ducts. As described above I have found these ducts in the young, and doubtless the same result will be obtained when the young of the scorpion is studied by means of sections. This is the more probable since Bertkau ('84) has found homologous glands in various spiders, which were without external openings in the adult, but in the young of *Atypus* the duct was found to open at the base of the third pair of legs (fifth pair of appendages).¹ Michael ('83, p. 21) describes similar glands in the Oribatidæ but failed to find their openings. The exact correspondence of these glands both in position and in their ducts, and their closely similar histological structure, is a point of no little importance in the argument for the union

¹ These glands have long been known in spiders, but had been regarded generally as belonging to the digestive tract. They were practically discovered and their true structure first described both in Scorpions and Spiders by Professor Lankester.

of the Arachnids and *Limulus* in a common group. It should be noted, however, that in complication, size, &c., the resemblance between the glands of *Limulus* and those of the spiders is closer than between those of *Limulus* and those of the most limuloid of Arachnids, the scorpions.

Packard ('75^a), discovered these organs and suggested their homology with the segmental organs of worms; Lankester ('82, p. 101) said "Possibly such coxal glands are the modified and isolated representatives of the complete series of tubular glands (nephridia) found at the base of each leg in the archaic Arthropod *Peripatus*;" while Michael ('83) suggests the homology of the glands in the Oribatidæ with those of *Scorpio*, *Limulus*, Crustacea and Worms. Packard, in a later paper ('83), while failing to see the argument for the close association of the Arachnids and *Limulus* derived from this organ, recognises the correspondence between the glands of *Limulus* and those of the Crustacea; but instead of making his comparisons with the "shell-gland" he refers only to the "green-gland" of the Decapods, an organ which occupies a different position in the body. His conclusion that "The occurrence of these organs in the Arachnida, as well as in Crustacea, indicates the independent origin of these two groups of Arthropoda" is intelligible only on the supposition that the word here italicised is a slip of the pen. This similarity of segmental organs in *Limulus* and the Arachnida neither loses nor gains in force by a comparison with the shell-gland of the lower Crustacea. This organ is a coiled tube with a cæcal inner extremity and an efferent duct which opens at the base of the second maxilla (a position which I shall show further on is exactly comparable to that where the segmental organs of *Limulus* and the spider's empty) but differs from the glands in the other groups in retaining its external opening through life. Thus the coxal glands of the one are the exact homologous of the shell-glands of the other.

In the Crustacea two of the primitive series of segmental organs are found, one being the shell gland, the other the organ variously termed antennal gland or green gland. Grobben

('80, p. 103) says that the antennal and shell glands agree in structure. Both terminate cœcally, and have a long convoluted duct opening at the base of the corresponding pairs of appendages.

The homology of the shell gland of the Crustacea with the segmental organs of the worms has been alluded to by many observers since Leydig first suggested it. Their similar origin,¹ structure, position, and ducts, all seem to point to their homology. The strongest arguments against it are that the series contains at the most but two pairs,² and that no connection with the body cavity exists. Recent authors (Leydig, '78, Weissman, '74, and Urbanowicz, '84) seem to strongly favor the homology.

The consideration of the evidence presented by the nervous, digestive, and circulatory systems I leave for another article; that by the respiratory system has already been alluded to. It may be well here to combine the various points of similarity between *Limulus* and the Spiders, on the one hand, and the Crustacea on the other. In this I embody the results gathered by Professor Lankester in his valuable paper ('81), so often referred to.

Limulus agrees with the Arachnida and differs from the Crustacea (1) in having six pairs of primitively post-oral pediform appendages; (2) a seventh pair bearing the outlets of the reproductive organs; (3) the ninth, tenth, eleventh, and twelfth, modified for respiratory purposes (the eighth pair in each shows a readily homologised structure, but different functions); (4) in the character and structure of the upper lip; (5) in the presence of a metastoma derived from the sternal portion of the sixth cephalothoracic segment.

¹ Reichenbach ('77) claimed that in *Astacus* the antennal gland was epiblastic in origin, a mistake which was corrected by Grobben ('79). Though Ishickawa ('85) repeats the statement for *Atyephira*.

² Huet ('82, I have not seen his final paper) describes a series of what he regards as segmental organs in the thorax of terrestrial Isopods (Oniscidæ), which are arranged one pair in each segment. The caudal glands of Lereboullet ('52) would appear to belong to the same series. Some of these have been found in the aquatic Oniscidæ.

The same agreements and differences are seen in (6) the possession of an entostermite with the same shape, position, and histological structure; (7) in the backward extension of the tergum of the head, so as to form the dorsum of the cephalothorax; (8) in the distribution of the eyes; (9) in the existence of a blood colored blue by the presence of hæmocyanin (10) in the branching and anastomosing spermatic duct (Benham, '83); (11) in the mode of formation of the mesoblast, its segmentation, and the early extension of the body cavity into the limbs; (12) in the mode of formation and structure of the alimentary canal and its appendages;¹ (13) the elongate stomodæum and the short proctodæum; (14) in the origin of the sternal artery and its intimate association with the ventral nervous cord; (15) the early closure of the duct of fifth (the only) segmental organ; (16) the absence of the second segmental organ (antennal gland).

Besides these points there are a number of other points in which the two agree, and which are but rarely paralleled in the Crustacea, and then not in groups which anyone would think of placing near *Limulus*. Among these may be mentioned the possession of vibratile spermatozoa (paralleled in the barnacles²), the concentration of the nervous system around the œsophagus (also in *Brachyura*), a brain which never supplies any of the appendages.

This array of similarities is almost conclusive, but we must turn to the other side of the question, and seek the arguments against the association of *Limulus* with the Scorpions. Dr. Packard is by far the most able advocate of the Crustacean affinities of *Limulus*, and in his latest paper ('82), in which he deals with this subject (confessedly a reply to Lankester's "*Limulus* an Arachnid"), we find the following summary of the arguments against placing *Limulus* in the Arachnidan phylum. In the quotation I have inserted numerals for convenience of reference below: "At the outset it will be remem-

¹ These points will be discussed in the second part of this paper now in preparation.

² They also have a slight motion in some other Crustacea.

bered that *Limulus* differs from the Tracheates, including the Arachnids, (1) in having no tracheæ, (2) no spiracles, and (3) no Malpighian tubes. It differs from the Arachnids in these characters, also (4) in having compound eyes, (5) no functional mandibles or maxillæ, (6) the legs not terminating, as generally the case in Tracheates, in a pair of minute claws, while (7) its brain does not, as in the Arachnida, supply both eyes and the first cephalic appendages. On the other hand, *Limulus* agrees with the Crustacea (8) in being aquatic (9) and breathing by external gills attached to several pairs of biramous feet, in having (10) a simple brain, which, as in some typical Crustacea (Branchiopoda, &c.), does not supply any of the appendages, while the structure of (11) the circulatory, (12) ingestive, and (13) reproductive organs agrees with that of the Crustacea; and, (14) as we have shown in our embryology of *Limulus*, . . . the development of *Limulus* is like that of certain other Crustacea with a condensed metamorphosis, (15) the possession of an amnion being paralleled by that of *Apus*. In all essential points *Limulus* is a Crustacean, with some fundamental features in which it departs from the normal Crustacean type, and with some superficial characters in which it resembles the Scorpion."

Of these points numbers 1, 2, and 15 have already been discussed in this paper, while numbers 5, 6, and 8 are trivial and of no importance. Since Dr. Packard wrote the above, Mr. Benham ('83) has shown that the thirteenth of these points is not true, while the answer to 11 may be found in Professor Lankester's paper. In regard to number 12 I would say that in development, except to a slight extent in some Tetradecapods, *Limulus* does not agree with the Crustacea, the hypoblast being solid and a midgut not appearing until after hatching. The origin of the liver and the structure of its ducts are greatly different in the two groups. Points 7 and 10 are the same and deserve more attention. It has been shown by Balfour and by Schimkewitch that in the spiders the ganglia of the first pair of appendages are primitively post-oral, and that with development they acquire a pre-oral position and eventu-

ally fuse with the "brain." In *Limulus* the same process occurs but stops just short of the fusion of the corresponding ganglia with the pre-oral ones. For a knowledge of the condition of the brain in the Scorpions, one must await a detailed account of the structure. As the case is at present Dr. Packard distinctly states ('80^a) that the brain supplies the first pair of appendages; while Newport's figure ('43, pl. xii, fig. 15) shows the nerves as arising from the side of the brain. Newport was a very careful worker but the subject needs further study. On the other hand, in all the Crustacea, not excepting *Apus* and *Limnetis* (Branchiopoda), this coalescence of ganglia has gone still further than in *Limulus* or Arachnids, and even in the earliest stages the first pair of appendages are pre-oral in innervation, while the ganglia of the second pair (*Apus* excepted) move forward with growth from a primitively post-oral position and form an important part of the brain.

Fourth in the series comes the presence of simple lateral eyes in the Arachnids and compound eyes in the other. I have not yet studied my sections of the eyes of the young carefully enough to throw any light on the question. Since Dr. Packard wrote, Lankester and Bourne have shown ('83) that if a comparison be made of the whole compound eye of *Limulus* with the entire lateral group of the Scorpion the correspondence is very nearly perfect; and that "if we supposed a common ancestor of the Scorpion and King Crab to have exhibited a lateral 'ocular area' which possessed a single feebly developed cuticular lens, then by two slightly divergent lines of differentiation we can obtain the grouped eyes of *Scorpio* on the one hand, and the polymeniscous eye of *Limulus* on the other hand." The same authors also show that "the essential agreement of the central eyes of *Limulus* with those of Scorpions is obvious." As to Professor Lankester's well-known accuracy in histological work no comment is necessary and no confirmation is needed, but I would say that before his results were published I carefully studied the eyes of the adult *Limulus*, and so far as that

animal is concerned I can vouch for the accuracy of his account.

In regard to the eighth point of Dr. Packard's paper, it will at once be recalled that the gills in the Crustacea are formed on several distinct plans, and an effort to homologise those for instance, of forms so closely related as the Lobster and *Squilla* is not easily carried out. I regard the gills of *Limulus*, like those of *Apus*, as derived from some ancestral form with expanded and flattened appendages, which exposed a large surface to the water and hence became largely the seat of respiration. With a thickening of the cuticle and increase in size, the necessity for increased respiratory surface led in *Limulus* to the formation of outgrowths (gill-lamellæ) from these appendages just as occurs (though not from the same reason) in the individual to-day. The not very plainly marked biramous character of the abdominal appendages of *Limulus* is an ancestral feature which may have been lost in the Arachnid stems from the early change which they undergo. Nothing approaching a biramous condition is found in the six cephalothoracic members of either spiders¹ or horseshoe crabs except in the sixth pair of the latter, and to homologise the joints of that member with the protopodite, exopodite, endopodite, and epipodite of the "typical" crustacean limb is a task that I do not care to undertake. It seems, on the other hand, to be much more like one of the thoracic feet of *Apus*.

The condensed metamorphosis mentioned in the fourteenth point is, I suppose, another method of saying that the development is direct, for certainly *Limulus* shows nothing that could be regarded in the light of a metamorphosis, and it is just this lack of any larval forms which renders it so difficult to decide upon the affinities of the forms in question. Had we any nauplius or zoea stage the problem would be an easy one to solve. As it is the development is direct just as it is in Tetradecapods, Spiders, and many other forms.

The third of the points is the most difficult to explain. In

¹ Croneberg's observations on *Dendryphantès* ('80, pl. xvi, fig. 14—16) need confirmation.

both Hexapods and Arachnids two or more urinary tubules are developed from the proctodæum (their development in Arachnida has not been described); in *Limulus* nothing of the sort is found, nor is anything of the kind certainly known in the Crustacea. As I shall have again occasion to refer to these organs I will leave the enumeration of the horns of the dilemma until then.

The close relationship existing between *Limulus* and the Trilobites has often been insisted upon by naturalists since Lockwood first saw a young horseshoe escape from its egg. The recent work of Walcott ('81), though I cannot accept his interpretations in many respects, serves to show that the resemblance between the two are not so great, or rather the differences are too great, to warrant a close association of these forms. This is more apparent from the discovery of the Ohio specimen described and figured by the same gentleman ('84). The veteran carcinologist, Henri Milne Edwards ('81), also fails to recognise these affinities, though he places his objection on different grounds from those that I hold. I do not care to enter into a discussion of the problem, but would state that according to these results and specimens the Trilobites had a series of non-chelate ambulatory limbs extending to the extremity of the body. Each limb consisted of a basal joint, from which arose an endopodite with six cylindrical joints, a three-jointed setose epipodite (exopodite?), and outside of these, just as in the lobster, the branchial organs. These latter were filamentary and straight or spirally coiled. With such a different appendicular structure it seems to me that we must have more than a strained resemblance of dorsal surfaces before admitting any close resemblance between the two, though it must be said that there is a certain resemblance between the four anterior legs of the Trilobite and their relationship to the mouth (as restored by Walcott, '81, pl. vi, fig. 1) and the four posterior cephalothoracic limbs of *Limulus*.

If we are to accept these resemblances as indicative of a homology between the two we must conclude that the first two pairs of appendages of the Trilobites have been lost, to say

nothing of the change in form and function of the abdominal appendages. It also necessitates a change in the nomenclature of the regions of the Trilobite body. The head will correspond to the cephalothorax of *Limulus*, and the thorax and abdomen or pygidium together will equal the abdomen of the horseshoe crab.

THE SYSTEMATIC POSITION OF THE ARACHNIDA.

Since 1858, when Leuckart divided the old group Articulata into Worms and Arthropods, and the latter group into the equivalents of Branchiates, not a single author, so far as I am aware, with the exception of Van Beneden and Lankester, has questioned the close association of the Arachnids with the Hexapods and Myriapods in a common group called either Insecta or Tracheata. Entirely independently of Professor Lankester's papers ('77 and '81) I came to somewhat similar conclusions, which may be stated as follows:—Omitting Peripatus, the Arthropods should be divided into three equivalent groups or classes, one embracing the Crustacea, the second *Limulus* and the Arachnids, and the third the Hexapods and possibly the Myriapods. The last of these for convenience may be called Insects, the second Acerata (a modification of the name given by Latreille to the Arachnida alone). The Crustacea and Acerata are more closely allied to each other than either to the Insects, and the nearest representatives to-day of their common ancestor are *Limulus* and *Apus*. Before these two classes diverged the Insects had left the primitive Arthropod stem.

The points of difference between the Arachnids and the Insects are many, those between the former group and the Crustaceans less in number and more readily to be considered as derivations of a common ancestor. These points and their bearings I will consider in a rapid manner beginning with the anterior appendages, the posterior in all of the groups showing too many variations to afford any decisive results.

First, in the Insects we have antennæ which are primitively pre-oral, and not to be homologised in position or character

with any structures as yet found in Crustacea or Acerata. It has been shown by several students that in the latter group all of the appendages are, in the embryo, post-oral both in position and in nerve supply. The same is true of the second pair in the Crustacea, and in the adult Phyllopods (which are admitted by all to be the most primitive of the Crustaceans), both anterior pairs receive their nerves from the œsophageal commissure, the corresponding (?) ganglia being distinctly post-oral in position.¹ It would appear possible that in the very early stages of other Crustacea the same condition may exist, as in several forms the rudimentary first pair of appendages has not a distinctly pre-stomial position. The first to suggest itself is *Moina*, where, according to Grobben ('79), the first pair of appendages to appear have a position decidedly posterior to the stomodeal invagination. This pair Grobben interprets (and possibly correctly) as the second antennæ, but there is not certainty on this point. In the Nauplius of *Palæmon*, according to Bobretzky² ('73), the first pair are on a level with the labrum, and show distinctly the similarity to the rest of the post-oral series. In the corresponding or a little earlier stage of *Astacus* (Reichenbach, '77, pl. x, fig. 8) they are some distance behind the labrum and the oral depression. The same is true of *Eupagurus* (Mayer, '77, pl. xiii, fig. 18) and of *Crangon* (my own studies).

The antennæ of Insects, on the other hand, always arise from the procephalic lobes. The possibility that *Peripatus* is a but slightly modified descendant of the ancestors of the Hexapods and Myriapods makes its evidence of some importance in this connection. Balfour, after a careful study of the anatomy, concludes that in *Peripatus* ('83, p. 217) "the antennæ are prolongations of the dorso-lateral parts of the anterior end of the body;" and his figures show that the eyes intervene between the antennæ and the other appendages. Kennel, from a study of two other species of the same genus,

¹ Pelseneer's results as to the brain of *Apus* ['85] require a modification of this statement.

² Teste Faxon ('82, pl. xi, fig. 6).

comes to a similar conclusion, and carries it further, as follows ('84, p. 200):—"Obwohl nun dieses segment [the 'praeorale Abschnitt'] seiner Entstehung nach allen anderen des Körpers homodynam ist, glaub ich doch es denselben gegenüberstellen zu müssen da es sich in ganz anderer Weise umbildet und niemals Organe erzeugt, wie sie allen anderen Segmenten ausnahmslos eigen sind; es entstehen in ihm keine Segmentalorgane, keine Drüsenbildung, auch keine Extremitäten; denn ob die Tentakel für Gebilde gehalten werden dürfen, welche den Extremitäten der Rumpfsegmente homolog sind, ist auch bei den übrigen Tracheaten, sofern man die Antennen derselben als gleichwertige Bildungen durch die ganze Reihe hindurch auffast, nicht ausgemacht."

A considerable difficulty arises when we try to homologise the antennæ of Insects with those of Peripatus. In the latter, as has just been said, these organs receive their nervous supply from the brain in front of the eyes. In Myriapods, according to Newport, the case is the same; but in Hexapods the case seems to be different; but careful study is yet needed to settle this point. In the embryo Hexapod the antennæ rise from the posterior side of the procephalic lobes, and there appears to be much evidence that they are innervated from a distinct ganglion from that which supplies the eyes. On the other side, Ayres ('84 pl. 20, figs. 22 and 23) represents the antennal lobe in *Æcanthus* as being in front of the ocular lobe and between it and the origin of the nerves to the ocelli, a condition which needs confirmation.

Should this view that the antennæ of Peripatus and Hexapods are not homologous prove true it would throw considerable doubts upon the comparatively close relationship which has been supposed that they hold to each other, a relationship which may be doubted on several other grounds, some of which will be mentioned later.

In the Spiders but one recent author (Croneberg, '80) has, so far as I am aware, found what he regards as antennæ. He figures (pl. xvi, figs. 14—16) the embryo of *Dendryphantès*, showing the upper lip (rostrum) arising as two appendage-like

lobes, in front of the rudimentary chelicerae and between the procephalic lobes. His figures clearly show however, that on account of their relations to the nervous system these lobes cannot be regarded as homodynamous either with the post-oral appendages, or with the appendages of insects.

Assuming for the moment that the view that the antennae of Insects are not represented in either the Acerata or the Crustacea is correct, a comparison of the three groups may give us some further interesting points. In the following schedule only the anterior segments are included, and the appendages are called by their usual names, which no one regards as indicative of homologies extending through the whole Arthropodan phylum.

HEXAPODA.	ACERATA.	CRUSTACEA.
(1) Antennæ . .	Absent . .	Absent.
(2) Mandibles . .	Chelicerae . .	Antennulæ.
(3) Maxillæ . .	Pedipalpi . .	Antennæ.
(4) Labium . .	1st legs . .	Mandibles.
(5) 1st pair legs . .	2nd pair legs . .	1st maxillæ.
(6) 2nd pair legs . .	3rd pair legs . .	2nd maxillæ.
(7) 3rd pair legs . .	4th pair legs . .	1st maxillipeds.

This comparison is a strictly serial one and starts on the assumption that the first pairs of primitively post-oral appendages are homologous throughout. That this is true in the cases of the two last groups is, to my mind, very probable, but with regard to the Hexapods there is some reason for doubt. In following it out we are led to some interesting regional coincidences. It brings the end of the thorax of the Hexapod and Spiders into exact correspondence. In the case of the Crustacea a line of demarcation at the same spot is frequently visible, and one needs but to mention that it corresponds exactly to the posterior end of the head of the Tetracepods, and is well paralleled in Squilla, and in the larva of Palinurus. In the Entomostraca a division at the same point may be seen in the larvæ as also in the protozoa of Lucifer. These may all be analogies, and the fact that no such regional distinctions

are found in the most primitive group of Crustacea, the Phyllopods, is against their having much significance.

The comparison also leads to another correspondence in the Crustacea and Acerata, which goes as far to prove its validity as did the regional comparison in the case of the Spiders and Hexapods. In both Crustacea and Arachnids the segmental organs (shell glands of the former, coxal glands in the latter) empty at the same point; at the base of the third pair of walking legs in the Spiders and *Limulus*, and at the base of the second maxillæ in the Crustacea, or, in other words, at the base of the fifth pair of appendages in each. It seems to me that this persistence of exactly the same segmental duct in these two groups and the absence of any corresponding organs in the Hexapods is an argument of no little weight.

If, however, it be shown that a variation or a disappearance of segments or appendages may take place at the anterior end of the Arthropod body this comparison will lose part of its force. That such obsolescence in the adult occasionally occurs is well known, but the presence of the appendages in the young readily enable us to check our results. Setting aside the parasitic forms the best known cases are presented by certain Copepods, Apus, and the Oniscidæ, but the fact that the normal condition is found in their near relations shows that this fact is of no morphological importance in this connection. In *Eurypterus*, according to Lankester, there is a case of an apparent disappearance of one pair; but until it is proved that the Trilobites are related to the Acerata (a point on which, as mentioned above, Walcott's observations throw considerable doubt) the assumption that the cephalic buckler of these forms is the exact homologue of the cephalothorax of *Limulus* is not warranted, and in case it turns out that the two are different these fossils throw no light on the subject. Until it is proven that a segment or an appendage may disappear in the anterior end of the adults of a large group of animals, it is justifiable to assume the exact homology of the first pair in all three groups, as I have done above. It is possible that an embryological study of the cement glands,

together with the mandibular glands of Hexapods and the chelicerai glands of Spiders, may throw some light on this point.

If, as pointed out by Lankester, the tracheæ of the Arachnids have arisen from the gills of the *Limulus*,¹ then either those of the Hexapods must have been derived from those of the Arachnids, or those in the two groups must have arisen independently. The latter I believe to be the true case, and without entering into any argument to establish this point, I would call attention to the fact that in the terrestrial Isopods (*Oniscidæ*) the gills become permeated with trachea-like air-tubes. Long ago Lereboullet ('52, pl. vii, figs. 148 and 149) figured these ramifying tubes, while, to consult a more recent student, Leydig ('78, p. 265, pl. xi, fig. 32) describes the mode of their formation. The cells of the blood-spaces of the gills secrete an internal cuticula, and in the branching cavities which this contains the air circulates. This forms tracheæ, certainly without any phylogenetic connection with those of the so-called tracheates, but which present many analogies with them. It also affords good grounds for the supposition of Professor Lankester that the trachea, at least in some groups, have followed the course of pre-existent blood-vessels.

Another fact of some weight in this connection lies in the position of the tracheal openings. In the Arachnids they

¹ Schimkewitsch (84*) denies this, but offers no reasons, but rather seems to misapprehend the whole argument relative to the relationships of *Limulus* to the Arachnids. He says (l. c., p. 67), "Les poumons mêmes peuvent être considérés comme une modification des trachées en faisceaux des chenilles et des myriapodes. Il est très probable que les ancêtres des Arachnides et des autres Trachéates avaient cette forme des trachées en faisceaux, laquelle a été transformée chez les Araignées en poumons. Tout cela me fait croire que les formes trachéennes et les Tetrapneumones sont plus anciennes que les Dipneumones." Further on (p. 84) he says, "Par leur appareil circulatoire et leur système musculaire, les Arachnides supérieures se rapprochent au contraire des Limulides; mais cette ressemblance peut être expliquée par l'identité qu'existe dans la configuration générale du corps de ces deux formes; car les Limules, d'après leur évolution (état Nauplius et état de Trilobite) et d'après la constitution des l'appareil respiratoire, sont des vrais Crustacés privés d'antennes."

perforate the ventral plates, as also in the diplopod Myriapods. In the Hexapods and the chilopodous Myriapods the stigmata are placed outside these plates. These differences in position of the external openings may indicate a separate origin in all these groups, especially when we consider Sedgwick's speculations ('84) on the origin of tracheæ. Again, it should be noticed that no traces of cephalothoracic stigmata or tracheæ occur in the Spiders.

One objection to the separation of the Hexapods and Arachnids, and the closer connection of the latter with the Crustacea, lies in the fact that biramose appendages are characteristic of the branchiate and simple of the tracheate Arthropods. This, however, may be regarded in two lights. In the ancestral Arthropod both exopodite and endopodite may have been present, and both branches may have been retained in the aquatic and only one in the terrestrial forms, or the ancestor may have had broad and flattened but unbranched appendages which have been variously differentiated in different groups. There are several facts in favor of either of these views, though the evidence presented by *Apus*, together with many other points render the latter the more probable. To mention one or two of these: *Apus* is by nearly all morphologists regarded as the most ancestral type of Crustacea. Its members (Lankester, '81^a) are broad and flattened plates bearing typically six internal and two external lobes, but studying the adult alone no one would ever arrive at the idea of exopodite, endopodite, and epipodite. In the Nauplius stage, in the second and third appendages, a biramose condition exists. This is, however, to be regarded as secondary in its nature, just as is the Nauplius itself. In the maxillæ of forms even as high as Decapods, this lamellar condition persists, and all attempts to trace the homologies of exopodite and endopodite meet with but partial success.

The evidence on the other side is fragmentary. Croneberg ('80, pl. xvi, figs. 14—16) describes and figures an embryo Arachnid (*Dendryphantès*) in which the pedipalpi are distinctly bifid at the tip. This, however, has never, so far as I am

aware, been seen by any other observer, and needs confirmation. Among other groups of Tracheates are the peculiar antennæ of the Pauropids, with their basal joints bearing two branches, one of which in turn is bifid. The investigations of Mr. Wood-Mason ('79) show that in some of the Thysanura and in the Cock-roaches some of the appendages exhibit a biramose condition. While some of his facts and many of his speculations need confirmation,¹ I think that in some instances (enough for our purposes) he has proved his points. Probably more extended studies on the Thysanura will throw important light on the relationships of the Hexapods to other forms. Patton ('84, p. 596) describes a similar condition in *Blatta germanica*: "A rather striking variation was found in the first and second maxillæ of *Blatta*, which were formed respectively of two and three branches, the second maxillæ thus attaining the typical trichotomous structure of the Crustacean appendages."

The existence of Malpighian tubes in Spiders and Hexapods is, without doubt, the greatest obstacle to the arrangement of the Arthropods here advocated, since they are absent in *Limulus* and the typical Crustacea. Their mode of development debars us from considering them as modified segmental organs, and we can only say that they are either inherited from an ancestor common to all Arthropods and have disappeared from some groups, or we must admit that they have appeared independently in two or more branches of the Arthropods. Which of these two alternatives we must take cannot be at present decided, though some facts may throw light upon the subject. The first thing that we notice is that those groups (Hexapods, Myriapods, and Arachnids) which possess them are terrestrial, while the great bulk of the Crustacea are aquatic; and this at once suggests that the organs may have an origin from similar physiological causes without any phylogenetic connection existing between them. Turning to those Crustacea which lead a terrestrial life we meet with some striking confirmations of this hypothesis.

Zenker ('54, pp. 106, 107) describes in the young *Asellus*

¹ *E.g.*, The structure of the mandible in *Machilis*.

(a fresh-water form) six glandular spots on either side of the abdomen, which later unite to form a tube, though he did not find the place where it opened. Weber ('79, p. 237) mentions and ('81, pp. 608—612) describes and figures tubes emptying into the hinder intestine in *Trichoniscus*, and says that they also occur in other *Oniscidæ*. He also states that he found depositions of urates, a fact which at once deprives the opinion of Wrzesniowski ('79, pp. 514, 515) of much of its force. The investigations of Nebeski ('80, pp. 122—127) are the most interesting. This author describes certain organs arising at the beginning of the hind gut of certain *Amphipods*. In the strictly aquatic genera these glands are small, but in the more terrestrial *Gammarus* they become well developed, while in *Orchestia*, a form living in the sand above high tide, they are very long and tubular, and the histology shows that they have active secretory or excretory functions. In position and origin they correspond closely with the Malpighian tubes. His series on pl. ii, fig. 14, is very instructive.

Nebeski's observations, however, are not conclusive, for he shows the rudiments of the same organs in *Amphipodous* genera which are solely aquatic. Gamroth ('78, pl. x, fig. 14) figures two globular glands occupying the same position in *Caprella* which he regards as urinary, and Haller ('80, p. 384), studying the same genus, agrees with him. These forms are all confined to the *Tetradecapods*, and so far as I am aware, no similar organs have been found in any other *Crustacea*. Still they may be derived from an ancestor common to them and to all the *Tracheates*. These ancestral glands may have been very small, possibly mere glandular surfaces, and changed conditions in life have caused their increased development. A somewhat parallel case is that noted by Grobben ('80) that the antennal gland differs in its length and complication in the salt- and in the fresh-water members of the same genera of *Copepoda*.

This of course is but analogy. It seems at present as if these organs had arisen in the *Crustacea* independently of their existence in other *Arthropods*. If this be the case, their

existence in Hexapods and Myriapods loses some of its force. If the reverse be true the argument, derived from these organs, for the maintenance of the group Tracheata has even less weight.

From these and other facts it seems to me probable that the ancestral Hexapod left the main Arthropod stem some time before the separation of the Crustacea and Acerata. The common ancestor of all three was an elongate animal with flattened ambulatory appendages, some of which (except possibly the first) were adapted for the purposes of eating. The head bore on its dorsal surface scattered sensory (optic) organs. In most, if not all, the segments of the body were segmental organs, through which passed the products of the genital glands, no genital ducts being differentiated. The reproductive glands were probably ventral in position; the nervous system consisted of a single supra-oesophageal ganglion, a ventral chain and a supra-intestinal loop (*vide* Peripatus). The alimentary canal traversed the whole length of the body; and, contrary to the opinions of the Hertwigs ('81), it seems probable that circulation was effected by the pulsation of the dorsal splanchnopleural muscles, the coelom containing the circulatory fluid, and that this portion was constricted off to form the heart.

The Hexapods left this stem at a time when the first pair of originally post-oral appendages were moving towards a pre-oral position.¹ The Spiders and Crustacea continued together until they had the following characters in common:—One pair of appendages had a distinctly pre-oral position, and the basal joints of at least the two succeeding pairs were employed in the comminution of food. The segmental organs had disappeared from the first, third, fourth, and sixth body segments and possibly from others. The genital glands became concentrated near the middle of the body, and the reproductive products passed out through the segmental organs in the same region. The genital glands themselves had assumed a dorsal

¹ Hatschek ('77) says that the ganglia of the mandible of the embryo Bombyx becomes transformed into part of the oesophageal connectives.

position. Most of the post-oral parts were concerned in respiration.

In the foregoing I have taken no account of Pauropus and the Myriapods, the facts concerning them being not yet well enough known. It seems possible that they have no connection with the Hexapods. The structure and relationship of the trachea, the ventral position of the genital glands, the mouth parts, the innervation of the antennæ, the existence of segmental organs in *Peripatus* and their possible homologues in the foramina repugnatoria of the Myriapods, all need to be taken into consideration in this connection.

I do not intend to defend in extenso these points at the present time; a few explanatory notes may, however, be of value. The relationship of the oviducts to the exterior in the Arthropods seems to point to the conclusion that here, as in many other animals, they are modified segmental organs. The positions in which these ducts empty would then warrant the conclusions given above regarding the relationships of the segmental organs. Several authorities (especially Grobben, '79 and '81^b) have pointed out that the genital glands of Arthropods are ventral in origin, and that they later assume a dorsal position. This author also points out, as an indication of inferiority, that they permanently retain a ventral position in *Peripatus* and Myriapods.

Whether the first pair of appendages in the ancestral Arthropod played a part in eating is uncertain, though the facts that it now does so in the Hexapods, Myriapods, and *Peripatus*, and that in the other groups it at first has a post-oral position is in its favor. In *Limulus*, as in *Apus*, and in the Nauplii of various Crustacea, the basal joints of at least two pairs behind the first are so employed, and in the two forms first mentioned the series is extended further. In all it is the basal joint which is so employed, and in the young of some and the adults of others the distal portion is used for ambulatory purposes.

NOTE.—Since this article was sent to the printer several papers have appeared which have more or less bearing on the subjects here discussed, though

none cause any serious modification of the views here held. Professor Lankester ['85], entirely independently, has arrived at essentially similar views as to the homology existing between the lungs of Arachnids and the gills of Limulus. The causes assigned for the change differ, a matter of no importance in this connection. Mr. Pelseneer ['85] has shown that the brain of Apus is a "syncerebrum," a fact which modifies some of the statements in the text. The discovery by Mr. Spencer that the urinary tubules of the Amphipods are mesenteric ['85] is more important, though I must say that my argument demands analogies rather than exact homologies.

Dr. Packard ['85] has studied some sections of a stage about equal to my figure 5, and from them he draws the conclusion that the development of the brain of Limulus is entirely different from that of Arachnids. He distinctly states that the stage cut had the first pair of appendages in a post-oral position, but still he regards the nervous invagination in sections which pass through the first pair of limbs as the brain. This being the case, his argument falls to the ground. Contrary to his statements, I would say that the development of the brain of Limulus is closely like that of the Arachnids, and that Crustaceans do have procephalic lobes.

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EXPLANATION OF PLATES XXXVII, XXXVIII,
AND XXXIX,

Illustrating Dr. J. S. Kingsley's Paper on "The Embryology
of *Limulus polyphemus*."

Reference Letters.

a. Anus. *ab.* Abdomen. *ap.* Appendage. *b.* Modified blastopore. *bc.* Blood-corpuscle. *bl.* Blastoderm. *bs.* Blood-sinus. *c.* Cœlom. *cm.* Commissure. *cn.* Connective. *co.* Connective tissue. *ct.* Second larval cuticle. *cx.* Cephalothorax. *dt.* Deutovum. *e.* Eye. *ec.* Edge of carapax. *ei.* Epiblastic invagination for brain. *eo.* External opening of segmental organ. *ep.* Epiblast. *f.* Flagellum of sixth pair of legs. *fn.* ? Funnel of segmental organ. *ga.* Gill-bearing appendage. *gl.* Gill-lamellæ. *gn.* Ganglion. *h.* Heart. *m.* Mesoblast. *mo.* Mouth. *mp.* Mesoblastic partitions. *mt.* Metastoma. *mu.* Muscle. *n.* Nerve. *nf.* Nerve-fibres. *ng.* Neural groove. *nr.* Neural thickening. *nu.* Nucleus. *o.* Operculum. *oc.* Ocelli. *p.* Proctodæum. *pab.* Abdominal appendage. *pc.* Procephalic lobes. *pl.* Pulmonary lamellæ. *pn.* Pulmonary invagination. *sg.* Segmental organ. *so.* Somatopleur. *sp.* Splanchnopleur. *st.* Stomodæum. *stg.* Stigma. *t.* Telson. *x.* Problematical organs of Fig. 3. *y.* Yolk. *yg.* Yolk-granules.

The Roman numerals, I, II, III, &c., refer to the segments; the Arabic, 1, 2, 3, &c., to the appendages of the body.

PLATE XXXVII.

FIG. 1.—Surface view of egg half an hour after attempted artificial impregnation.

FIG. 2.—Same egg twenty-one hours later.

FIG. 3.—Surface view of an egg twenty-nine hours after artificial impregnation, showing two peculiar protuberances on the surface. For detailed description of Figs. 1—3 see p. 544.

FIG. 4.—Early embryo of *Limulus*. The lighter area (*m*) indicates the extension of the mesoblast; the key-hole-shaped centre (*b*) is the modified blastopore. Osmic acid preparation.

FIG. 5.—Embryo after the appearance of the compound eyes (*e*), the six pairs of cephalothoracic appendages (1—6), and the operculum (*o*). The blastopore has now divided into the pyriform mouth and anus. The neural groove (*ng*) is seen. Osmic acid preparation.

FIG. 6.—“Germinal disc” of embryo after the appearance of the eighth (first gill-bearing) appendage (*ga*¹). The distinction between the cephalothoracic and abdominal regions is now distinct. Osmic acid preparation; camera drawing.

FIGS. 7 and 8.—Surface and sectional views of deutovum after separation from the embryo. $\times 160$.

FIG. 9.—Diagrammatic upper and, Fig. 10, side views of segmental organ, constructed from sections. I am not certain about the internal termination, *f*. Cf. Fig. 27.

FIG. 11.—Embryo at the time of moulting. The second larval cuticle (*cl*) viewed obliquely from the front to show the procephalic lobes (*pc*).

FIG. 12.—Embryo at the time it escapes from the chorion and assumes a Limuloid appearance. The position of the eye (*e*), extending across a mesoblastic partition, is noticeable.

FIG. 13.—Horizontal section of an embryo of the stage shown in Fig. 14, taken above the level of the eyes, to show the extent of ingrowth of the mesoblastic partitions (*mp*). $\times 14$.

FIG. 14.—Under surface at the “trilobite stage,” constructed from camera drawings. Owing to difficulties of manipulation the brain could not be seen, and the metastoma may not be correct.

FIG. 15.—Reproduction of Metschnikoff's figure ('71, Pl. xvi, fig. 12). “A part of the embryo [of Scorpio] to show the first formation of the lung.” *p. ab*. Abdominal appendage. *pn*. Pulmonary sac.

FIG. 16.—Dorsal and, Fig. 17, ventral views of young Limulus at the escape from the deutovum and beginning of a free life. $\times 14$.

FIGS. 18, 19, and 20.—Diagrams illustrating the derivation of the pulmonary sacs of the Arachnids from the branchiæ of Limulus.

FIG. 18. A single gill-appendage with the gill-lamellæ, as shown in the adult Limulus.

FIG. 19. The gill-appendage is partially sunk in the ventral surface, and the gill-lamellæ exhibit a condition shown in Figs. 37 and 38.

FIG. 20. Diagram of pulmonary sac of an Arachnid. The gill-lamellæ are replaced by the pulmonary lamellæ; the pit of invagination has narrowed above and forms a spiracle.

PLATE XXXVIII.

FIG. 21.—Transverse section through fourth segment of embryo, shown in Fig. 12. The mesoblast has met above and below. $\times 64$.

FIG. 22.—Longitudinal section through the fourth to the seventh segments of an embryo in stage shown in Fig. 12. The section passes to one side of the median line, and shows the metastoma as a portion of the sternum of the sixth segment. $\times 76$.

FIG. 23.—Longitudinal section of embryo, Fig. 12, showing the opening of the segmental organ and the vesicular enlargement. $\times 150$.

FIG. 24.—Section through the nervous cord (not yet separated from the epiblast) behind the eighth ganglion of Fig. 12. $\times 380$.

FIG. 25.—Section through seventh ganglion of Fig. 12. The separation of the nervous tissue from the epiblast is complete in the middle, though not at the sides.

FIG. 26.—Section parallel to and outside of Fig. 23, cutting through three folds of the segmental organ. A thirteenth of a millimetre intervenes between the two sections.

FIG. 27.—Transverse section of half of fifth segment, showing three portions of the segmental organ and its internal opening, *fn*. $\times 150$.

FIG. 28.—Section of middle portion of segmental organ. $\times 1000$.

FIG. 29.—Median sagittal section of embryo, Fig. 15. The section passes through the edge of the mouth (*mo*) and shows the epiblastic involution (*ei*) which later takes part in the formation of the brain. Though the first pair of appendages are distinctly preoral (cf. Fig. 12), the first ganglion of the ventral chain (*gn* 1) retains a postoral position. Behind the eighth ganglion the nervous tissue has not separated from the epiblast. $\times 75$.

PLATE XXXIX.

FIG. 30.—Transverse section of third appendage and adjoining region of Fig. 6 at the first appearance of the coelom, showing it to be a schizocoel. $\times 150$.

FIGS. 31—33.—Formation of the heart, Fig. 31 being the most posterior. A twentieth of a millimetre behind Fig. 31 no lumen occurs in the solid mesoblast. A thirteenth of a millimetre intervenes between Figs. 31 and 32, and a fifth of a millimetre between Figs. 32 and 33. The conversion of mesoblast cells into blood-corpuscles is shown in all three figures. The thickening of the dorsal epiblast immediately above the heart is noticeable. $\times 442$.

FIG. 34.—Constructed from three longitudinal sections of Fig. 6, showing portions of the coelom in each segment of the body.

FIG. 35.—Transverse section through the middle of the fourth segment of Fig. 14, showing the segmental organs and the origin of the nerve to the fourth pair of appendages. $\times 75$.

FIG. 36.—Section through the metastoma (*ep*) of Fig. 14, showing the mesoblastic outgrowths (*co*) to form the artery surrounding the ventral nervous cord. $\times 150$.

FIGS. 37 and 38.—Longitudinal section of abdominal appendages, Fig. 14, showing the mode of formation of the gill-lamellæ, the inpushing being as marked as the outgrowths. Compare with Fig. 19.

FIG. 39.—Origin of deutovum as a cuticle secreted by the blastoderm. The section is taken from an egg in the stage represented in Fig. 4. $\times 300$.

FIGS. 40—43.—Transverse sections of the mouth region of Fig. 6, illustrating the formation of the stomodeum by a closing-in of the epiblast. Fig. 40 is the most posterior. $\times 200$.

FIG. 44.—Transverse section of the germinal area of Fig. 4, showing the origin of the mesoblast from the elongate "germinal groove" (modified blastopore).

FIG. 45.—Relative proportions of blastoderm and deutovum at the stage shown in Fig. 5.

FIG. 46.—Transverse section through anus of Fig. 5. $\times 175$.

FIG. 47.—Transverse section through the fourth pair of appendages of Fig. 5, showing the extension of the mesoblast and the absence of a cœlom at this stage.

Fig. 2.

Fig. 3

Fig. 1.

Fig. 12.

Fig. 13.

Fig. 16.

Fig. 17.

Fig. 5.

Fig. 6.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 14.

Fig. 15.

Fig. 18.

Fig. 19.

Fig. 20.

Fig. 21.

Fig. 22.

Fig. 25.

Fig. 26.

Fig. 27.

Fig. 28.

Fig. 29.

Fig. 23.

Fig. 24.

Fig. 30.

Fig. 31.

Fig. 32.

Fig. 33.

Fig. 34.

Fig. 35.

Fig. 36.

Fig. 37.

Fig. 38.

Fig. 39.

Fig. 40.

Fig. 41.

Fig. 42.

Fig. 43.

Fig. 44.

Fig. 45.

Fig. 46.

Fig. 47.

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