

Resumen por el autor, Alexander Petrunkevitch.

El sistema circulatorio y la segmentación de los Arácnidos.

El presente trabajo se basa principalmente en el estudio del sistema circulatorio de embriones, jóvenes y adultos del escorpión, varias arañas y *Limulus*. El autor hace notar el hecho de que en todos los Arácnidos la válvula cardio-aórtica presenta la misma estructura y posición con referencia al cefalotórax. El autor propone que se use este carácter permanente como el punto de partida para el estudio comparativo de la segmentación. Después investiga cuidadosamente el sistema arterial del escorpión sirviéndose de secciones e inyecciones. Corrige también los errores de varios investigadores que le han precedido en estos estudios. Se ocupa del plan general de estructura del sistema circulatorio, demostrando que las arañas también le presentan. La segmentación es objeto de discusión en detalle, estableciéndose homologías. También describe la aparición de un segmento falso en los escorpiones. En una comparación con *Limulus* indica que el caparazón de esta forma no es exactamente homólogo del caparazón de los arácnidos, sino que representa este más dos tergitos abdominales fusionados con él. La naturaleza aracnoidea de *Limulus* es, según el autor, dudosa, volviendo a reviver la idea de su origen trilobítico.

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THE CIRCULATORY SYSTEM AND SEGMENTATION IN ARACHNIDA

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TWO TEXT FIGURES AND TWO PLATES (SEVEN FIGURES)

The circulatory system in Arachnida has been made repeatedly the subject of studies and is fairly well known. Nevertheless, several points have escaped observation, partly on account of technical difficulties, partly because the attention of the investigators was directed toward other aspects of their study. Thus it came to pass that the relation of the circulatory system to the problem of segmentation in arthropods received less attention than it deserves. Indeed, in this respect the circulatory system may be more valuable than the nervous system and may, with a certain portion of the alimentary canal, of which I shall speak in a later contribution, help to establish definite homologies within the phylum of arthropods, and thus not only clear the relationships between the various classes belonging to that phylum, but also throw light on their phylogeny.

Many years ago, in the spring of 1905, while on a trip to Jamaica, West Indies, I collected scorpions and spiders, preserving them in the only fluid then obtainable in Jamaica, a mixture of alcohol with ether. The specimens were simply thrown into a jar and left in the fluid, as I did not intend to use them for any anatomical or microscopical study. Quite recently I wanted a few sections through scorpion embryos for class demonstration, so I imbedded and sectioned some quite young scorpions which had been carried by their mother on her back and of which I had many specimens representing stages before and after the first moult. I also took embryos out of the uterus. My surprise was great when I found that the fixation of the tissues was

remarkably good and that prolonged sojourn in the preserving fluid made the material considerably less brittle than it usually is on account of the voluminous yolk. A cursory examination of the sections has revealed so many interesting deviations from the usually accepted descriptions of the anatomy and embryology of scorpions, that a number of carefully oriented and sectioned series of various stages were made. All sections were purposely made 20μ thick. Exact orientation for sagittal, frontal, and transverse series was comparatively simple on account of the size, shape, and coloration of the material. A few of the series are absolutely symmetrical. The most satisfactory staining proved to be haematoxylin followed by orange G.

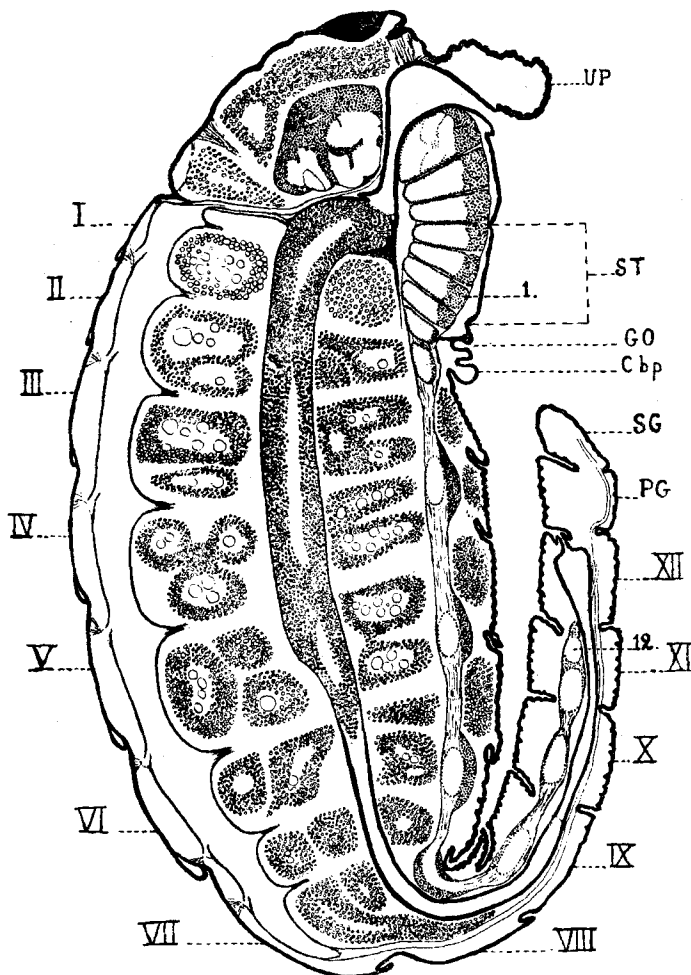
When the study of the circulatory system revealed the remarkable similarity in this respect between scorpions and spiders, I prepared corresponding series through very young spiders fixed for the purpose in my sublimate mixture. Two species of scorpion (*Centrurus insulanus* and *C. carolinianus*) and three species of spiders (*Agelena naevia*, *Lycosa carolinensis*, and *Pholcus phalangioides*), belonging to three different families, form the basis of the present study. While it would be very interesting to extend it over other groups of Arachnida, the diversity of the material leaves no doubt that similarity here is not accidental, but is the expression of true homology, and that generalization is therefore warranted and helpful.

To avoid possible misinterpretation of results, obtained only from the study of sections however perfect, a few scorpions were injected through the heart. These scorpions, *Centrurus carolinianus* of Texas, were obtained alive through the courtesy of Professor Painter, of the University of Texas, who kindly took the trouble to collect and mail to me a dozen specimens. Injection was made in a manner similar to that which I used for *Lycosa* several years ago, but the technique in the case of the scorpion is somewhat more complicated, owing to the fact that the heart is only imperfectly visible through the chitin. For this reason it becomes necessary to open the chloroformed specimen in a saline solution to expose the heart. The tergites of the second to sixth abdominal segments are carefully removed,

beginning with the posterior edge of the sixth tergite. The ligaments of the heart are cut close to the hypodermis with a sharp scalpel, as otherwise the heart would sustain injury. Freshly precipitated carmine as injection fluid proved to be quite satisfactory. Not only the large vessels become injected to their end near the base of the claws in the legs, but many ramifications of pedal arteries appear dark red. The injected specimen is next fixed in 95 per cent alcohol, dehydrated in absolute alcohol, and cleared in cedar oil, in which it becomes sufficiently transparent for further preparation. All organs obstructing the view are now carefully removed with the aid of two needles under a binocular dissecting microscope and the entire circulatory system exposed to view.

Usually the circulatory system in scorpions is described as consisting of a dorsally situated heart which gives rise anteriorly to the cephalic aorta and posteriorly to the posterior aorta. The heart itself is said to consist of eight chambers with a pair of ostia each, or eight pairs of ostia altogether, typically one pair for each segment of the body. The cephalic aorta is described as giving rise to a pair of arteries near its base, and a little further to another pair. The latter assume a downward course, pass on each side of the oesophagus, forming a ring from which six pairs of arteries are said to be given off to the appendages, while a single median supraneural artery runs from the ring backward above the nervous system. The usual description of the finer ramifications, as well as of the arteries given off by the heart, is irrelevant to our purposes and may be entirely omitted.

The microscopical structure of the heart seems in all Arthropoda to be more or less the same. Its wall is composed of three layers. The outer layer, the adventitia, consists of connective tissue. The heavy media or muscularis is formed either by a spiral muscle or by symmetrically arranged semicircular muscle fibers which meet in the middorsal and midventral line, as has been described by Bergh for insects. The inner layer or intima is, whenever present, nothing but a very thin transparent membrane which, according to Verson, may be nothing but the sarcolemma of the muscle fibers of the media.



Text figure A. *Centurus insulanus*, late embryo. Sagittal section in the plane of symmetry, showing all organs developed at that age. The black spot above is one of the median eyes. In front of the eye is the dorsal dilator of the pharynx. Abdominal tergites marked with Roman numerals I to XII without reference to their embryological history. 1, the first abdominal neuromere; 12, the last neuromere; Cbp, basal plate of comb; GO, genital opening; PG, poison gland; SG, sting; ST, sternum; the dotted lines showing its anterior and posterior margins; UP, upper lip (rostrum). Further explanation in the text.

This description of the gross anatomy of the circulatory system is, as we shall see, not quite correct, but served to show the similarity between the scorpion and *Limulus*. On the other hand, it created differences between scorpions and spiders especially, since the circulatory system of the latter had only recently been described correctly. Moreover, the exact position of the heart in both groups remained unnoticed, and yet therein lies its value from the morphological point of view.

The best material for the study of the circulatory system in the scorpion is furnished by that stage of embryos represented in our text figure A, in which all organs are already fully developed, but the nervous system has not yet reached its final state of contraction. The postabdomen is still short, the length of each segment being smaller than the diameter. The last neuromere has already begun to fuse with the preceding one and is almost entirely withdrawn into the fourth postabdominal segment. The first and second abdominal neuromeres have moved forward, passed the diaphragm, are completely within the cephalothorax, and are fused with the thoracic ganglia into one mass in which the separate neuromeres remain however clearly defined as they do, even in adult scorpions. The third abdominal neuromere is just on the verge of passing the diaphragm, while the fourth, which in the adult scorpion forms the last portion of the thoracic ganglionic mass, is still in the abdomen just behind the genital opening and on a level with the basal plate of the comb. In this connection we may state that Buxton had recently shown that the comb receives its nerves from the eighth postoral ganglion of the suboesophageal mass, i.e., from the third abdominal neuromere—an observation which I am able fully to confirm.

In median sagittal sections the diaphragm appears as a thin line. Its ventral portion runs from the ventral body wall just in front of the genital opening to the endosternite which lies above the nervous system. Its dorsal portion arises from a vertical transverse crest of the endosternite and proceeds upward to the dorsal body wall, where it is attached between the carapace and the first abdominal tergite.

The midgut may easily be recognized because of the presence of a cardiac valve, because of its thin walls and, further, because it is still filled with embryonic yolk. It has the appearance of a wide tube with larger lateral branches or diverticula usually known under the name of 'liver.' The anterior portion of the midgut proper runs at almost a right angle to the longitudinal axis of the body and belongs to the cephalothorax because it lies in front of the diaphragm. Its posterior end extends only to the end of the fifth abdominal segment. The diverticula of the midgut extend forward almost to the anterior end of the cephalothorax and backward through the entire preabdomen, the last dorsal diverticulum reaching even into the first post-abdominal segment. The gross anatomy and segmental arrangement of the diverticula are not easy to understand. Sagittal sections show a clear separation of the diverticula into ten metamerically arranged groups, two of which are in the cephalothorax and eight in the preabdomen. Their metameric nature is especially emphasized by the dorsoventral muscles and the hypocardiac ligaments. The ligaments shown in text figure A as ventral projections of the heart exist only in the preabdomen. Of the muscles, one pair is in the cephalothorax where they are attached by one end to the carapace between the two cephalothoracic diverticula and by the other to the endosternite above the nervous system. There are eight pairs of dorsoventral muscles in the preabdomen passing between the diverticula, right and left of the midgut, from the back to the ventral surface of the body. The first pair is easily overlooked as it lies closely applied to the posterior surface of the diaphragm. Dorsally, these muscles are attached to the anterior end of the first abdominal tergite on the outside of the epicardiac ligaments. Ventrally, they are attached, like the cephalothoracic pair, to the endosternite above the nervous system. All other dorsoventral muscles are attached at both ends to the chitin of the body wall. The dorsal attachments are to the outside of the epicardiac ligaments. The ventral attachments are slightly farther apart than the dorsal, one pair for each abdominal sternite, the second pair lying at the sides of the genital opening, and the third at the sides of the basal plate of the comb.

Although the diverticula are divided by the dorsoventral muscles into ten groups, there are only six pairs of ducts connecting them with the midgut proper. The first pair of these transverse ducts is in the cephalothorax and connects the two cephalothoracic diverticula with the anterior portion of the midgut. The first, second, third, and fourth abdominal diverticula have a pair of transverse ducts each in the corresponding segments. The last pair of connecting ducts opens into the midgut in the fifth abdominal segment. These ducts are long, extending backward over three segments and establishing a connection between the midgut and all four posterior metameric groups of diverticula.

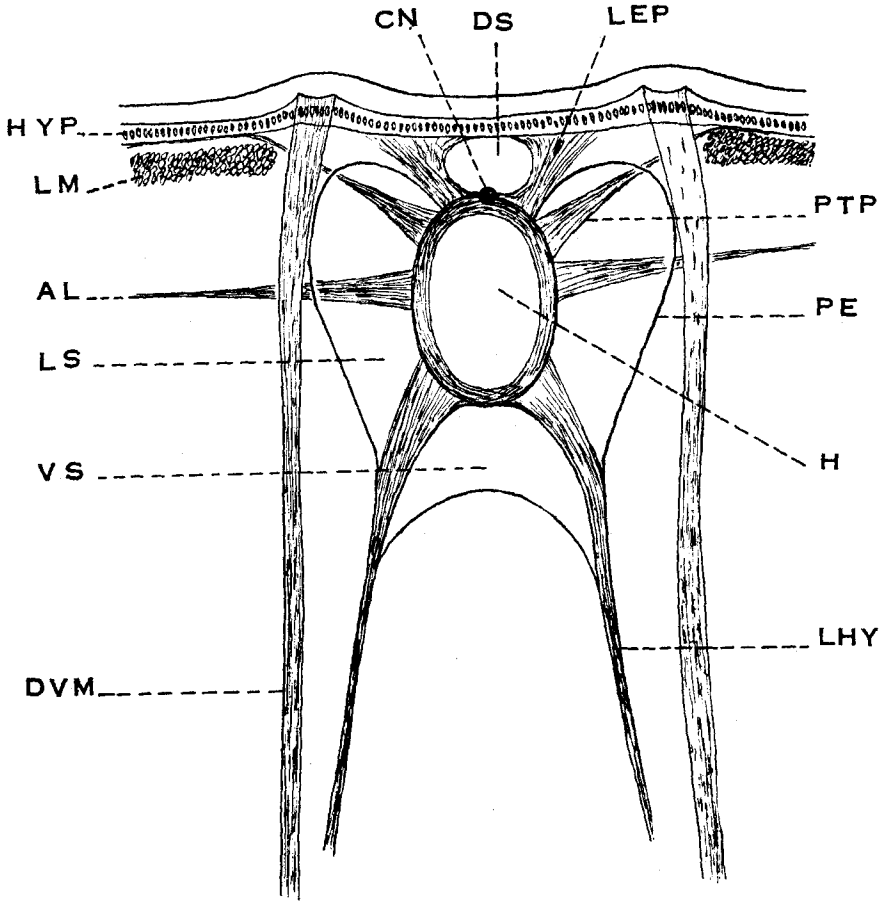
Transverse sections through the second to fourth abdominal segments show that each pair of diverticula is composed of two dorsal, two ventral, and one lateral lobes. All lobes are filled with embryonic yolk and all those on the same side are naturally connected with each other near their base. The dorsal right and left lobes are separated by the pair of dorsoventral muscles. Below the midgut proper, which occupies approximately the center of a transverse section, the dorsoventral muscles pass on the outside of the inner pair of ventral lobes. In the cephalothorax only dorsal lobes are present. The last pair of transverse ducts gives off side branches to the fifth and then to the sixth abdominal diverticula, while the ends of the ducts lead into the seventh pair into which the eighth pair also opens.

The hindgut begins in the terminal region of the fifth abdominal segment. It is considerably smaller than the midgut, but has both relatively and absolutely much thicker walls. It is devoid of embryonic yolk and in the last postabdominal segment forms a considerable widening beyond which it is again suddenly constricted and opens with a small anus in the midventral line at the end of the segment.

The heart lies entirely in the preabdomen, extending from the diaphragm which separates the latter from the cephalothorax, almost to the end of the seventh abdominal tergite. Its anterior and posterior limits are clearly defined by the valves of which I shall speak later. The heart has seven pairs of ostia

(not eight as usually erroneously stated). The presence of the ostia gives the heart the appearance of an eight-chambered organ. In reality there are neither valves nor any constriction or impediment in the spaces between the successive ostia. There is, therefore, nothing that would have the morphological value of chambers. In transverse sections the ostia occupy a position approximately half-way between the dorsal pole and the equator of the heart. The first pair lies exactly at the posterior edge of the first abdominal tergite. The position of all seven pairs may be best understood from text figure A. It is the same in all specimens and does not change with maturity. The structure of an ostium with its valve is represented in figure 3 on a large scale. This is a frontal section, and the media or muscularis is therefore sectioned at right angles to its muscle fibers. Each fiber has the appearance of a rectangle. The adventitia of connective tissue is well defined and shows long, darkly stained nuclei. Multinuclear fibers of connective tissue run from the edges of the ostium laterally, converging and forming a ligament, the so-called pteripyle.

The position of the ligaments by which the heart is suspended is well known in spiders, owing to several researches, especially those of Causard. There is scarcely any difference in this respect between spiders and scorpions. Text figure B, drawn from a complete series of transverse sections through a late embryo, represents the heart of the scorpion with all its ligaments of a single group projected into the same plane. All told, there are eight metamerically arranged groups of ligaments, each group, except the first, composed of four pairs. The shortest of these are the epicardiac ligaments which pass on each side of the dorsal sinus and are attached to the basal membrane of the hypodermis, thus clearly demonstrating their connective nature, since all muscular fibres, as for example those of the dorsoventral muscles represented in the figure, pass between the hypodermal cells and are inserted in the base of the cuticle. The second pair are the pteripyles. Their distal end merges with the somatic connective-tissue layer which separates the dorsal longitudinal muscles of the abdomen from the hypodermis. The third pair,



Text figure B. *Centurus insulanus*, late embryo. Transverse section through the heart in the region of the third abdominal segment, showing the ligaments. The drawing was made from two sections, as not all ligaments are in the same plane. The epi- and hypocardiac ligaments are in one plane, while the pteripyles and alar are ligaments in another. *AL*, alar ligaments; *CN*, cardiac nerve; *DS*, dorsal pericardial sinus; *DVM*, dorsoventral muscle; *H*, heart; *HYP*, hypodermis; *LEP*, epicardiac ligaments; *LHY*, hypocardiac ligaments; *LM*, dorsal longitudinal muscles; *LS*, lateral pericardial sinus; *PE*, pericardium; *PTP*, pteripyle; *VS*, ventral pericardial sinus.

often called alary muscles, are the alary ligaments. Their ligamentary nature has been elucidated by Causard. They are directed at almost right angles to the longitudinal axis of the heart. Distally they are not attached to the body wall, as usually stated, but merge with a layer of connective tissue, evidently representing the splanchnic coelom covering and separating the diverticula of the midgut from other organs situated above the latter. The fourth pair are the hypocardiac ligaments. They are by far the strongest and longest, and are easily mistaken for muscles, especially where they intercross with the dorso-ventral muscles. From here on they continue diverging and unmistakably and finally merge with the splanchnic layer of connective tissue which covers the diverticula of the midgut from below. The first group of ligaments consists of two pairs only. The epicardiac ligaments are attached to the anterior edge of the first tergite. The hypocardiac ligaments are more or less normally developed, but the pteripyles and alary ligaments are wanting.

Since there are no muscles for the dilatation of the heart, diastole is accomplished through the elasticity of the heart ligaments. This explains why the muscularis of the heart is so powerfully developed. During systole the heart has to overcome the resistance of the ligaments, while the contraction of the latter during diastole is not impeded by the relaxed muscles. There is nothing unusual in such arrangement, as a similar condition exists in almost all joints of the appendages in Arachnida, where flexing is accomplished by muscular contraction and extension by the elasticity of the interarticular chitinous membrane. I have counted 120 pulsations of the heart in one minute.

The pericardium appears as a thin membrane, and the space between it and the heart is, in sections, invariably filled with coagulated blood plasm, and consequently is clearly discernible. Owing to the presence of epicardial and hypocardial ligaments, this space is subdivided into four regions which may be termed sinuses, though they communicate with each other in those regions of the heart where there are no ligaments. The lateral sinuses are the largest, next in size is the ventral sinus, while the dorsal sinus, almost round in shape, is the smallest of the four.

In the dorsal midline of the heart, partly imbedded in a groove in the wall of the heart, the cardiac nerve extends from one end of the heart to the other (text figure B, *CN*). The nerve is clearly visible in all transverse sections and unquestionably corresponds to the cardiac nerve described in Chilopoda (Dubosq), Protracheata, and other Arthropoda. As my material is not specially prepared for the study of nerves, I am unable to find a connection of the nerve with the brain, but such connection has been described by Police in Euscorpius.

The structure of the anterior aortic valve is best understood from median sagittal sections and sections which traverse the valve more or less at right angles. In the first (fig. 1, *AV*) the valve appears as a line attached to the dorsal wall of the heart exactly under the epicardiac ligaments, inclined downward, and about two and a half times as long as the diameter of the heart at the place of the attachment of the valve. In reality the valve is a muscular membrane arising from the dorsal half of the wall of the heart and attached to the sides of the vessel throughout its length. The anterior edge of the valve is longer than the diameter of the vessel. The valve has, therefore, a peculiar shape, being concave or troughlike at its free edge and convex or arched at its base. About half-way between its base and end the valve is drawn tight in the equator of the transverse section of the vessel. Such a section is represented in figure 4, which also shows that the valve is not a fold, but consists of a single layer of transverse muscular fibers with elongated nuclei. There is always a greater accumulation of blood-cells above the valve than below it, showing that the action of the valve is perfect.

The structure of the posterior aortic valve is more difficult to ascertain, and is somewhat different from the anterior one. Text figure A represents the position of the posterior valve as being not far from the posterior edge of the seventh abdominal tergite. This position is constant in specimens of all ages. The valve seems to have the shape of a cone, the open free apex of which is directed posteriorly, while the broad base is attached to the wall of the heart along its entire circumference. This valve, too, has a single layer of circular muscle fibers composing it,

but the length of the posterior valve is many times smaller than that of the anterior valve. Indeed, the posterior aorta which begins at this place is a thin vessel gradually becoming smaller as it traverses all the segments of the postabdomen. It may be traced through the poison gland into the sting, where it ends apparently without any ramifications.

I have stated that the valves are muscular in structure. It may be objected that I have adduced no evidence in support of this assertion and that one may just as well claim that the valves are internal projections of the same connective tissue which as its adventitia surrounds the heart. Indeed, I have no sections through either the anterior or posterior aortic valves to prove or disprove either of the contentions. But I have already mentioned the fact that spiders possess the same types of valves. A comparison of figure 6 with figure 1 will show that the position and appearance of the anterior valve in both scorpions and spiders is the same. Similarly, a comparison of figures 4 and 7 will disclose the identity in structure of the anterior aortic valve in these two orders of Arachnida. Now I happen to have a great many sections through young spiders, and these show the intima lining both surfaces of the valve and continuing directly as intima of the heart itself. In many cases there is a slight loosening of the intima from the muscularis, with the consequence that it appears as an uninterrupted line. The intima of the heart being the sarcolemma of the muscle fibers, it is not conceivable that it could line any but muscular tissue.

Let us now turn our attention to the anterior aorta and the arterial blood vessels of the cephalothorax (fig. 1). The anterior aortic valve, having the exact direction of and lying immediately in front of the diaphragm represents the exact demarkation line between the heart and the aorta. Otherwise, the transition from the heart to the aorta would be scarcely perceptible. Shortly beyond the valve the aorta gives rise to a pair of small arteries supplying with blood the pair of dorsoventral muscles which separate the first cephalothoracic diverticula of the midgut from the second.

The aorta itself continues as a considerable vessel under the brain until it reaches the third neuromere of the suboesophageal ganglionic mass. Here the aortic arch around the oesophagus is formed. The arch is very short and connects the aorta with the right and left thoracic sinus opposite the base of the second pedal artery as shown in figures 1 and 2. Two pairs of vessels issue from the aortic arch. The first pair are the large cephalic arteries shown in figure 1. The second pair cannot be shown to advantage in the planes chosen for our drawings and is therefore not represented there. But these vessels are nevertheless constant in their position and easily found. Their roots are in the right and left anterior inner edge of the aortic arch, near its junction with the sinus and almost directly above the third vessel connecting the sinus with the supraneural artery. The two vessels run convergingly upward, feeding the wall of the oesophagus.

Each thoracic sinus gives rise to small and thin vessels connecting the sinus with the supraneural artery, and to four large vessels for the appendages. Of these vessels the first is the largest and splits almost immediately into two branches. The outer branch (fig. 1 and 2, *1, AP*) is the first pedal artery, while the inner, longer, and stouter branch is the pedipalpal artery (*APP*). The latter gives off a thin branch directed inwardly, following in its course the curvature of the ganglionic mass, and connecting with the supraneural artery just behind the pharynx. A branch of this supplies the tissues in front of the pharynx.

Posteriorly, the right and left sinus merge with each other and form a connection with the supraneural artery. This artery is single and runs in the median line above the ventral nervous system and closely applied to it. Anteriorly it runs to the very end of the ganglionic mass, turning downward in its course and now continuing backward in the midventral line below the ganglionic mass as subneural artery. Posterior to the thoracic sinus the supraneural artery continues as a straight vessel in the median line above the nervous system and closely applied to it through the entire abdomen. I have not followed its course in the post-abdomen.

Nine single interneural vertical arteries connect the supra-neural with the subneural artery. These vertical arteries pass exactly between adjoining neuromeres, the first artery separating the pedipalpal from the first pedal neuromere, the ninth lying immediately behind the fourth abdominal neuromere of the suboesophageal ganglionic mass. Median longitudinal connecting vessels seem to exist between all vertical arteries, but only between the fifth and sixth, and between the sixth and seventh vertical arteries the connecting vessels are invariably well discernible, as shown in figure 1.

The subneural artery does not extend beyond the suboesophageal ganglionic mass, but ends behind the fourth abdominal neuromere, where it receives the ninth vertical artery, which may be, therefore, in a way regarded as a direct continuation of the subneural artery. At the place of their junction a single blood vessel is given off ventrally. This is the comb-artery shown in figures 1 and 5. It gives off a pair of branches, one for each comb, and another pair of smaller branches for the genital opercula.

Each cephalic artery gives off several branches, the most important of which is the ophthalmic artery shown in figure 1. Beyond the ophthalmic artery the main vessel may be termed cheliceral artery. Inside the chelicera the cheliceral artery forms two ramified branches, one for the flexor and the other for the extensor of the movable finger.

COMPARISON WITH SPIDERS

Having thus described the most important features of the circulatory system in scorpions, we now may proceed to its comparison with the corresponding system in spiders. A glance at plate 3 of my paper published in the *Zoologische Jahrbücher* for 1920, vol. 31, will reveal both the similarities and diversities of structure. What I described there as 'Kopfarterie' corresponds with the cephalic artery of the scorpion almost to the minutest details, and shows the same ramifications. On the other hand, in the spider the cephalic arteries represent the upper branches of the thoracic arteries, the lower branches of which

lead to the thoracic sinuses, whereas in the scorpion the cephalic arteries arise from the aortic arch. This means simply a further extension of the arch in the spider, so that the aortic arch of the scorpion corresponds with the thoracic and connecting arteries of the spider. The homology is unmistakable, and it may be wiser to speak in the spider also of an aortic arch instead of a thoracic and a connecting artery.

The thoracic arch, then, of the spider opens into the thoracic sinus at the base of the second pedal artery as in the scorpion. As in the scorpion, the pedipalpal and the first pedal arteries are branches of the first arterial stem given off by the thoracic sinus. The aorta recurrens of the spider, shown in my drawings, is the supraneural artery. But for the comparison of the supraneural and subneural arteries of the scorpion and spider we have to consult the description of these arteries given by Causard, and his figures on plate IV. Instead of quoting passages in the original, I translate them with such omissions as have no relation to our subject.

"We will now consider the arteries which issue from the aortic arches. For a long time two roots were described issuing from the posterior end of each goose-foot [my thoracic sinus,—*A. P.*], forming by their junction a sort of supraganglionic anastomosis which gives rise to a longitudinal artery directed backward and running along the dorsal surface of the ganglionic mass. Schneider gave this artery the name *supraneural*. He has also shown that in front of this anastomosis there are five others. There are therefore altogether six anastomoses which this author describes as thin and delicate. This is true of the five anterior ones, but cannot be accepted as characteristic of the last one, which has a considerable diameter. Moreover, the supraneural artery is rather stout; how could it be fed by two such fine roots? These, as he shows, are often incomplete, the supraneural artery arising from a single root which may be either the right or the left one. When the root is complete this anastomosis has the shape of a V.

"The anterior anastomosis has the shape of a V open posteriorly [i.e., of an angle with a vertex directed forward—*A. P.*].

It is situated immediately under the oesophagus and gives rise anteriorly to a thin artery which is closely applied to the inferior surface of the oesophagus. This is the *suboesophageal* artery. The four following anastomoses are rectilinear and each gives rise to a vessel which issues from the middle of their ventral surface and traverses the ganglionic mass from end to end to its ventral surface. Schneider gave to these arteries the name of *median cerebellar arteries*, as he did in the case of the scorpion. I prefer to call them *ganglionic median arteries* [my vertical or interneural arteries—A. P.]. The supraneural artery gives also rise to a certain number of more or less short arteries of this kind, the first being omitted at the beginning of the supraneural artery and corresponding therefore with the sixth supraganglionic anastomosis. I was able to find seven or eight such arteries, thus bringing their total number to 12 or 13 What Schneider does not mention is the fact that all these arteries connect on the ventral surface of the ganglionic mass with a median longitudinal lacune” (pp. 61-62).

Although I have no conclusive evidence at this moment, either to confirm or to disprove some of the statements contained in the above quotation, it seems to me that Causard has been misled by imperfect injections. We easily recognize in the suboesophageal artery of Causard that portion of the supraneural artery, which is shown in the scorpion in our figure 2 as *SOA*. But I think that both Causard and Schneider have overlooked the connection of the ‘anastomoses’ with the supraneural artery. Causard, indeed, has seen their connection with the subneural artery by means of the vertical arteries (ganglionic median arteries). On the other hand, the number of these vertical arteries given by Causard as 12 or 13 seems to be decidedly too great. A careful examination of sagittal series of sections through young spiders shows invariably the presence of eleven distinct neuromeres in the thoracic ganglionic mass. The first belongs to the pedipalpi, the second to fifth to the legs; the tenth corresponds to the same neuromere in the scorpion, which in the latter is already in the abdomen. The eleventh neuromere is imperfectly divided into two. The anterior portion

is the eleventh neuromere proper, while the posterior portion represents the remnant of the abdominal neuromeres, whether contracted and fused or lost altogether makes no difference as regarding our proposition. We thus have at the most eleven interganglionic surfaces, if we count the partition of the eleventh neuromere as complete. Therefore, there cannot be more than eleven vertical arteries, since arteries passing through instead of between ganglia are not known.

The heart of the spider has four pairs of ostia in the Theraphosidae and only three pairs in the true spiders, as against seven pairs in the scorpions. From the position of the aortic valve, it is safe, however, to accept that the reduction in the number of ostia took place in a progressive direction from the rear end of the heart forward. What has happened to the rear portion of the heart, which has lost the ostia? I think it must have shrunk in size, become considerably thinner and changed into what became the proximal end of the posterior aorta. We have seen that the posterior aortic valve has a structure distinctly different from that of the anterior valve. It would be scarcely necessary to assume a progression of the posterior aortic valve, a shifting of its position with the loss of ostia. Is it not more likely that the posterior aortic valve is a modified remnant of the last pair of ostia valves which have become functionless as such, when the ostia themselves closed? With other words, that the posterior aortic valve of a Theraphosid is the remnant of the fifth pair of ostia valves, while in true spiders it is the remnant of the fourth pair?

From the above comparison of the circulatory system of the scorpion with that of the spider we may now draw the following important conclusions: the scorpion represents the more generalized and therefore more primitive circulatory system among Arachnida, the spider the more modified and therefore the more advanced. The most permanent structure in the circulatory system of Arachnida is the anterior aortic valve which is attached at the anterior edge of the first abdominal tergite and therefore marks the limit between cephalothorax and abdomen. The reduction in the number of ostia stands in direct relation-

ship with the loss of segmentation in the abdomen and proceeds in the same direction, that is, from the posterior end forward. The changes in the neural portion of the circulatory system do not extend over the thoracic haemomeres because of the permanency of the thoracic appendages, but follow the changes in the position of abdominal neuromeres. As the contraction of the longitudinal connectives between neuromeres brings abdominal neuromeres into the thorax, abdominal vertical arteries are also shifted in position, while the complete disappearance of the last abdominal neuromeres brought about a corresponding complete disappearance of the last vertical arteries.

COMPARISON WITH LIMULUS

The circulatory system of *Limulus* has been excellently described by Milne-Edwards, and such errors as he has admitted in his description have been later corrected by Patten and Redenbaugh. I have made injections of adult large specimens to verify the results, and can only confirm their correctness. It is different, however, with the interpretation of the structures, and here I disagree both with the older and later investigators.

Alphonse Milne-Edwards worked eight years before Lankester, and although the idea that *Limulus* is an Arachnid had been already advanced by Latreille and later by Owen, yet the knowledge was not sufficient to admit of incontrovertible homologies. Consequently, notwithstanding the great similarity in the structure of the nervous and circulatory systems, Milne-Edwards felt justified in pointing out the differences and in refusing to place *Limulus* either among Crustacea or among arachnids. For reasons which it is not worth while reviewing at present, Milne-Edwards considered the first pair of appendages in *Limulus* homologous, not with the chelicera, but of the pedipalpi in scorpions.

Lankester's interpretation of *Limulus* was colored by his theory of tagmata into which (according to him) the body of an arthropod is divided. He finds that the body of Arachnida is composed of three tagmata of six somites each and that the genital openings are placed on the first somite of the second

tagma or mesosoma. Following this idea, he finds the same tagmata in *Limulus*, the mesosoma being represented by the genital opercula and the five gill-plates, while the metasoma is reduced to a very small area around the anus, including the last pair of lateral spines.

Patten and Redenbaugh do not attempt to change the interpretation of Lankester, but correct it in regard to the chilaria. The presence of a distinct neuromere for this pair of appendages having been established by Kingsley, our authors naturally ascribe to them the value of a distinct metamere and consider the chilarial somite as belonging to the cephalothorax. For them, as for all previous investigators, the articulation between the carapace and the abdomen is the segmentation line separating the cephalothorax from the abdomen.

It would be useless to describe here in detail the entire circulatory system of *Limulus*, but certain features of it must be considered. The heart occupies the same position as in other arthropods and extends from about the middle of the line passing through the side eyes back to about the middle of the abdomen. The heart has no opening posteriorly and the superior abdominal artery is connected with the heart only indirectly through the collateral arteries. Therefore, though occupying the same position as the posterior aorta of Arachnida, the superior abdominal artery of *Limulus* cannot be regarded as homologous with the latter. The number of ostia is greater than in the scorpion, inasmuch as *Limulus* has eight pairs. Patten and Redenbaugh describe and figure a pair of rudimentary ostia in front of the aortic valve. These may be the last remnants reminiscent of a still older time when the ancestor had a heart extending farther forward. The aortic valve has almost the same structure as in Arachnida. In front of the valve "a pair of tendinous bands, comparable to a pair of alary muscles, run forward and upward a short distance beyond the limits of the pericardium, and attach themselves to the carapace close to the insertions of the tergo-proplastral muscles" (p. 127). I may add that this connection is so strong that in removing the carapace the heart is easily injured, unless particular care is given to sever the connection of

these tendinous bands, which is certainly not the case with the heart ligaments of the subsequent metameres.

The aorta is exceedingly short and forms almost at once two vessels which are rightly regarded as the aortic arch. These vessels are large and long, run at first forward, then curve downward, pass the oesophagus on each side and open into the 'vascular' ring a little to the inside of and above the base of the first pedal artery. The entire ventral circulatory system of *Limulus* is perineural; i.e., it sheaths completely the nervous system. Not only the postoral neuromeres of the suboesophageal ganglionic mass, but the supraoesophageal forebrain as well is enclosed in this perineural circulatory system. The haemal sheath extends through the entire length of the ventral nervous cord in the abdomen. Accordingly, neither supraneural, nor subneural, nor interneural or vertical arteries are present. The cheliceral arteries issue from the ventral surface (actual, not morphological) of the vascular ring. In all this *Limulus* is very different from the scorpion and other Arachnida. Yet the similarity is nevertheless quite striking. If the forebrain portion of the vascular ring were removed, the rest of it would present an identical appearance with the two thoracic sinuses of the Arachnida. The similarity is increased by the existence of five nervous bridges connecting the right and left ganglia of the five pedal neuromeres. These nervous commissures are naturally ensheathed by the corresponding perineural vessels which, therefore, represent the five arteries in the scorpion connecting the thoracic sinuses with the supraneural artery. But in what way could we explain the origin of the scorpion type of neural circulatory system from the *Limulus* type or vice versa? Has the perineural system broken up into two sinuses and neural blood vessels, or have the latter altogether a separate origin?

The relatively great size of the oesophagus and the position of the forebrain in front of and not above the suboesophageal ganglionic mass in *Limulus* may have something to do with the differences between this animal and Arachnida. But this position itself is by no means original. Notice the position of the mouth in the middle of the ventral surface of the cephalothorax

and the position of organs in front of the mouth, which morphologically have to be considered as postoral. Notice the plastro-buccal muscles going "from the anterior neural side of the plastron to the oesophagus" and the strands of muscles attaching the proventriculus to the carapace in the region of the median eyes. The former undoubtedly represent the pharyngeal dilators of Archnida, the latter the dilators of the sucking-stomach in spiders and the corresponding pair of dorsoventral muscles in the scorpion. Although considerably in front of the posterior edge of the carapace in *Limulus*, these muscles are not far in front of the aortic valve. Notice that in severing the carapace from the abdomen with a knife, the opercular plate remains with the carapace. Notice, further, that the suboesophageal ganglionic mass in *Limulus* consists of seven neuromeres, the sixth belonging to the chilaria and the seventh to the opercula; that, owing to the perihæmal type of blood system, the vessels for the chilaria and opercula issue from the vascular ring; notice all this and you get the idea of what happened to *Limulus* in the course of its phylogenetic development. On the ventral surface two somites, corresponding to the first and second abdominal somites in Arachnida and characterized by the chilaria and opercula, became fused with the thoracic somites, while at the same time the corresponding neuromeres moved forward and fused with the suboesophageal ganglionic mass. On the dorsal surface a general displacement forward took place. In this displacement two things remained unchanged: the position of the mouth and the attachment points of the foregut and of the heart in the region of the aortic valve. What was above and behind the mouth, with the forward bending of the back came to lie in front and above the mouth. Part of the heart followed the displacement because of the permanent attachment at the aortic valve. Of the tergites, those of the chilarial and opercular somites had to follow the forward motion of the original carapace and were drawn into the hollow of the horseshoe-shaped carapace as it was formed through the forward displacement. These tergites fused with the carapace along their front and sides, but are still visible even in the adult and especially in the so-called trilobite stage of the

young. The cephalothorax of *Limulus* is therefore the result of fusion of the original cephalothorax with the chilial and opercular somites, and the articulation between the carapace and abdomen is in reality an articulation between the opercular and first gill somite, or what corresponds to the division line between the second and third abdominal somites in Arachnida, as exemplified by the genital and comb somites in the scorpion. The division line between the last thoracic and first abdominal (chilial) tergites lies immediately in front of the attachment of the heart, i.e., somewhat in front of the line passing through the two lateral eyes.

The history of this forward displacement and fusion of originally abdominal somites cannot be gleaned from a study of the external segmentation of *Limulus* embryos. On the ventral surface segmentation is clear, but on the dorsal the first visible segment is already the first gill segment. Something similar may be seen in the scorpion. Here, in the adult, the third abdominal tergite corresponds to the first lung sternite and therefore in reality representing the fourth abdominal somite. The second tergite, corresponding to the comb, represents the third abdominal somite. But the first abdominal tergite is the result of a fusion of the first and second tergites of the corresponding embryonic somites. The external segmentation is clear in young embryos on the ventral surface, and in quite young embryos is at least indicated by the even segmentation of the nervous system as seen in longitudinal sections through these stages. But when segmentation appears in the shape of transverse depressions on the dorsal surface, the first visible abdominal tergite corresponds already with the same tergite of the adult and is therefore already the result of fusion. It may be argued that if in *Limulus* abdominal tergites fused with the carapace, the same may have happened in the case of the missing first tergite of the scorpion. But this interpretation meets with too many objections. Of these perhaps the clearest is presented in the case of solpugids in which the thorax is still externally segmented.

In my monograph of Palaeozoic Arachnida ('13) I have pointed out that the Xiphosura must have developed independently

of the scorpions. The idea that *Limulus* is an arachnid as it is usually expressed, or more correctly that the Arachnida have a common ancestor with Xiphosura, must now be completely abandoned. Geologically, *Limulus* is older than the scorpion and already the oldest limuloid shows the same type of segmentation as the recent. Neither has the idea of Versluys on the origin of gills from lung books any bearing upon the question of origin of *Limulus* or Arachnida. With a stress on imagination one may derive *Limulus* from a eurypteroid ancestor, but to derive the latter from originally air-breathing Arachnida on the basis of no other evidence than conjectures which rest on a comparison of gill-plates with lung books and in the absence of any remains of air-breathing Arachnida antedating eurypteroids, seems to be a rather hazardous undertaking.

It may be interesting to mention in this connection that early stages in the embryonic development of scorpions show clearly eighteen postoral neuromeres, the first of which soon passes in front of the mouth and represents the cheliceral somite. The study of preoral neuromeres in the same stages is too complicated to admit of impartial judgment. In later stages, after the passage of the mouth behind the cheliceral neuromere, one may clearly count three pairs of nerves issuing from what appears to be three corresponding neuromeres. The first pair are the optic nerves of the median eyes, the second the nerves of the lateral eyes, and the third the nerves of the upper lip. These nerves are much finer than both optic nerves and can be traced with certainty only in sections parallel to the plane of symmetry (sagittal). The adult scorpion has therefore four preoral and seventeen postoral neuromeres. Five of the latter belong to the thorax and twelve to the abdomen. It happens that the abdomen of the scorpion shows twelve tergites. Yet one should not conclude from this coincidence of figures that each of the neuromeres mentioned belongs to a corresponding tergite. Nothing of the kind. I have already mentioned that the comb receives its nerves from the third abdominal neuromere, as may be easily demonstrated on sagittal and frontal sections. In early stages the neuromeres do not possess longitudinal connectives and

are recognizable without difficulty only because of the constriction between adjoining neuromeres. The last neuromere is clearly situated in the last abdominal segment, and only later moves forward and fuses partially with the penultimate neuromere. There is, therefore, in the adult scorpion an abdominal segment in excess of neuromeres. From an examination of numerous series I have no doubt that it is the first postabdominal or caudal segment and which therefore may have the value not of a true somite, but of an anterior subdivision or segment of the same somite to which the second postcaudal segment also belongs. Here, then, something happened the reverse of the fusion of sclerites in the first two abdominal somites, namely, the subdivision of the sclerite ring of a single somite into two distinct sclerite rings or segments, without a corresponding subdivision of other structures in the same somite.

It may be objected that such formation of pseudo-segments has not as yet been described, either for Arachnida or other Arthropoda, and that it were simpler to accept that the neuromeres really correspond to the visible segments, but in moving forward lost connection with them and began to furnish nerves to the next following. In other words, that the first abdominal neuromere originally furnished the nerves for the genital opercula, lost connection with the latter, and ceded this morphological and physiological function to the second neuromere; that the same happened to the second neuromere in relation to the comb, which now received its nerves from the third neuromere. But this explanation, besides being more complicated, suffers from another weakness. The roots of nerves follow the displacements of their neuromeres, but the nerves themselves obtain their connection with the original appendages, even if some branch of the nerve passes to another somite. This may be seen in *Limulus* and in many other arthropods. But in the case of the first abdominal neuromere of the scorpion there is not even a considerable or appreciable displacement forward, so that there would be no morphological reason of any kind for a loss of connection with the genital opercula if these belonged to the first neuromere.

We may therefore form the following conclusions regarding segmentation in scorpions and in Arachnida in general. The body of an Arachnid is composed of twenty one somites, to wit: 1 the first ocular (median eyes in the scorpion, anterior median eyes in the spider); 2 second ocular (lateral eyes in the scorpion, eyes with inverted retina in spiders, i.e., anterior lateral, and the four posterior ones); 3 rostral (upper lip); 4 cheliceral; 5 pedipalpal; 6 to 9 thoracic pedal; 10 to 21 abdominal. The first three are originally preoral in position. The fourth or cheliceral becomes preoral during development. The attachment of the heart to the anterior edge of the dorsal wall of the first abdominal somite and the formation at this place of the aortic valve indicate the division line between the thorax and the abdomen. The tenth somite is always rudimentary, having lost its identity in all but its neuromere. The genital opening is on the eleventh somite (second abdominal). A further fusion and ultimate loss of the identity of somites in Arachnida involves the posterior end of their body, beginning with the twenty-first somite and proceeding forward. In some cases, as in the eighteenth somite in the scorpion, secondary or spurious segmentation may take place, which has no relation to the original metamerism. If there be more than three originally preoral somites, these would have to be sought for in front of the first ocular somite.

Turning once more our attention to *Limulus*, we may first of all consider the homology of the thoracic and abdominal somites established in a way excluding all doubt. The six pairs of appendages belong to the same somites as in Arachnida, the chilaria represent the tenth, the opercula the eleventh somite, the five branchial neuromeres correspond to the twelfth to sixteenth somites, and of the three postbranchial ganglia the last is the result of fusion of the nineteenth to twenty-first neuromeres, if the ancestor of *Limulus* possessed that many postbranchial somites.

The homology of the preoral somites is more troublesome. Patten and Redenbaugh describe three preoral neuromeres, the olfactory, median ocular, and lateral ocular. Shipley following Carpenter recognizes only two somites, the median ocular and

the rostral. I think we may consider it as fairly conclusive that the median ocular and lateral ocular somites are homologous in *Limulus* and the scorpion. Whether the rostral somite of the scorpion corresponds with the somite designated as rostral in *Limulus* by Carpenter, is not so sure, but if it does not, then *Limulus* must possess just the same some evanescent somite between the lateral ocular and cheliceral. As for the olfactory somite, its homologue in Arachnida would have to be sought in one of those two pairs of obscure parietal ganglia described by Schimkewitsch for tetraneumonous spiders.

In the presence of a perineural circulatory system, in the existence of eight pairs of ostia in the heart, and of a pair of chilarial nerves, *Limulus* shows evidence of its origin from an arthropod ancestor lower and more primitive than the Arachnida. But in every other respect *Limulus* shows advanced development different from that in Arachnida and most likely standing in direct relationship to its particular mode of life. It seems as if the older interpretation of *Limulus* as a descendant of Trilobites must be revived. The shape of the trilobite carapace, the position of the mouth, the probable similarity in the position of the foregut as suggested in figure 24 of Raymond's beautiful monograph, the larval stages showing segments which were interpreted as cephalothoracic, but some of which probably are abdominal tergites drawn into and fused with the thoracic ones, point to a similarity more than casual. At any rate, the problem should be reinvestigated from the new point of view.

COMPARISON WITH OTHER ARTHROPODA

We have seen that the aortic valve has a uniform structure and a permanent position in Arachnida, permitting of strict homologies within that class. We have also seen to what conclusions we arrive through the assumption that the rule holds good in the case of *Limulus* also. One would expect that a structure so permanent in one or perhaps two classes would prove to be the same in the case of all other Arthropoda, if the diverse forms united under this immense phylum are of monophyletic origin. Unfortunately, this is not the case.

In his work on the organs of circulation in Schizopoda, published in 1883, Delage writes (I translate the original): "To determine exactly the length of the heart one should first of all well define its limits. It happens that these limits are not easily traceable because the diameter of the heart is not greatly different from that of the aortae at their points of origin. (Delage has in mind both the anterior and posterior aorta.) They are marked by the presence of cardioaortic valvules which have not yet been described by anyone. Moreover, these valvules are identical with those which are found in the same place in Amphipoda." "Within these limits the heart extends from the level of the last maxillary segment to the superior portion of the last thoracic segment." The anterior aorta, the median stem of which ends in the upper lip, gives off four branches in its course: the common trunk of the ophthalmic arteries, the cerebral artery, and the two antennal arteries. It may be of interest to notice that the sternal artery in Schizopoda arises from the heart.

The structure of the aortic valves themselves is different from those of Arachnida. They are paired lateral structures, as in all other Crustacea. The position indicated by Delage, taking into account evidence derived from the study of all other organs, is two somites nearer the head than in Arachnida. In such Decapoda as the crayfish and the lobster the heart is distinctly limited and considerably modified. Instead of arising from the aorta, the antennal arteries arise directly from the heart and have their own valves. Yet the aorta has also valves at its base and these are of the same type as in Schizopoda and Amphipoda. The position of these valves coincides exactly with the semilunar sulcus of the carapace, the two ends of which open into the so-called cervical groove. There are therefore differences in regard to structure of the circulatory system in closely related orders of the same sub-class—differences which cannot be understood without special study directed to their elucidation.

We know still less of the Protracheata, Pycnogonida, and the four classes formerly comprised under the general name of Myriapoda. Although I have some investigations under way, I am not prepared as yet to make any definite statement.

The circulatory system of insects is somewhat better known in this respect, yet here also the data are quite inadequate to form a clear judgement. Popovici-Bazosanu has described the heart in the *Chironomus* larva and states that the aortic valves are situated close to the anterior end of the fifth segment. In other larvae the heart had been described by other authors as situated near the rear end of the body. In some larvae the heart is not even situated directly under the dorsal body wall, but lies considerably deeper in the body cavity. The structure of the cardio-aortic valves, too, seems to be not only different from that of the aortic valve in *Arachnida*, but not always of the same type in all insects. Moreover, according to Zawarzin there are modified ostia in the aorta itself. It is evident that the first step must be in finding the true limits of the heart itself in insects. Meanwhile all conjectures would be entirely out of place.

SUMMARY AND CONCLUSIONS

1. In comparing the segmentation in arthropods the uncertain method of counting somites beginning with the anterior end should be abandoned. Instead, some structure should be chosen which has permanent value for a number of forms within a class and used as a starting-point of comparison.

2. Such structure in the case of *Arachnida* is furnished by the cardio-aortic valve which marks the division line between the last thoracic and first abdominal segments.

3. The method applied to *Limulus* leads to the conclusion that the carapace of *Limulus* is more complicated than in *Arachnida*, having two abdominal tergites drawn into the horseshoe-shaped thoracic tergite with which they have fused anteriorly and laterally.

4. A further conclusion is that the midcorporal articulation in *Limulus* is not between thorax and abdomen, but between the second and third abdominal somites.

5. The structure of the circulatory system in *Arachnida* follows a general plan given in the text.

6. The number of postoral somites in adult *Arachnida* is seventeen. Five of these are thoracic and twelve abdominal.

7. The genital opening is on the second abdominal somite.
8. The first caudal segment in scorpions is not a true somite, but merely the anterior division of the fourteenth postoral somite.
9. If the number of preoral somites in Arachnida is not more than four, as represented by the median ocular, lateral ocular, rostral, and cheliceral somites, then the total number of somites in Arachnida is twenty-one.

EXPLANATION OF PLATES

ABBREVIATIONS

<i>AC</i> , Cheliceral artery	<i>GB. 2</i> , Gnathobase of the second leg
<i>AO</i> , Aorta	<i>GP</i> , Genital plate (operculum)
<i>AP</i> , Pedal artery	<i>H</i> , Heart
<i>APP</i> , Pedipalpal artery	<i>LC</i> , Longitudinal connective between
<i>1. AT</i> , First abdominal tergite	the fourth and fifth abdominal
<i>AV</i> , Anterior aortic valve	ganglia
<i>BR</i> , Brain	<i>M</i> , Mouth
<i>CA</i> , Comb-artery (ninth vertical ar-	<i>MA</i> , Anterior edge of carapace
tery)	<i>ME</i> , Median eyes
<i>Cbp</i> , Basal plate of comb	<i>MG</i> , Midgut
<i>CO</i> , Aortic arch connection with	<i>MP</i> , Posterior edge of carapace
thoracic sinus	<i>PH</i> , Pharynx
<i>D</i> , Diaphragm	<i>SAA</i> , Supraneural (epineural) artery
<i>DP</i> , Dilator muscle of the pharynx	<i>SBA</i> , Subneural (hyponeural) artery
<i>DS</i> , Dorsoventral muscle separating	<i>ST</i> , Sternum
the first cephalothoracic diverticle	<i>UP</i> , Upper lip (rostrum)
of the midgut from the second	<i>VA</i> , Vertical or interneural artery

PLATE

EXPLANATION OF FIGURE

- 1 The circulatory system of a young scorpion, *Centrurus insulanus*. A very perfect median sagittal section, 20μ thick, was first drawn with the Edinger drawing apparatus. The section contained everything shown in the figure except the cephalic arteries, the thoracic sinus and the arteries leading to the appendages. All these were introduced into the drawing on the basis of results obtained from the study of a series of frontal sections through scorpions of the same age and species and of adult injected specimens of *Centrurus carolinianus* from Texas. To avoid confusion, the corresponding arteries of the right side are omitted. The cephalothoracic diverticula of the midgut are also omitted. In the section from which the figure was made they extend as far as the median eyes.

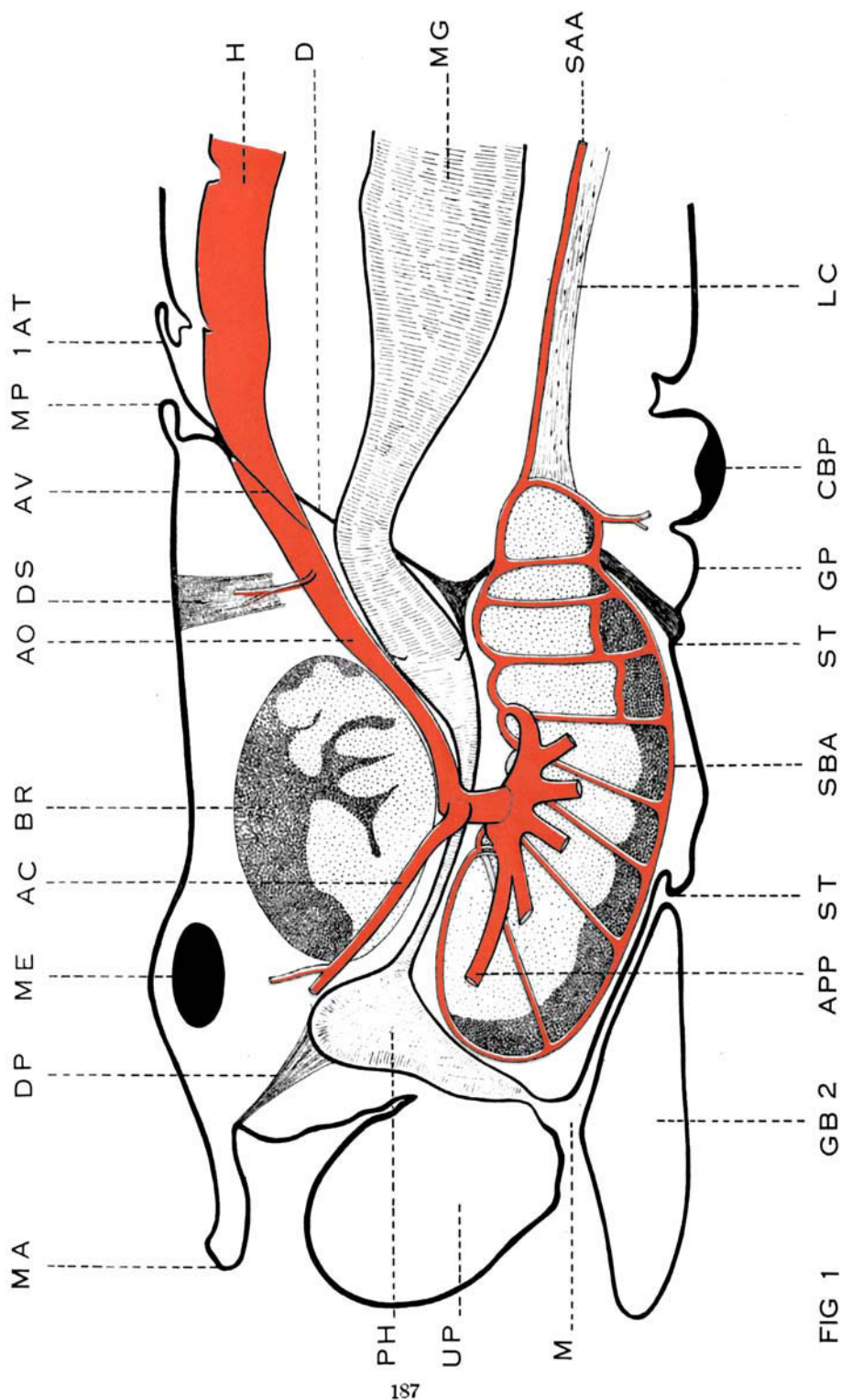


FIG 1

PLATE 2

EXPLANATION OF FIGURES

- 2 The circulatory system of a young scorpion, *Centrurus insulanus*. Dorsal view of the thoracic sinus with its arteries and of the supraneural artery. This figure represents a combination drawing of three consecutive sections of a frontal series. The drawing was made with the Edinger drawing apparatus under the same magnification as figure 1. Heart, aorta, cephalic arteries and subneural artery are not shown because they belong to quite different levels. The place where the aortic arch connects with the thoracic sinus of the corresponding side is indicated by the black oval opposite the base of the second pedal artery. Similarly, the vertical arteries connecting the supraneural with the subneural artery are represented by small black circles. The dotted parts represent the nervous system.
- 3 One of the right ostia in the heart of a young scorpion, *Centrurus insulanus*, drawn from a frontal section under high power. Between the fibers of the peripyle ligament blood corpuscles are shown.
- 4 Transverse section through the aorta of a young scorpion, *Centrurus insulanus*, showing at a high power the aortic valve.
- 5 Comb-artery of a young scorpion, *Centrurus insulanus*, drawn from a thick transverse section. The drawing shows the fourth abdominal ganglion and the genital duct with its muscles.
- 6 Sagittal section through the heart of a young spider, *Lycosa carolinensis*, in the region of the aortic valve. The drawing shows the relation of the valve to the carapace for comparison with figure 1.
- 7 Transverse section through the aorta of a young spider, *Lycosa carolinensis*, showing the aortic valve, for comparison with figure 4.

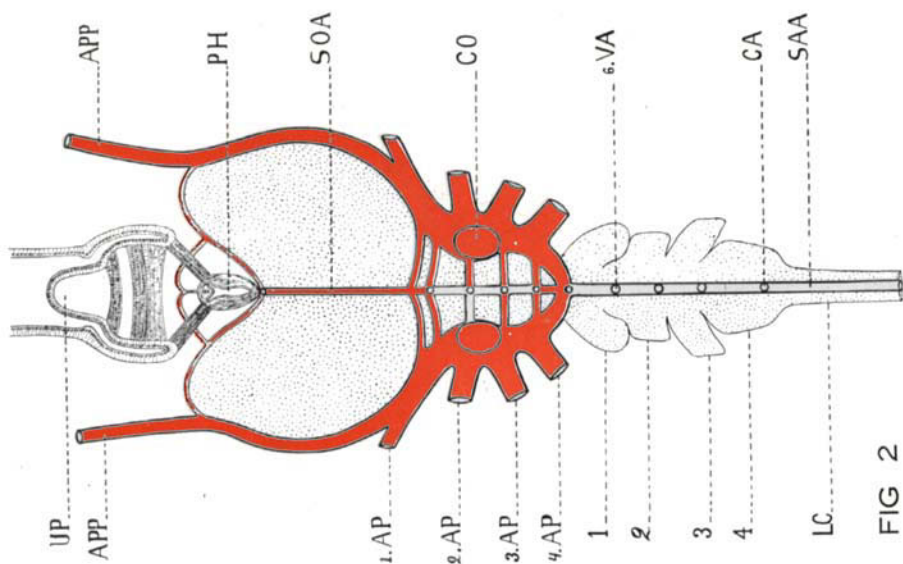


FIG 2

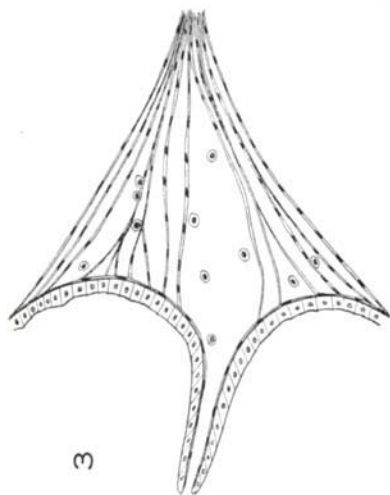


FIG 3



FIG 4

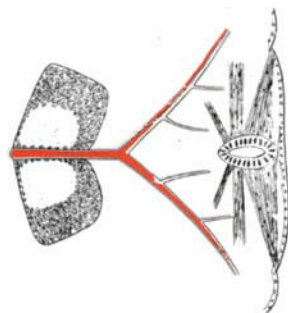


FIG 5

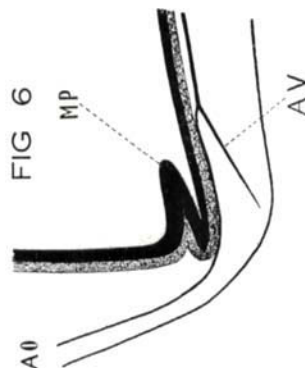


FIG 6



FIG 7