The Innervation of the heart of the Crustacea.
I. Decapoda.

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With Plates 13-15 and 25 Text-figures.

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N
INTRODUCTORY.

The innervation of the heart is one of those problems of comparative anatomy and physiology which are always being discussed with the liveliest interest. It must be stated that considering the importance of this problem our information about the plan of distribution of the nervous elements in the heart is still very scanty. With regard to the vertebrates we know that different fibres run to the heart from the central nervous system and from the sympathetic trunk; further, that many ganglion cells are present on the heart itself and abundant nerve-fibres in the muscles. But the legitimate demand for the analysis of the structural relations of all neurons which build up this very complex system gets but meagre satisfaction. The observation of preparations stained with methylene blue leads to the conclusion that the possibility of distinguishing the fibres of different provenance is very doubtful, and that the criterion for diagnosis of the several types of ganglionic cells as they have been described by some authors is more than uncertain. This opinion, to which I was led when examining many preparations of the mammals’ heart, I find also expressed by Stöhr in his recent work about the involuntary nervous system.

A study of this question in the Invertebrates should yield better results, and there is no doubt that a minute knowledge of this system in the lower animals is also very desirable. It is, of course, to be borne in mind that one has to be careful when attributing general value to conclusions based on statements made in one group of animals and extending them to other groups, but it is very probable that there are analogies in the general plan of the distribution of the nervous elements, and, therefore, some light might be shed on this problem in the higher animals. Accordingly, in the larger treatises on physiology dealing with the innervation of the heart, references may be found to the lower animals, but from the examination of the bibliography on the subject it appears that our knowledge is rather unsatisfactory. There are, however, numerous accounts regarding the nerves running to the heart from the central nervous system (e.g. Carlson’s) but the data concerning the
nerve elements in the heart itself are few, and even in recent works one finds now and then doubts as to the presence of ganglion cells in it. This state of things is due to the great difficulties in making preparations of the nervous system by means of all specific methods. For my own part, more than twenty years ago I tried to apply the vital staining and the silver methods in different groups of Invertebrates, such as the Tunicates, Molluscs, and Arthropods; but although it could be asserted that in all these animals the heart is provided with abundant nerve-fibres, the general staining effect was not sufficiently satisfactory.

Some years ago I repeated my attempts, and then I obtained better results with Periplaneta (1926) and Potamobius (1929). In the paper on the latter I expressed the opinion that for many reasons it would be advantageous to investigate various species of the marine Crustacea. My sojourn at the biological stations in Plymouth and Naples in the summer and autumn of 1930 made it possible to realize these plans, and I was able there to make observations on the heart in Decapods, Stomatopods, and Isopods. In the present paper I propose to give an account of my results in the Decapods.

I have much pleasure in expressing my most sincere thanks to Dr. E. J. Allen of Plymouth and Professor Dr. E. Dohrn of Naples for all the facilities which they afforded me while working in the laboratories of these two stations. I cannot refrain from expressing as well my grateful indebtedness to the Board of the Fund for the Advancement of Arts and Science in Poland, whose assistance has enabled me to pursue my researches abroad.

HISTORICAL.

On referring to the literature of the subject, we find that the chief attention, when dealing with the innervation of the heart of the Crustacea, has been paid to the nerve discovered by Lemoine in 1868, which runs alongside the anterior median blood-vessel. Other nerve-fibres approaching the heart from its sides have also been seen by several authors, e.g. Dogiel (1894), Carlson (1905), and Police (1908). The nerves of the arterial
valves are mentioned in the paper of Newmywaka (1928). Attention was drawn to the presence of nerve-cells by Berger in 1876. His discovery was confirmed by several authors, e.g. Pogoschewa (1890), J. Dogiel (1894), Nusbaum (1899), Stecka (1903), Alexandrowicz (1913), Newmywaka (1928).

In 1929 the present writer gave a description of the innervation of the heart of *Potamobius astacus* (= *Astacus fluviatilis*) distinguishing three systems of nervous elements, as will be explained later. In order to avoid needless repetition, I do not give here a detailed account of the opinions of the writers mentioned above, as their contribution will be referred to in the following chapters.

The bibliography of the foregoing investigations will also be found in the papers of Police (1908), Alexandrowicz (1913), and Newmywaka (1928).

**MATERIAL AND METHODS.**

The investigations recorded in the present paper were made on such different species of Decapod Crustacea as *Maia squinado*, *Cancer pagurus*, *Eriphia spinifrons*, *Carcinus maenas*, *Palinurus vulgaris*, *Homarus vulgaris*, *Scyllarus arctus*, *Munida rugosa*, *Galathea stri-gosa*, *Eupagurus bernhardus*, *Pagurus striatus*, *Leander serratus*. Not all of these were examined with the same exactness, for either the size of some species was not suitable for dissection of the heart or the animals were not obtainable in sufficient numbers.

The observations have been made on preparations stained with methylene blue or rongalit white.

**Methylene blue Staining.**—I used mostly the 'Methyl-enblau chem. rein, chlorzinkfrei' from Merck, Darmstadt, or 'Methylenblau zur vitalen lnjektion n. Ehrlich' from Gruebler (Hollborn). As is well known, the staining of the nervous elements can be obtained in different ways, viz. by submerging the tissues in a weak solution of the dye or by injecting a more concentrated solution into the body of the living animal. By trying both these methods it was found that the nerve-cells in the ganglionic trunk of the heart are better stained when sub-
merged in a solution, while injection gives clearer preparations of the nerves of the pericardium and of the arterial valves. Being chiefly occupied with the distribution of the nerves in the heart-wall itself, I mostly applied the former method.

It was my practice to keep a standard solution of methylene blue 0.5 per cent. in distilled water, of which 15 to 20 drops were mixed with 100 c.c. of sea-water immediately before the organ was submerged. It seemed to make the preparations clearer when to the above solution a small quantity of hydrochloric acid (1 to 2 c.c. of n/100 HCl for 100 c.c.) was added.

Rongalit White.—The rongalit white (Rongalitweiss) was prepared according to the prescription of Unna (v. Zeitschr. f. wiss. Mikroskopie, Bd. 32, p. 302) viz.:
Methylene blue 0.5 p.c. in dist. water acidulated in the proportion of 7 drops of 25 p.c. HCl to 100 c.c. 10 c.c.
Rongalit . . . . . . . . . . . . . . . . . . . 0.8 gm.
Dilute and warm in a test-tube until the blue colour changes to pale-yellow; filter after cooling. As I have already indicated (Archives de Zoologie exp. et gén., t. 66, 1927) this standard solution should be kept in an open test-tube protected by a piece of paper, and may be used for about 10 days. Its staining properties are better the next day than immediately after preparation. For staining it was added to sea-water in proportion of 10 drops to 100 c.c.

I have been using rongalit white since 1924 and find that it often gives better results than methylene blue, but during my latest work I have had many failures with it, due, as I was able to demonstrate, to the quality of the drug. The last remark may be found useful by those who after the first trial will be inclined to distrust completely this method of staining. Satisfactory results were obtained by me at Naples with the rongalit obtained from Gruebler & Co.

Some measures ought to be taken for facilitating the penetration of the dye into the nervous elements. In the first place it is necessary to have the heart-wall flattened as much as possible.

To secure this the heart of the animal, previously killed with chloroform, was cut in the median line of the ventral wall. Then it was attached, the inner side upwards, to a paraffin plate
8 to 5 mm. thick with hedgehog spines; these are more advantageous than common needles, not only because of their not being acted on by different fluids but because of the possibility of shortening them as desired when observing the preparations with the microscope. The paraffin plate with the heart was put into the solution of the dye, and from time to time was taken out in order to watch the staining process under the microscope, the plate being transparent enough to permit tolerable illumination of the tissues. Usually after 15 to 30 minutes, the superficial nerve-fibres begin to stain. But even if we succeed in spreading the heart, the methylene blue does not reach all the nerve-cells, as they are included in the nerve-trunk, which is covered more or less with muscle-bundles. Therefore, in order to expose the nervous elements freely to the stain it is necessary to remove a part of the muscle-fibres. This is a very delicate operation which has to be done under the microscope with needles or fine scissors. It should be begun as soon as possible, i.e. when the main nerve-trunk becomes distinguishable; then, with the advance of the staining process, new incisions of the muscle-fibres should be made.

The objects remain attached to the paraffin plate during the whole time of staining and fixing. In order to facilitate the access of the reagents from both sides of the heart-wall a part of the paraffin may be removed, though generally I preferred not to do this.

The preparations were left in the dye for 2 to 6 hours and then, in order to obtain the more complete staining, they were exposed to the action of the air in a moist chamber. In some cases the process of staining took 20 hours in all. The point when the preparation is ready to be fixed is very difficult to determine. It is easy to say that it must be fixed when the staining is at its best, but it is not easy to know when a given preparation shows the best that could be obtained with it, especially as the nervous elements can behave very differently in the same organ. So, e.g., 10 hours may elapse between the beginning of staining of the small ganglion cells and that of the large ones, and very often the former have already lost their colour when the latter are not yet blue enough.
Injection.—The following was the solution usually employed for injection: methylene blue 0·5 per cent. or rongalit white (the standard solution) 1 vol. + sea-water 2 to 7 vol.

Of this mixture in the thorax or the abdomen of the animal 1 to 6 c.c., according to its size, was injected. After 1 to 6 hours the heart was taken out. Sometimes the animals were left alive for a longer time, viz. up to 24 hours after injection; but this method, which produced good results in Astacus, did not improve them in the marine Crustacea. The method of injection was serviceable for staining the system of the nerves of the arterial valves in the Macrura and Anomura, whilst in the Brachyura I had but little success with it.

Fixation.—It is well known that up to now there is no good method of fixing methylene blue preparations in all their beauty, and so it is understandable that every one who works with vital staining endeavours to improve the fixation of the stained nerves and tissues. Schabadasch (1930) discusses the value of different methods of fixation and, suggesting that the action of the osmotic pressure may be responsible for the conservation of the tissues, gives prescriptions for isotonic fluids with ammonium picrate as the fixing agent, declaring himself satisfied with the results. The formulae of Schabadasch are, however, not suitable for the organs of marine Crustacea, as the solution of the salts he proposes, viz. ammonium iodide or ammonium thiocyanate and ammonium picrate, cannot in practice be obtained in a concentration corresponding to the high osmotic pressure in the tissues of these animals.

In the course of more than 20 years' experience with methylene blue staining I have made many experiments in order to obtain the best fixation of my preparations, but have been obliged to confirm Dogiel's opinion that, for the most part, the simple solution of ammonium molybdate is the best. Some additions, however, as osmic acid and platinum chloride seem in some cases to be advisable and I have often made use of them previously (1909, 1913, 1927). Using mostly ammonium molybdate as fixing agent I have tried to make its solution isotonic and have found that cane-sugar may be employed for this purpose, as it does not influence the action of ammonium
molybdate in fixing methylene blue. The solution was prepared as follows:

Aqueous solution of 10 per cent. ammonium molybdate . . . . . . . 1,000 c.c.  
Cane-sugar (saccharose) . . . . . . 350 gm.

To this solution osmic acid and platinum chloride may also be added. The following formula was used by me for the majority of the preparations.

Solution of ammonium molybdate with cane-sugar . 30 c.c.  
Platinum chloride 1 per cent. in distilled water . 1 c.c.  
Osmic acid 2 per cent. . . . . . . 1 drop

To be mixed immediately before use.

The standard solution of ammonium molybdate with sugar becomes after some time more or less blue. This colour disappears after addition of osmic acid and platinum chloride.

I was able to convince myself on different organs of marine animals that the addition of sugar to the ammonium molybdate is really useful.

In the fixing solution the objects were left for from 4 to 20 hours. Then they remained in distilled water for the same time. In some cases I used for washing a solution of cane-sugar (35 gm. to 100 c.c.) and then diluted it gradually. From water the objects were brought into absolute alcohol, then into xylol and were mounted in xylol-dammar.

I also made some experiments in order to obtain a better fixation of the tissues. Of different reagents I experimented with, only formol seems not to damage the staining of the nervous tissue. Unfortunately, it gives a precipitate with ammonium molybdate solution. As this mixture still remains clear for some minutes I have profited by this property as follows: To the solution of ammonium molybdate with sugar concentrated formol was added (3 c.c. of formol to 27 c.c. of the solution) and the preparations were immediately put in. Within 10 to 20 minutes this fluid becomes turbid and has to be replaced by a freshly prepared mixture. As the preparations, being attached to the paraffin plate, swim on the surface, they do not retain the falling particles of the precipitate. The change of solution can be repeated; afterwards the objects are submerged in the
solution without formol. This proceeding is not convenient, but it is worth while trying it when the simple solution of ammonium molybdate appears quite useless. Some good preparations have been obtained by me by this method, but generally I have used the more simple one first described.

I also used fixation with ammonium picrate, but, except in some particular cases, I preferred the ammonium molybdate.

It may be added that when making and examining the preparations of the nervous system binocular observation is far superior to monocular. There are nowadays very comfortable binocular microscopes, but I preferred to use the simple Stereo-attachment 1 (Stereo-Aufszat) of Heimstaedt made by C. Reichert, Vienna. It has some inconveniences, increasing considerably the height of the microscope; 2 the clearness of the pictures also does not seem to be so perfect as in binocular microscopes, but it has two great advantages. First of all, a good stereoscopic effect is obtained; preparations of the nervous system, showing the nerve-fibres at different levels, are very good for demonstrating the possibility of the spatial perception, and I find that in this respect the Stereo-attachment is superior to the modern binocular microscopes. In the second place, a special advantage of this eyepiece is that it gives an upright picture, so that manipulations with the forceps and scissors are easy. With an objective of low power (I used for this purpose objective 1 b of Reichert with a changeable magnification 3 to 4 x), the common microscope can in many cases replace the Greenough microscope. At times even it offers some advantages, e.g. when during dissection a control with a higher power is needed this can be obtained by a single movement of the revolving nose-piece.

It may not be superfluous to call the attention of readers

1 This apparatus is introduced into the tube of the ordinary monocular microscope and clamped fast to it. I find that in practice the screw mechanism adopted in the new pattern of Reichert is less convenient than that of the older pattern.

2 In order to facilitate observation, especially in those cases when the microscope cannot be used in the bent position, I have in my laboratory a table made with an incision so that the microscope can be placed at a changeable level, 6 or 11 cm. below the level of the table.
working with similar objects, i.e. with fresh organs or with thick mounted whole preparations, to the fact that the choice of adequate objectives greatly facilitates their examination and is sometimes the only method which allows the necessary observations to be made. Of great importance when using objectives of medium or higher power is the so-called working-distance of the lens, which in ordinary histological work does not play a decisive part. As objectives of the same magnification have different constructions, I have selected, after comparing the data of several firms, such of them as have the greatest working-distance.

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<tr>
<th>Objective</th>
<th>Magnification</th>
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<td>E. Leitz</td>
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<td>1/8 immers.</td>
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The first of these (Leitz 4) is seldom used in ordinary work, but for our purpose it is very advantageous, since, keeping in focus at a distance of 2 mm. from the object, it gives, in combination with an eyepiece of high power, e.g. 15×, a fairly good magnification. For mounted preparations an immersion objective 1/8 is very useful, as even the thicker parts can be examined with it.

**DESCRIPTIVE.**

**I. GENERAL ARRANGEMENT OF THE NERVE SYSTEMS supplying the Heart.**

In a previous paper the writer has stated that in the heart of *Potamobius astacus* three systems of nervous elements may be distinguished:

1. A system of neurons situated in the heart itself and therefore constituting its proper or local system.
2. Fibres which connect this local system with the central nervous system and which are represented by the dorsal nerves —Nervi cardiaci dorsales.
3. A system of fibres innervating the muscles of the peri-
INNERVATION OF HEART OF CRUSTACEA

Cardium and those of the valves situated at the exit-points of the arteries. These are given off by nerves which will be called 'nervi segmentales cordis' and by an anterior nerve—'nervus cardiacus anterior'.

All these elements have been found also in the course of the present investigations on the marine Decapod Crustacea. Certain differences concern details only and will be referred to later. First of all an idea of the general arrangement of these nerves may be given, making use of the diagrammatic drawings representing the nerves of the heart in Palinurus vulgaris.

Text-fig. 1 shows the heart from its dorsal side considered as transparent so that the main parts of the local system, which lie on its inner surface, can be seen. This system consists of a stout trunk (Tr gang) containing ganglion cells, and of the branches arising from this trunk and distributed in the heart-muscles and the muscles of the ostia. The finer branches are not represented.

The dorsal nerves (N dors) enter the heart from its dorsal side and join the main trunk.

Text-fig. 2 shows the system of nerves going to the valves. The heart with the pericardium left on it is represented from its ventral side. The fibres of the local nervous system are omitted in this drawing. The nervous elements represented originate in 4 pairs of nerves coming from the sides, which I had already named segmental nerves of the heart (Nn seg). They unite in a bundle—fasciculus longitudinalis pericardii (Fasc long)—lying on the ventral surface of the pericardium. From this fasciculus—in other species they may be two in number—branches are given off whose destination is the muscles of the pericardium and the valves of five arteries, except the ophthalmic artery (aorta anterior). The valve of the latter receives its nerve-fibres from the anterior nerve of the heart—nervus cardiacus anterior (N card ant).

II. LOCAL SYSTEM.

1. Elements of the Local System.

The nerve-cells which with their processes build up the local system are of two sizes, large and small. Their number, as could
be ascertained for several species of marine Decapods, amounts to five large elements and four small ones. It may be emphasized that even if that number may not be identical in all these animals it is at any rate very close to it. *Potamobius astacus,*
however, possesses, as I noted before, eight large cells and the same or nearly the same number of small ones.

The nerve-cells lie in a nervous trunk situated in the dorsal wall of the heart near to its inner surface. This trunk containing

![Text-fig. 2.](image)

Semi-diagrammatic representation of the nervous system of the valves and the muscles of the pericardium in *Palinurus vulgaris*. *Nn seg*, segmental nerves of the heart; *Fasc long*, Fasciculus longitudinalis pericardii; *Mm peric*, muscles of the pericardium.

the ganglion cells will, in later descriptions, be called the ganglionic trunk. It gives origin to branches passing to the different parts of the heart-wall. It is important for the staining process
that the posterior part of this trunk is not covered with muscle-bundles, while the anterior part of the trunk lies under the muscles. The latter, as has already been explained, must be removed during the staining process.

Diagrams showing the shape of the ganglionic trunk and the situation of the nerve-cells of the local system in A, Palinurus and cyllarus; B, Brachyura; C, Homarus; D, Galathea, and E, Astacus.

There is some variation in different species with regard to the shape and relative size of the ganglionic trunk (Text-fig. 3). In the Brachyura (B) it is relatively shorter and bifurcates on the anterior edge. The large cells are so distributed that one of
them is situated at the point of the anterior bifurcation, two are lateral on both branches of bifurcation (fig. 8, Pl. 14), and the remaining two are placed on the posterior end of the trunk, where, too, the small cells are situated. This arrangement is by far the most frequent I met with in the Crabs, though some deviations from it have been found by examining a considerable number of the hearts of Maia squinado and Cancer pagurus. The three anterior cells may be situated either nearer to or farther from the median line, or they may lie asymmetrically; two elements on the one side and the third on the other. Further the two posterior cells or one of them may be placed in the trunk more anteriorly and in consequence at some distance from the small cells (fig. 11, Pl. 14). Variations in the number of the cells seem to be rare. In Maia in one preparation six large cells were found, in another five small ones. The supernumerary large cell was lying in one of the anterior branches of bifurcation of the anterior trunk. In one preparation of Cancer six large and five small cells were present.

With regard to Eriphia spinifrons, I am not sure whether this species possesses two posterior large cells or only one.

The lobster (Homarus vulgaris) has the median trunk relatively longer than in Brachyura, as it surpasses the half of the length of the heart. It bifurcates equally, forming a Y-shaped figure (Text-fig. 3, C); the disposition of the three anterior cells is similar to that of the Crabs, while the posterior cells are never found at the posterior end of the trunk, being placed nearer to the bifurcation and at some distance from one another. The small cells are situated in the posterior part of the trunk but never grouped together.

In Pagurus striatus the arrangement of the nervous elements in the main trunk resembles that in Homarus. The exact number of the small cells, however, could not be ascertained.

The trunk of Palinurus vulgaris is represented in Text-figs. 1 and 8, A. The microphotograph (fig. 9, Pl. 14) shows its anterior part. The trunk does not bifurcate, the large cells
being placed in one line in the anterior half of the trunk. They may be nearer to or farther from one another, the two in front apposed quite close to one another. It seems to be certain that they are always five in number. The situation of the small cells is like that in Homarus but their staining is not so distinct as in the latter form. Scyllarus arctus shows the same arrangement as Palinurus.

Munida rugosa and Galathea strigosa have the trunk bifurcated and forming a T-shaped figure (Text-fig. 3, D, and fig. 10, Pl. 14). The two lateral cells are remote from the median line, in consequence of which the transverse part of the trunk is approximately of the same length as the median one.

In Potamobius astacus the arrangement of nervous elements differs from that represented above. The shape of the trunk is somewhat like that of Munida and Galathea. Yet the transverse part is still longer in comparison with the median, and curving forwards and outwards resembles in its outlines the antlers of a stag (Text-fig. 3, E). The large cells are placed in the transverse part and generally lie nearer the lateral edges of the trunk. The small cells are situated in the median part. There is also a remarkable difference in the number of ganglion cells, as no fewer than sixteen elements are here present. It is surprising that the arrangement and the number of the chief nervous elements in the heart of the lobster is much nearer to that of the Crabs than to that of Astacus. The difference in the number of the cells is really striking, if we accept the view—as I am inclined to do—that this number in the Decapods bears some relation to the number of metameres which go to make up the heart reduced in its length during phylogenetic development.

We shall give later a detailed description of the elements which are included in the ganglionic trunk, only mentioning here that it contains: (a) ganglion cells; (b) their processes; (c) the fibres of the dorsal nerves; (d) neuropile-like networks. The nervous elements of the trunk and of its main branches are bound together by a thick sheath of connective tissue.
Some data may be useful regarding the size of the ganglionic trunk, but I can only give approximate values, as it is correlated with the size of the animal. In the smaller specimens of Homarus the trunk from its posterior edge to the bifurcation is about 1 cm., in the larger specimens up to 1-6 cm. In Palinurus the size is the same or even somewhat longer. In the Crabs the trunk is shorter. In large specimens of Maia squinado, the carapace of which was 16 cm. in breadth, it was 0-7 cm., in large Cancer pagurus 0-8 cm.

The general course of the nerves arising from the ganglionic trunk is indicated in the Text-fig. 4, which represents a methylene blue preparation of the heart of Cancer pagurus and shows the dorsal wall of the heart viewed from its inner side. The two branches originating from the anterior bifurcation go to the sides, turn backwards, and take a circular course till they reach the posterior end of the ganglionic trunk. In this way they put into communication the anterior and posterior part of the median trunk. From the latter and from the circular anastomosing branches, which consist of five stout fibres, nerves to different parts of the heart are given off. One branch—not always present—runs forwards in the median line or a little asymmetrically on one side of it. Two or three branches on each side, consisting of a small number of fibres of unequal calibre, also take their course towards the anterior part of the heart. Tracing the circular anastomosing trunks, we meet branches the direction of which is antero-lateral (N a-l), lateral (N l), and postero-lateral (N p-l). These branches (a-l, l, and p-l), which are made up of five fibres each, pass farther on the ventral wall. The nerves destined chiefly for the median part of the dorsal wall arise directly from the ganglionic and circular trunks. In the subsequent description of the cells and their processes details will be given concerning the participation of the individual neurons in these branches.

Regarding the further distribution of the nerves in the heart it may be pointed out: (1) that the branches arising from the larger trunks do not remain on one level but penetrate the heart-wall; and that the figures do not show the real course of the nerves which undergo many subdivisions at various depths,
nor do they indicate their abundance; (2) that the thick and thin branches are in different ways connected with each other, but it is difficult to give the detailed plan of these anastomoses.

It ought to be emphasized that in our diagram the nerves of the dorsal wall only are figured. It is obvious that they pursue their way on the lateral and ventral parts of the heart.

The nerves of other Crabs examined show the same plan in their arrangement, differing in some points of little importance.
In *Maia* the lateral trunks are not so regular, and the fibres both in them and in the large branches lie more closely together.

In *Homarus* and *Palinurus* the situation of the main branches does not correspond to that in *Cancer* in the following points. Firstly, more branches run laterally from the ganglionic trunk (Text-fig. 1), and, further, the large posterior branches do not arise from the end of the ganglionic trunk but forward of it. The lateral anastomoses which soon take a deeper course among the muscles are also less regular in their outlines.

In *Munida* I have found the anterior median branch more developed than in other species (fig. 10, Pl. 14).

The arrangement of the nerves in *Astacus* was figured and described in my previous paper.

It may be added that there are some other modifications in the distribution of the nerves in the various species. I will not give an account of all the details observed, as the general plan seems to be the same.

The nerves for the ostia spring from the same branches which supply the muscles adjacent to the muscles of these orifices. The nerves reach the ostium from both its angles and break up in fine fibres which stain easily in this place. The relationship of the nerves of the ostia to those of other muscles is of such a kind that I think I am justified in concluding that they form an anatomical and physiological unit (Text-fig. 5).

Regarding the nerve-endings in the muscles little need be said. The nerves after many subdivisions accompany the muscle-fibres as very fine fibrils. I agree with Montalenti (1926) that these fibrils end in the muscles without forming any special end-organs (Text-fig. 6).

It is to be noted that besides these terminations originating from the long branches given off by the subsequent divisions of the axons, there are others which spring from short but mostly stout branches breaking up in the muscle-bundles into a considerable number of arborescent fibres. They always lie in the neighbourhood of the ganglionic trunk and, as will be described later, may be regarded as the ramifications of the dendrites.
2. Ganglion Cells.

(A) Large Cells (figs. 1, 3, 4, Pl. 13; Text-figs. 7, 8, 9, 11).

The size of these elements is related to the size of the heart and therefore to the size of the animals themselves. It is obvious that this is a consequence of the limited and constant number of the nerve-cells, each of them in the larger organs having to

Text-Fig. 5.
Nerves of the ostium drawn from a preparation of the heart of Galathea strigosa. The branches going to the ostium give nerves also to the adjacent muscles.

Text-Fig. 6.
Ramification of the terminal nerves in the muscles of the ostium of Eriphia spinifrons. a, small nerve consisting of two fibres.
supply a greater quantity of muscle-fibres. In the large specimens these cells measure up to 200μ and therefore, when stained, may be seen with the naked eye; in the smaller Crustacea such as Eriphia, Munida, Galathea, Scyllarus, they are 60 to 100μ, and thus they belong to the very large cellular elements.

The large cells present in the methylene blue preparations various appearances and might be classified as unipolar, bipolar, and multipolar. When several processes have stained they show considerable variations in their calibre (Text-fig. 7). There is reason to believe that all cells possess several processes some of which are seldom seen because of their refractory behaviour to the staining. Usually the anterior cells appear as unipolar or bipolar, the posterior generally as unipolar. In Homarus
the anterior cell situated in the bifurcation of the trunk shows as a rule three processes.

The methylene blue preparations do not reveal cytological details in these cells. The cytoplasm has a varied appearance during the staining process. At the beginning, i.e. about one hour after the organs had been placed in the methylene blue solution, numerous small granulations stained pale blue are seen in the protoplasm. They become after some time completely colourless and then the cells themselves cannot be distinguished. Only after some hours do they begin again to take little by little a deeper and uniform colour. It is probable that the former reaction occurs in the living cells, while the diffuse staining proceeds in those elements which are dying.

The nucleus, which is of relatively small diameter and of compact appearance, stains more deeply, but after the protoplasm has taken a deep blue colour it can no longer be distinguished in the cell.

The large cells are encased in a tissue of the same appearance as that forming the sheath of the main trunk. This tissue stains but very little with the methylene blue.

In Cancer, Eriphia, Palinurus, and Homarus numerous thin and mostly beaded fibres can be observed surrounding the cells in a kind of basketwork (fig. 3, Pl. 13, and fig. 20, Pl. 15). They are closely apposed to the cell, but whether the fibrils penetrate into it and what is the exact histology of the junction, I am unable to say. The proximal parts of the axons are often surrounded by the same fibres which enter the pericellular network (fig. 3, Pl. 13). All these elements arise from the dorsal nerves and therefore belong to the efferent system. This matter will be dealt with further in a later section.

(a) Axons.—The long processes of the large cells give to the heart the majority of all the nerve-elements whose distribution we have already described. As the microphotograph (fig. 16, Pl. 15) shows, the branching of the axons may present very clear images. Their whole course in the ganglionic trunk and in the main branches is very interesting, and I will give here some details observed in Cancer pagurus, the most favourable object for these investigations.
The axons of the three anterior cells at first run backwards down the ganglionic trunk at the posterior edge of which each of them divides into two (Text-fig. 8). In the first part of their course they give off two kinds of ramifications (Text-fig. 11):

(1) short and mostly stout branches which break up in rich arborescences in the vicinity of the trunk, and which we shall call dendrites, and (2) short collaterals to the neuropiles situated in the trunk. In the microphotograph (fig. 12, Pl. 14) is represented the anterior median cell, situated here a little asymmetrically; the thick fibres ($ax$, $ax$) in the same figure belong to the lateral cells.
The branches of the posterior bifurcations, three on each side \((a_1, a_2, a_3, \text{Text-fig. 8})\), take a circular course in the lateral trunks which, as was said before, run again to the anterior part of the main trunk (cf. Text-fig. 4). The postero-lateral, lateral, and antero-lateral nerves springing from the circular trunks receive fibres from each of these neurons. The fibres given off to the antero-lateral and lateral nerves are of different calibre; this fact being evidently correlated with the unequal distribution of the neurons in the heart, as may also be ascertained from their further course. The axon \(a_1\) sends only a thin branch to the antero-lateral and lateral nerves, and taking a curved course to the median trunk emits several branches running in different directions. One of them, being the thickest of all the fibres in this part of the heart (Text-fig. 8, and fig. 12, \(a_1\), Pl. 14) can be traced far forward. The branch of axon \(a_1\), pursuing the circular course of the axon, reaches the median line and for a short distance runs backwards in it, but soon enters one of the branches arising from this trunk and passes sideways and backwards. Before doing so it sends off some fibres which cross the median line.

Axons \(a_2\) and \(a_3\) give off to the lateral and antero-lateral nerves branches of more considerable diameter. In consequence the other branches of this division running to the median trunk are thinner than that of axon \(a_1\). Their further course is difficult to trace with certainty among the fibres of different origin. At any rate, it can be stated that they give off dividing branches which run in various directions. Some of them accompany the branches arising from the fibre \(a_1\).

The branches of the posterior bifurcation, which run on the opposite side, show the same plan of division though some asymmetry on both sides may be sometimes observed.

I am unable to state to which of the anterior cells each of the fibres \(a_1, a_2, \) and \(a_3\) belong, as in their course in the median trunk they could not be traced separately. It may be that axon \(a_1\) the territory of which seems to lie nearer to the middle line, originates in the anterior median cell.

The two posterior cells which, for the sake of clearness, are represented in a separate diagram (Text-fig. 9) send their pro-
cesses forwards in the ganglionic trunk. After giving off several shorter branches these axons bifurcate on the anterior end of the ganglionic trunk and take their course in the same circular trunks as the processes of the anterior cells, but, as is obvious, in the opposite direction. On their way they send branches to the three lateral nerves, so that these are formed of five fibres,

![Diagram illustrating the course of the axons of the two posterior cells in Cancer pagurus.](image)

Our diagrams are not complete since more branches arise to the posterior part of the heart, reach the ganglionic trunk and, after passing by the cells from which they have started, run forwards to end partly on the opposite side.
from the main trunks, and I have omitted those the origin of which was uncertain.

It would without doubt be of the greatest interest to know exactly the detailed distribution in the heart-wall of all fibres springing from each of these neurons. This problem may perhaps be solved when particularly good preparations may by chance be made; but up to the present my attempts to trace further individually the longer branches have had little success as in these observations errors easily creep in. Thus I am obliged to limit my description to some points only.

TEXT-FIG. 10.

A small nerve arising from the circular trunk made up of two fibres only.

The first question was whether all nerves running to the muscles contained elements given off by all five neurons. To this question I can give a negative reply; though, as a matter of fact, five neurons are represented in the circular trunks and, as has been pointed out, several nerves arising from the trunks receive each five fibres. But in one of the subsequent divisions of these nerves branches are given off consisting of four, three, or two fibres only. Already in the smaller branches arising directly from the main trunks, various numbers of fibres had been noted. Text-fig. 10 shows a nerve given off by the circular trunks near to the postero-lateral nerves. It is formed of two fibres only belonging to the posterior cells.

The analysis of components of further divisions is difficult, the more so since anastomoses join the nerves, but the preponderance of evidence indicates that the neurons are not equally
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distributed in the heart. From the examination of features represented in our diagrams the conclusion may be drawn that the axons of the anterior cells, though making a long loop and giving off many branches, predominate finally in the anterior part of the heart. The contrary is the case with the axons of the two posteriorly situated cells. On the other hand, we cannot assert that each of the neurons has to supply a definite territory isolated and independent from the others. On the contrary, it may be assumed that the area of distribution of one neuron overlaps the areas of the other neurons, since terminal branches of different origin can be observed in different parts of the heart. We see further in many preparations two fibres which belong to two neurons running in the branches of subsequent divisions parallel to each other. Even in the fine branches immediately before their breaking up in the terminal filaments the presence of two fibres sometimes can be observed (Text-fig. 6, a). However, there is no such regularity of double innervation such as may be seen in the muscles of the body, a fact which had already been stated by Montalenti (loc. cit.).

It may be mentioned here that this question is complicated by the fact that the fibres of the local system are joined by the efferent nerves. Fibres from these efferent nerves seem to run directly to the muscles. Very fine fibres which can sometimes be seen accompanying the branches of the axons of the local system might perhaps belong to these efferent nerves. On the other hand, they might be simply thin anastomosing branches of other neurons of the local system. The terminations of the fibres in the muscles have already been mentioned.

The collaterals for the neuropile are thin fibres which arise from the axons at that part of the latter which passes by the side of the neuropiles. In consequence they are of but short length. They are numerous when well stained, but this is rarely the case (Text-fig. 11; fig. 2, col. Pl. 13). Similar thin collaterals are given off also by the proximal parts of the dendrites.

(b) Dendrites. Short Arborescences of the Axons.—These short branches had been observed by me for the first time in Astacus and description and figures are given
in my previous paper. They are like a bush or a tree with very numerous and dense short branches, so that the most typical of them can be, when well stained, at once distinguished from other ramifications of the axons (Text-figs. 7, 11; figs. 1, 3, 4, Pl. 18; figs. 14, 15, Pl. 14). They are always situated in the vicinity of the ganglionic trunk, for they arise not far from the cells. Every axon seems to send off several such branches, but it is not easy to fix their exact number especially as the thinner ones may not be of a very characteristic shape (Text-fig. 11). These arborizations penetrate among the muscular bundles and end on the muscle-fibres. The striking richness of short and continually branching nerves offers some difficulties in describing and figuring them. In their general arrangement these terminations differ from those of the long branches. Their ramifications are shorter, branch at more varying angles, and are more tightly interwoven. On the other hand, these short branches of the axons have, in their terminations, the same appearance as the short processes arising directly from the cells. Sometimes they branch at the point of exit of the axons, and in such cases might be described as projections of the axons as well as of the cells themselves (Text-fig. 11; fig. 3, Pl. 18). Therefore, I decided, not without hesitation, to give all these arborescences the general name of dendrites.

Short Processes of the Cells.—The short projections of the cells are of various size both as to their length and breadth, and, as has been said, do not stain readily. They run in various directions and, when taking their course in the large branches, are difficult to trace, so that I am not quite able to say definitely whether all these processes have similar terminations. Those, however, which go sidewards are more easily observed, especially when they are of larger calibre (fig. 12, Pl. 14), and then it may be ascertained that they really end in the muscles with richly arborescent branches just as do the short branches of the axons described above.

Already during my investigations of the heart of Astacus it was observed that the same muscle-bundles may be connected with two short arborizations. Moreover, the presence in them of fibres, which I called accessory fibres, was assumed. After
examining different species of Crustacea I can confirm these statements. It is not easy to ascertain the relationship of such double arborescences to the respective neurons. Smaller doubts may arise when they both, as represented in the figs. 3, 4, Pl. 13, belong to the same neuron; but in some cases they appear as if springing from different elements (fig. 14, Pl. 14).

As to the 'accessory fibres', they are thin fibres accompanying the arborescent branches (figs. 3, 4, ac, Pl. 13). They belong to
the system of efferent nerves and we shall return again to these elements when dealing with the distribution of the dorsal nerves.

(B) Small Cells. (Text-figs. 12, 13, 14, 15; figs. 5, 6, Pl. 18; figs. 11, 13, Pl. 14.)

The small cells, the position of which we have already indicated, measure in the large specimens about 80\(\mu\). Therefore they differ distinctly in size from the large cells (fig. 11, Pl. 14). In smaller Crustacea, however, this difference is not always so noticeable, but, at any rate in Astacus, the two kinds of elements can easily be distinguished from each other. The cells are multipolar. Sometimes elements may be seen with one process only and of pyriform shape, yet this appearance is doubtless due to incomplete staining, though the cells themselves and their projections take the dye much more readily than those of the large neurons.

Two small cells of Mai\(a\) are represented in the fig. 5, Pl. 13. In one of these cells the nucleus can be seen, but, generally, the cytoplasm, when stained well, becomes so deep a blue that the nucleus cannot be distinguished any more.

As in the large cells two kinds of processes, the long and the short, are present. In the Crabs the polar differentiation of the cells can sometimes hardly be observed, as the processes springing from them may seem to be all alike (fig. 5, Pl. 13; figs. 11, 13, Pl. 14); only from its further course can the long process—let us call it the axon—be ascertained. The short processes stain very easily in Cancer, more easily than in Mai\(a\) and Eriph\(i\)a. In the latter form the cells often appear as unipolar, and when examining them superficially one might conclude that two forms of small cells are present, one unipolar and the other multipolar. This, however, is certainly not the case.

In Palinurus and Homarus the small cells differ somewhat in shape from those in the Brachyura. They are more elongated, and though multipolar in fact they present often only two stained processes, one of which, the axon, runs forwards, the other springs from the opposite pole and takes its course backwards in the main trunk; the latter is nothing else than one of the short arborescences (dendrites) which is thicker than the others.
The axon of the small cells gives off short arborescent branches (fig. 17, Pl. 15) which are similar to those of the large neurons. Consequently we shall call them dendrites too. In the Brachyura they arise in the vicinity of the cell, while in the Macrura they branch out at a greater distance from the cell (Text-figs. 12 and 13). Text-fig. 15 shows the small cells in Homarus. The situation of the cells in the trunk and the distribution of their projections should be noted. The dendrites are, as a matter of fact, more abundant than they are represented in the figure; but they rarely stain simultaneously in one and the same
preparation. Especially those running backwards in the ganglionic trunk are difficult to trace, except in the last cell, the posterior dendrites of which can often be seen distinctly, their shape being quite characteristic. The short thin fibres ramifying in the ganglionic trunk, which we regard as collaterals running to the neuropile, are also scattered to a greater distance if compared with their topography in the Crabs.

The axon pursuing its course forwards, though giving off some
branches, does not decrease in diameter and even may appear thicker at some distance from the cell than when near to it. Unfortunately, its whole course could not be traced and its final destination is uncertain. It was, however, established that it gives collaterals to the anterior neuropiles, and, on entering the anterior bifurcation of the ganglionic trunk, divides into two main branches and also gives off some arborescent branches (Text-fig. 14). The insufficiency of these observations, which is the cause of this, perhaps the greatest, gap in our present investigations, is due to the close apposition of the fibres in the ganglionic trunk, especially in those parts where they pass near the neuropiles. Any one who has had to deal with similar investigations knows quite well how difficult it is to follow one nerve-fibre for any distance without losing it among the others. In my large specimens the distance from the small cell to the anterior end of the trunk may amount to 10 mm. and more. For these investigations the smaller Crabs, as *Eriphia spinifrons*, are more appropriate.

The number of the dendrites springing from the cell body is usually from two to four; the greatest I have noticed was seven in *Maia squinado* and eight in *Astacus*. However, if we take into account the short branches originating from the proximal part of the axon, which, as we have agreed, may also be considered as dendrites, the total number of the latter will evidently be greater.

The dendrites belonging to different cells often travel parallel to each other and are accompanied by fibres of other provenance. The proximal parts of the outgrowths from even two cells present a complicated image of reciprocal relations (fig. 5, Pl. 13), in consequence of which their course is difficult to trace, especially in Crabs, in which the length of the dendrites may be considerable (Text-fig. 12). When describing these processes in *Astacus* I expressed some doubts as to their destination, but the observation of these elements in *Homarus* and *Palinurus* has cleared up the uncertainties. In these specimens the dendrites of the small cells are shorter and end in arborizations of characteristic shape (Text-figs. 13, 15). In Crabs, too, whenever the dendrites of the small cells can be followed up to their
endings, one finds them breaking up in tree-like terminations. They are found at various depths in the heart-wall but always entangled between muscle-fibres. I was unable to see any constant difference between the short arborescences springing from the axons and those originating in the cell itself. Moreover, they present the same features as those which we have described.

**Text-fig. 14.**
Small cell of *Eriphia spinifrons* in its whole course in the median trunk. The anterior bifurcation of the trunk is drawn as a dotted line.

**Text-fig. 15.**
Small cells of *Homarus vulgaris* (1-4). *ax*, axons; *col*, collaterals; for the sake of clearness the space between the axons is enlarged in the drawing.
before as dendrites of the large cells. There are, of course, differences in the length and calibre of the outgrowths as well as in the size of the areas occupied by the terminal filaments; but all these differences may be observed in the processes of one and the same cell and thus, from an histological point of view, all these elements appear to belong to the same class.

From the axons and the dendrites thin collaterals arise, which soon ramify in closely interwoven coils lying in the ganglionic trunk (fig. 5, Pl. 13). They are here in connexion with the endings of the efferent fibres (fig. 6, Pl. 13). The branches of the latter, too, accompany the dendrites as thin beaded fibrils. Thus the processes of the small cells have also their 'accessory fibres'.

The question now arises whether the difference between the large and small cells lies only in the size or in a totally different function. Some data of comparative anatomy seem to speak in favour of the first of these possibilities. The heart of the Decapods is derived, as is well known, from the more elongated form of the lower Arthropods and in some of these animals even bears the name of 'Dorsal pulsating vessel', which defines its shape sufficiently well. The ganglion cells of the local nervous system are in this case scattered along the heart tube. The observations concerning the topography of the cells in the heart of the Arthropods are not numerous but so far all agree as to this point. In Insects—I described the nerve-cells in the heart of Periplaneta orientalis in 1926, and, since then, have been able to observe the same arrangement in some other specimens—the ganglion cells are placed in two nerve-trunks accompanying the heart tube throughout its entire length. A single ganglionic trunk is present in the Isopoda, Stomatopoda, Decapoda, Xiphosura, and Scorpionidae. Very interesting is the arrangement of the nervous elements in Squilla. Claus (1889) has already pointed out that the nerve-cells lie at regular intervals, one cell for each segment. This writer stated it when investigating the larval form, but the same features were observed in the adult by Nusbaum (1899), and I can confirm his results. From the regular arrangement of the cells in Squilla it appears that their number bears a constant relation to the number of segments

\[1 \text{ I propose dealing with this question in a subsequent publication.}\]
in which the heart is situated. As to the Decapods, it may be admitted that a smaller number of segments contributes to the making up of the heart, which would explain the relatively small number of nerve-cells in it.

Regarding the difference of the cell-sizes it might be suggested—this is hypothesis only—that the amount of muscle given by different metameres for the constitution of the definitive form of the heart is not the same, and in consequence the ganglion cells having to supply a greater territory become hypertrophied, while the others preserve their smaller size. With regard to the probable distribution of the neurons, we may suppose that the middle part of the dorsal wall of the heart is left for the smaller ones. According to this interpretation both large and small cells would have the same function, and the various sizes would result from the unequal amount of muscle supplied by each of the two kinds.

Two objections come to mind: firstly, some difference was noted in the staining properties of the two kinds of cells, and hence the conclusion may be drawn that they possess essentially separate functions; but another explanation of this is also admissible, viz. that these various staining effects depend on the size of the cells only; in the small elements the surface, being relatively larger, makes the penetration of the dye easier and hence the conditions of the reaction needed for the staining with methylene blue are not the same in the two cases. Secondly, the large and small cells differed in the fact that in the latter the basketwork surrounding the cells seems to be wanting. On the other hand, however, it may be recalled that in some species (Maia, Potamobius) the large cells also appear in our preparations without the fine fibres entangled around them.

The assumption that these small cells represent sensory elements must also be considered. They would differ, of course, completely from the common bipolar form of sensory cells which are well known in Crustacea, but I do not think that this fact alone renders the supposition untenable, for I have many doubts as to the completeness of our knowledge of the nervous elements in the Crustacea.\(^1\) Therefore it is not improbable that some

\(^1\) In this connexion it is interesting to note that in the peripheral nervous
elements may have a sensory function although their appearance does not fit into the customary scheme.

On the other hand it may be said that the behaviour of the long processes of the small cells in the heart does not support the view that they are sensory elements. Their dendrites and the axons, the latter so far as they could be traced, do not differ essentially from the processes of the larger cells; there would be also difficulty in explaining their connexions with the efferent system and even with the same branches of it if the small cells were sensory elements.

Lastly the possibility has to be considered that the small cells have in the local system some associative function but, until direct evidence has been brought forward as to their exact relationship, we must be satisfied with the statement that of the three possibilities discussed the first one, viz. that the small cells differ only in size from the large ones, is more probable than the others; yet none of them is completely excluded.


The discovery of the nerve-cells in the heart of the Crustacea is attributed to Berger who mentioned the presence of these elements in 1877. His statement was confirmed by several authors of whom J. Dogiel seems to be the first who made more precise observations by means of the gold-chloride method. From the figures illustrating his paper (1894) one may draw the conclusion that the elements represented there are certainly the nerve-cells in question, but the description given by Dogiel was inexact, for he stated that the nerve-cells in the heart of Astacus were grouped in two clusters ('Knoten') anterior and posterior, situated in the median line of the heart. A similar error was made by Stecka (1903) who also investigated the heart of Astacus. She gave a drawing in which we see large and small nerve-cells, fifteen (or sixteen?) in all, but the direction system of these animals I observed peculiar cells with processes ending in the muscles. These cells, which are undoubtedly nervous elements resembling somewhat the small cells of the heart, were found in the Decapods and the Stomatopods. In the latter, moreover, there are other unknown elements and even systems in the peripheral innervation of the abdomen. I intend to describe them elsewhere.
of the trunk including these cells as given in her description is incorrect. As to the cells stained with methylene blue in the heart of Palaemon treillanus by J. Nusbaum (1899) it is difficult to ascertain whether they belong to the nervous elements. The writer himself pointed out that no connexion of these cells with other nerves could be observed. It may be that in this species the staining of the nerve-trunk did not succeed and consequently the cells appear as isolated. In 1913 I described ganglion cells in Palinurus vulgaris and Cancer maenas which could be made out by means of the methylene blue method. Their nervous character and the presence of the connexions with the nerve-trunk were beyond doubt, but the distribution of the local neurons in the heart and their relation to the efferent system were not traced out. Newmywaka in 1928 investigated the heart of Astacus, using also the methylene blue method. The greatest number of cells stained by him in one preparation was sixteen, but Newmywaka expresses the opinion that these cells are probably much more numerous. This writer figured the nerve-cells as unipolar, bipolar, and multipolar. As to their function he says: 'Es ist sehr möglich, dass diese Zellen einen diffusen rezeptorischen Apparat vorstellen, welcher den rezeptorischen Endigungen im Herzen der Wirbeltiere analog ist.' The results of my investigations on the same subject published in 1929 have been referred to in the foregoing description.

III. Nervi Cardiaci Dorsales.

The dorsal nerves (regulator nerves of the heart) consist of fibres by means of which the heart communicates with the central nervous system. They certainly contain the efferent fibres conveying the impulses from the infra-oesophageal ganglion to the heart. Whether there are also others which, as afferent fibres, run in the opposite direction I have no positive knowledge. The term ‘dorsal nerves’ was proposed by the writer when describing this system in Astacus, as these nerves coming from the sides pass to the dorsal wall of the heart and penetrate into it. The addition ‘regulator nerves’ seems to be advisable owing to the fact that in the meantime in another
group of Crustacea, namely, in Isopods, nerves had been found, which are evidently homologous with the 'dorsal nerves' of the Decapods but differ in their topography.

1. Historical.

The nerves which reach the heart from the sides and influence its rhythm were investigated by J. Dogiel in 1894, who noted that before him Eckhard in 1867 had made some experiments on a nerve having an inhibitory action on the heart. J. Dogiel, by his own physiological experiments, was led to the conclusion that two kinds of fibres, inhibitory and accelerator, run to the heart of Astacus, yet from the drawing he gives it is not clear whether the nerve he found in the microscopical preparation really represents the fibres in question. Much more precise are the observations of Carlson (1905), who described the course of two nerves springing from the large thoracic ganglion and illustrated the results of his investigations by a diagram which is well known from several reproductions in works dealing with the comparative physiology of the heart.

G. Police in 1908, unaware of Carlson’s paper, described in Maia three pairs of nerves approaching the heart from the sides. One pair of them, figured by this writer in Maia and Scyllarus and called by him nervi cardiaci, seems to correspond to our nervi dorsales, although their relation to the heart and to the other nerves is represented in a different manner from that which we shall describe later. Police has also endeavoured to find out the origin of these nerves and says that they spring 'con tutta probabilità' from the infra-oesophageal ganglion, being independent of the 'visceral nervous system'.

2. General arrangement of the dorsal nerves.

The dorsal nerves can be well observed when, after the injection of methylene blue or rongalit white—in the Macrura the staining succeeds more easily—a part of the dorsal carapace is taken off and the heart exposed. When the staining is favourable a pair of nerves is to be seen branching from the nerves running on the thoracic muscles. They cross the lateral border of the heart at about the middle of its length, pass on the
dorsal wall and penetrate it approximately midway between the lateral border and the median line.

In some rare cases a branching of these nerves was observed at some distance from the heart and in consequence two branches reached the ganglionic trunk, but I could not as a rule find two nerves on each side.

It is a very difficult task to find out the origin of the dorsal nerves by anatomical methods. They branch, as was said, from the nerves lying on the muscles of the epimeral plates; by following the latter nerves we find that they spring from the infra-oesophageal ganglionic mass. But precisely these nerves are interconnected by numerous anastomoses, and, therefore, I was not able to trace with certainty the course of the heart nerves in them. According to Carlson the inhibitory nerves for the heart take their origin 'near the roots of nerves to the third maxilliped and the accelerator near the roots of the first ambulatory nerves'. Thus, the heart nerves have different roots, but whether they run independently up to the heart seems to me more than uncertain. In all species I could see one pair of nerves taking part in the innervation of the heart itself and therefore, if it is not a peculiar case in that another nerve remains always resistant to the staining with methylene blue, I am inclined to conclude that the fibres originating from different roots join in one bundle, i.e. our dorsal nerve. The structure of the nerve itself, which is composed of two kinds of fibres of different calibre, is not incompatible with this interpretation.

Mention may be made here of particular swellings on the dorsal nerves just before they enter the heart. I observed them in Astacus and called them 'apparatus nervi dorsalis'.

After piercing the heart-wall the dorsal nerves join the local nervous system (Text-figs. 2, 4). It is not difficult to trace their course through the wall (fig. 7, Pl. 13) and after some experience to distinguish them from the branches of the local system as they differ somewhat in their appearance (N dors, Text-figs. 16, 17). This difference may be yet more pronounced owing to the unequal staining reaction of the two systems in consequence of which the fibres of the dorsal nerves generally take up the dye sooner (especially in Eriphia and Palinurus) or, when
stained, differ sometimes in colour from the fibres of the local system. These properties enable us to follow them in favourable cases through their whole course in the ganglionic trunk. However, this relative facility in examining the dorsal nerves does not apply to all their elements but merely to one kind, viz. the fibres which, as will be seen, communicate in the ganglionic trunk with the cells and their projections. For the sake of facilitating the description I will call them 'System I', which is made up of the thicker fibres. The thinner elements we shall call 'System II'.

3. System I of the dorsal nerves.

The fibres of System I, after entering the ganglionic trunk, run throughout its whole length. In the species in which the trunk bifurcates at its anterior end they pass, following the branches of bifurcation, to the median line and, after reaching it, turn directly backwards. In Palinurus and Scyllarus
their course is somewhat different: as the microphotograph (Text-fig. 17) shows, each fibre on arriving at the ganglionic trunk divides into two, giving rise to a Y- or T-shaped figure, and sends one branch of this division forwards and the other backwards.

The fibres which make up System I are not numerous. In Palinurus, where the relations between the ganglionic trunk and the dorsal nerves are easy to examine because of their position, some preparations show three fibres on each side at the point of junction of the dorsal nerves with the ganglionic trunk (Text-fig. 17). This has been the largest number seen; usually only one or two of them have stained.

The characteristic feature of the fibres of System I is the abundance of thin and richly ramifying branches meeting in the ganglionic trunk and in its neighbourhood and giving off neuropile-like networks of fibrils. The latter establish connexions between the fibres of System I with each other, and between these fibres and both the large and the small neurons of the local system.

The connexions between the fibres of System I show a striking abundance and density of arborescences. The neuropiles which we have mentioned when describing the ganglionic trunk appear as if they were made up chiefly of these branches. The networks are situated in the Crabs mostly in the anterior part of the trunk, forming here one or, more rarely, two oblong masses and some smaller ones, the latter in the bifurcation of the trunk or in its main branches. Fig. 2, Pl. 13, represents a part of the larger neuropile in Maia and the numerous short collaterals arising from the fibre belonging to the System I. In Text-fig. 18 we see the networks and the shorter and longer branches reaching them. Observation of fixed and fresh preparations—the latter are more convenient for this purpose as the fixation of the neuropile is difficult and seldom gives clear images—teaches us that branches are sent to these neuropiles by different fibres from the same side, as well as from the opposite one.

In the posterior part of the ganglionic trunk of the Brachyura the same fibres of the dorsal nerves give off again networks of fibrils smaller than those in front (fig. 6, Pl. 13).
All these neuropiles may have various appearances in fixed preparations. Sometimes they present small irregular plates with uneven outlines and very fine granules; in other preparations the granulations are larger. As a matter of fact, these neuropiles consist probably of very dense networks of fibrils, which by the action of reagents are deformed in different ways.

In the Macrura the branching fibres of System I of the dorsal nerves do not give such convoluted masses and the networks, though very numerous, are arranged more loosely along the...
ganglionic trunk, yet they are denser in the anterior part of it. The diagrammatic figures (Text-fig. 19), in which only one fibre

on each side is represented, may illustrate the course of the System I in Palinurus (A) and Brachyura (B).

The fibres of System I travelling in the ganglionic trunk send out branches which are not confined to this trunk only. Some
run sidewards and soon ramify between the muscle-bundles. It is easier to observe them in the Macrura. As shown in the microphotograph (fig. 21, Pl. 15) these branches may consist of several fibres which come into close relation with each other. In Eriphia I observed these fibres ending in small coils.

It has been mentioned that in some preparations the dorsal nerves had already stained before all the others had taken the dye. In such a case the reciprocal connexions of all the fibres belonging to System I prevail to such a degree that one might assume that the function of all neuropiles is the mutual exchange of the impulses among the fibres of the dorsal nerves only. This is certainly not the case, all these structures being at the same time the fields of conjunction between System I of the dorsal nerves on the one hand and the neurons of the local system on the other.

There are various parts of the large neurons which are in close relation to System I, viz. (a) the cell bodies; (b) the dendrites; and (c) the collaterals to the neuropiles.

(a) In one of the foregoing sections when dealing with the histology of the nerve-cells, we described the pericellular networks which are made up of varicose fibrils. In Cancer, Eriphia, Homarus, and Palinurus these networks stain distinctly (fig. 20, Pl. 15) and I could convince myself that they belong to what we call System I, from which many fibres ramify round one cell. The most probable destination of a part of the branches of the dorsal nerves which cross the median line, as they are represented in the Text-figs. 18 and 19, B, is participation in the network surrounding the contralateral cells.

(b) The branches of the dorsal nerves accompanying the dendrites have also been mentioned before. Already when dealing with the heart of Astacus it seemed probable to me that the so-called accessory fibres (figs. 3, 4, ac, Pl. 13) of the short arborescences belong to the dorsal nerves. This assumption seems to be correct, for the connexions of the dendrites with the branches of the dorsal nerves were often observed; but, unfortunately, their relations cannot be discerned in detail. When the ramifications of the dendrites have stained well and are then very numerous, there is no possibility of tracing the finer fibrils
separately. I am, therefore, unable to say whether all the arborizations of the dendrites are accompanied by fibres of the dorsal nerves. The observations are rendered much more difficult by the fact that the dendrites rarely stain and mostly not at the same time in both systems. Many branches of the dorsal nerves which run sidewardly from the ganglionic trunk may be nothing else than these accessory fibres of the dendrites, the latter not having stained in this place. If such be the case we can assume that one dendrite may be in relation to the branches of different fibres of System I.

The thin collaterals given off by the proximal parts of the short arborescences to the neuropiles have already been mentioned.

It remains doubtful whether the 'accessory fibres' only accompany the dendrites or continue farther to other nerves or, perhaps, to the muscles. Thus, for instance, in the anterior part of the trunk thin fibres may be noticed which leave the trunk and go with the nerves of the local system (Text-figs. 19 A, 19 B, b). It is not improbable that they accompany one of the longer dendrites of the anterior cells. Alternatively, they may represent fibres of System I with some special unknown signification.

(c) The further fields of conjunction between the dorsal nerves and the neurons of the local systems are the neuropiles, and it seems most probable that this is the essential role of these networks. The collaterals of the axons are short and thin, and in their shape do not differ much from those of the dorsal nerves (fig. 2, Pl. 13), but they do not stain readily and even when stained remain mostly pale blue. In view of this fact we may conclude that the predominance of the fibres of the dorsal nerves in the neuropiles is only apparent and due to their staining properties.

The connexions with the small cells are, properly speaking, the same as with the large ones, except the network surrounding the cells, though fibres approaching the cells and lying on them can be observed. As to their dendrites they are accompanied by the 'accessory fibres' branching from the dorsal nerves. Junctions by means of networks to which both elements send thin fibres are also present. Fig. 6, P. 13, represents a
small cell of *Maia squinado* showing the connexions by means of small neuropiles in the ganglionic trunk.

According to this description, when we summarize all that has been said about System I of the dorsal nerves we come to the conclusion that at least the majority of its fibres end in synaptic junctions with the neurons of the local system, as illustrated by the diagrams, Text-figs. 20, 21. The neuropiles seem to be the largest field of these conjunctions. The question arises whether all cells send collaterals to the same part of the neuropile, when it forms such a convoluted mass as seen in Brachyura. I am inclined to answer this question in the affirmative, although this statement, so far as it concerns the small cells and the two larger ones which are situated in the posterior end of the trunk, cannot be made without some reservation, owing to the distance of these elements from the anterior part of the trunk and the possibility of errors in tracing the fibres. However, in some preparations, I was able to observe the collaterals lying far from the cell-body (Text-fig. 14).

4. **System II of the dorsal nerves.**

The fibres of the dorsal nerves which do not belong to System I are of smaller but not equal calibre. The term System II
employed in this description is used only in order to distinguish these fibres from the former system and does not imply that they belong to one and the same anatomical and physiological unit, as I am unable to give a more detailed account of their distribution in the heart. The nerves in question do not stain

**Text-fig. 21.**

Diagram showing the relation of a fibre of the dorsal nerve to the small cell.
satisfactorily, and even when stained cannot be traced with certainty among the other fibres. Some features only can be mentioned here.

In Astacus I found fibres of the dorsal nerves which, arriving at the trunk of the local system, take a separate course running in the opposite direction from other fibres of the dorsal nerve towards that part of the heart where no cells are present and ramifying between the muscles.

Similar bifurcation of the dorsal nerves could be observed in Scyllarus and Munida, and also, in some rare cases, in Palinurus and Cancer. This might be regarded as an accidental aberration of the usual course of the fibres. On the other hand, comparing the dorsal nerves before they join the trunk of the local system and after, it must be asserted that some of the fibres are lost somewhere, and, therefore, the cases in which they are found to be taking a separate course might indicate the real destination of these elements. Part of the thinner fibres accompany the fibres of System I in their course towards the ganglionic trunk, but I could not trace them farther. Possibly, those fine fibres which are sometimes found along the long branches of the local system are of this origin. If I am right in this conjecture, the System II, or a part of it, may be considered as consisting of fibres of efferent nerves which go to the heart muscles without giving synapses with the nerve-cells in the ganglionic trunk.

In Fig. 7, Pl. 13, the dorsal nerve of Palinurus is represented at the place where it pierces the heart-wall (indicated by the line a-a). The fibre SII ramifying on the inner surface of the heart-wall belongs to System II.

IV. Apparatus Nervi Dorsalis and the Nerves of the Pericardial Cavity.

In Astacus I had observed on the dorsal nerves peculiar short branches ending in irregular plates or cell-like bodies. I have called them 'apparatus nervi dorsalis' and suggested that the apparatus may be concerned with the appreciation of the pressure in the pericardial cavity. In Eriphila and Scyllarus cell-like bodies, and in different species thin
ramifying fibrils surrounding the dorsal nerves were seen in this situation. But so far I am unable to give an exact description of these elements and of their relation to the dorsal nerves. Possibly they form a part of peculiar terminations of the nerves entering the pericardial cavity, for in addition to the pair of dorsal nerves (regulator nerves), several other nerve bundles can be seen—especially numerous in *Palinurus* and *Scyllarus*—which spring from the thoracic nerves, and running to the dorsal surface of the heart, break up in a fine arborescence of thin fibrils which assume a beaded form. This fact suggests that the heart itself is supplied with many nerves, but microscopic examination convinces us that only one nerve-bundle on each side, viz. the dorsal nerve, penetrates the heart-wall, while the others remain in the pericardial cavity and terminate on the ligaments and in the connective tissue on the dorsal surface of the heart. Methylene blue does not give clear images of these endings, since the thin fibrils which originate from the thicker fibres actually present a mass of blue points like the 'punctate substance' of the neuropiles (fig. 7, Pl. 13).

Similar structures can be seen on the epimeral plates and I had previously observed them in *Potamobius*. In Stomatopods they are present in the abdomen and are in connexion with a peculiar nerve which I think is homologous with Newport's nerve in Insects. I think also that all these systems of peripheral neuropile-like structures must be regarded as sensory elements which may have some relation to respiration and to the circulation of the blood in the body cavities. The matter needs further investigation.

V. **Nerves of the Arterial Valves and of the Pericardial Muscles.**

The valves situated at the entrances to the arteries arising from the heart are innervated, except the valve of the anterior median vessel, by branches of the nerves which I called *nervi segmentales cordis*. The same nerves give off branches to the muscle-fibres of the pericardial plate. The valve of the median artery is supplied with a nerve which runs alongside that vessel,—*nervus cardiacus anterior*.
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1. Nervi segmentales cordis.

I adopted this term describing the innervation of the heart in Insects in order to point out their origin from different segments. The system found in Crustacea may be considered homologous with that of the Insects. In the Decapods, according to the shape and position of the heart, its segmental nerves are confined to the thoracic region only, whilst the segmental nerves in the abdomen run to the abdominal dorsal vessel and from that point might be called Nervi segmentales aortae abdominalis.

As regards the number of the segmental nerves of the heart, I have found in Astacus four of them on each side, and I think that the same number is possessed by the marine Crustacea also, but, since the latter specimens had been used principally for the investigation of the local system, my observations on segmental nerves have been more numerous in Astacus.

The methods employed in making the preparations demonstrating this system were somewhat different from those indicated above for staining elements of the local system. The segmental nerves take the dye much more readily when it is administered by means of an injection, and therefore this method of staining them was chiefly applied. Some hours after the injection the carapace must be removed from the thorax, and then the liver, the genital organs, the stomach, and the intestine must be taken out. The pericardium must be left intact and remains attached to the thoracic muscles. After longitudinal section of the ventral wall of the thorax, the underside of the heart and the segmental nerves on it can be seen. The whole preparation can then be fixed in ammonium picrate or ammonium molybdate. It is possible after washing to detach the muscles from the chitinous parts and mount the whole, i.e. the heart with the pericardium and the adjacent muscles. Then, the segmental nerves in connexion with the thoracic nerves from which they branch may be observed.

In the Brachyura I could not obtain similar preparations, this failure being due at first to the much less satisfactory staining of these nerves in the Crabs. On the other hand, tracing the
nerves is very difficult owing to the form of the chitinous parts of the thorax. The system of segmental nerves is of course also present in the Brachyura, and, so far as I could determine, is arranged similarly to that of the Macrura. In Astacus I found that the segmental nerves of the heart travel in the thoracic nerves II to V (denomination according to Keim, 1915). The point where they branch from these nerves may be easily observed, whereas their proximal course in the thoracic nerves could not be traced farther. Passing on to the pericardium they give off fibres to the muscles of the latter and running farther towards the middle line join in a longitudinal nerve bundle (Text-fig. 2). In a foregoing paper I called this bundle Fasciculus medianus pericardii—as in Astacus and Palinurus it was found lying in the median line. However, in Homarus, Scyllarus, and in the Brachyura, there are two bundles directed more or less longitudinally (Text-figs. 22, 23), and, therefore, the name fasciculus (l) longitudinalis fits better. In this bundle (or bundles) fibres meet from the segmental nerves and, taking various courses, are distributed among the branches running (1) to the pericardial muscles which, therefore, receive fibres directly from both the segmental nerves and from the longitudinal bundles, and (2) to the valves of 5 arteries, viz. the arteriae antennales, arteriae hepaticae, and aorta posterior. The microphotographs (figs. 22, 23, Pl. 15) show the longitudinal bundle and the nerves going to the pericardial muscles in Palinurus.

The nerves on arriving at the valves break up into a tuft of fibres which, ramifying again, are closely interlaced between the muscles. The arborizations of these nerves mark well the outlines of the valves and, in the two pairs of the anterior arteries, the longitudinal aperture between two parts of the valve may be seen (Text-figs. 22, 23). The nerves of the posterior valve have a much more complicated course, which I have described in Astacus. This is due to the peculiar arrangement of the muscular fibres, which is not the same in the various species, and further to the fact that the system of the segmental nerves of the heart is in connexion with the nerves of the aorta. The latter system is made up of some bundles travelling on the
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abdominal dorsal vessel and receiving in every segment branches from the abdominal nerves. I propose to call these branches Nervi segmentales aortae (Text-fig. 24, Nn seg ao). They supply the valves situated at the origin of the arteries arising from the abdominal aorta. In the diagrammatic drawing (Text-fig. 24) the relations of the system of the segmental nerves of the heart and those of the aorta are shown. We note that the fibres springing from the 1st abdominal nerve take part in the

TEXT-FIG. 22.
System of the nerves of the valves and of the muscles of the pericardium in Scyllarus arctus. Similar arrangement in Homarus vulgaris also.
The same as in fig. 22 in Eriphia spinifrons; similar arrangement in the other Crabs investigated. Figures 22 and 23, Pl. 15, should be compared with Text-fig. 2 representing this system in Palinurus.
TEXT-FIG. 24.

Systems of the segmental nerves of the heart and of the segmental nerves of the abdominal aorta and their relations to the somatic nerves in Potamobius astacus. Nn seg c, nervi segmentales cordis; N th I–V, thoracic nerves; Nn seg ao, nervi segmentales aortae abdominalis; N abd I, II, abdominal nerves; N card ant, nervus cardiacus anterior (Nerve of Lemoine); Mm depr, depressor muscles.

innervation of the posterior valve of the heart; whether some from the segments farther back reach the heart too, or, vice versa, how far the fibres of the segmental nerves of the heart pass on the aorta, I am unable to give any exact information.
Turning to the nerves of the valves of the heart, we have to note that their appearance is somewhat different from that of the nerves described in previous sections. The fibrils are more uneven, the shape of their swellings (beads) is not the same. Even their colour when stained with methylene blue has often a different nuance.

On the periphery of the valve some fibres end in small leaf-like plates showing no connexions with the muscles. They may perhaps be regarded as the sensory endings. In the neighbourhood of the valves oblong swellings on the fibres were also observed. They could not be identified as the true cells.

It is a fact of the greatest interest that connexions could nowhere be found between the system of the segmental nerves and the other nervous elements of the heart. This statement must be accepted with some reserve owing to the difficulties of observing the elements of the neighbouring systems of fibres, the respective muscles being in close connexion with each other. However, it is easy to determine the limits between these two muscular systems because of the peculiar staining properties of the valvular muscles, for they very often become a distinct blue and are then sharply delimitated from the muscles of the heart-wall (Text-fig. 25). Moreover, some details of the structure of the muscle-fibres of the valves are distinctive, since they are more loosely arranged and give off ramifying branches.

Attention may be called to the fact that these muscles, which are antagonistic to the muscles of the heart-wall, show a different behaviour when stained in methylene blue. This fact, which seems to prove that muscle-fibres in the same organ have various chemical or physico-chemical properties, may be of interest for the physiology of the involuntary (autonomic) system.

Notwithstanding a careful examination of all successful preparations I could find neither any irradiation of the local nervous system on the valves or of the nerves of the valves on the heart-wall, nor any anastomosis between the fibres of these two nervous systems.

Still more surprising is the fact that while the nerves of five valves are connected with each other, one valve only, namely,
that of the anterior median artery, is excluded from this common system and possesses its proper nerve.

2. Nervus cardiaicus anterior.

There exists considerable bibliography about this nerve which was discovered by Lemoine in 1868 and called by him 'nerf cardiaque'. Its presence was asserted by several authors. In some recent works it was described as the main or even unique nerve of the heart. Accordingly, it was represented as giving stout branches in the heart which, as a matter of fact, do not exist. There is, however, to be noted the accuracy of the investigations of Police (1908), who confessed not to have succeeded in observing this branching, and stated that he only saw the nerve penetrate the wall of the artery: 'In vicinanza del cuore l'ho visto approfondarsi nella parete dell’arteria'. This observation is the most correct of all.

Police called this nerve 'nervus arteriosus medianus', and perhaps there is some reason for changing its name, but I have
preferred to adopt the term nervus cardiacus anterior, firstly because it has been known by the name 'nervus cardiacus' for more than sixty years, and further, because, as a matter of fact, it reaches the heart at the origin of the artery. The name nervi arteriosi seems better reserved for the nerves of the artery in the abdomen. The addition of the adjective 'anterior' to the old name seems necessary in order to distinguish this nerve from other nerves of the heart.

The anterior cardiac nerve arises from a nerve lying on the anterior and dorsal surface of the stomach (nervus stomatogastricus). For details concerning the complex innervation of oesophagus and stomach the reader may be referred to the works of E. J. Allen (1894), Police (1908), Keim (1915), and Orlov (1929). The cardiac nerve runs alongside the ophthalmic artery and, approaching the heart, divides into 2 or 3 branches (Text-figs. 2, 22, 23, 24). Staining with methylene blue reveals the destination of this nerve, viz. it penetrates the wall of the artery and breaks up into many fibres which supply the muscles of the median arterial valve. The appearance of these fibres, their branching, endings, and staining properties are the same as those of the nerves in other valves.

As already said, contrary to my expectation no communication with the latter could be found. Even if we suppose that some fibres escaped our observation, there might be only thin fibrils which certainly could not be got out by mere anatomical dissection. At any rate, the nerve of Lemoine, which ranked high in the innervation of the heart, must now be relegated to a much more modest place.

PHYSIOLOGICAL CONSIDERATIONS

In the foregoing description I touched in several places upon the probable functions of the nervous elements which had been found in the heart of the Crustacea. I shall now endeavour to summarize those points which may be of interest for physiology.

As to the local nervous system, its arrangement and relations with all the muscle-fibres of the heart lead to the conclusion that these muscles are under the influence of impulses originating in the ganglion cells of this system. The suggestion that the latter
may be sensory elements seems to me untenable, and I am strongly inclined to think that this system rules the beat of the heart.

Experimental evidence may be obtained with regard to the significance of the local system. Thus, in the heart of *Maia squinado*, though it is prepared for staining in the usual way, i.e. sectioned on its ventral side and stretched on the paraffin plate, the muscles, during one hour or more, continue to contract in a regular rhythm provided the ganglionic trunk be not damaged. But if now the latter be divided with fine scissors—this operation when the staining reveals the nerves may succeed without hurting the muscles—the heart stops beating at the very moment of the incision, and thenceforth only irregular contractions of various muscle-bundles take place. In cases in which, without this experimental incision, either such irregular contractions were observed or the heart did not beat at all, it could be ascertained that the ganglionic trunk or the main branches of it had been unintentionally injured when cutting the heart-wall.

It was tempting to make some experiments, also, on the cells themselves. But this is rendered difficult owing to the situation of the cells which, at least the anterior ones, lie under the muscles. At the section of the latter a part of the dendrites of the cells must be cut away and, moreover, it is almost impossible to work without hurting the ganglionic trunk.

From the above statements it would seem that the local system of ganglion cells in the Crustacea has the same function as, according to the investigations of Carlson, the corresponding system in the Xiphosura possesses. With regard to this question some experiments made by me when working on Isopoda may be of interest. In *Ligia oceanica* the ganglionic trunk is not covered by the muscles and, therefore, is more easily accessible. If it be divided by an incision, the heart continues to beat; but then each part of the heart containing one-half of the ganglionic trunk beats in a different, though regular, rhythm. It is even possible to cut the nervous trunk in two places, and then a separate rhythm of three portions of the heart may be perceived. On the contrary, if the heart itself be divided into
two, without cutting the nervous trunk, which is left like a bridge between the two parts, their beat remains synchronous (Alexandrowicz, 1931). The description of the nerves of the heart in Isopoda will be given in a subsequent publication.

Turning to the neurons of the local system in the heart of the Decapods, the problem to be solved is the function of the different projections of the cells. As for the long branches of the axons the preponderance of evidence indicates that the impulses are conveyed in them from the cells to the muscles. But what is the direction of the impulses in the short arborescent processes which arise both from the cell-body and from the axons? Are they transmitted from the cell to the periphery or in the opposite direction? As we have seen, these short processes also ramify in the muscles; would this not serve as an indication that they carry the impulses to the muscles, and, in consequence, that the cells of the local system possess several axons? We are, of course, accustomed to the schematic conception of nervous cells with one efferent fibre only, but there is no reason to assert that cells with several axons do not exist. Describing the innervation of the digestive organs in Cephalopods I suggested that the cells found there might have two or more efferent processes. Stöhr, in his recent work dealing with the histology of the involuntary nervous system, states that the distinguishing of the axon among the processes of the sympathetic ganglion cells has no sufficient base. Yet with regard to the neurons of the local system in the heart of the Crustacea we must take into consideration two facts: (1) the different aspect of endings of the short processes in the muscles when compared with the terminations of the long branches; and (2) the connexions of these arborescences with the efferent nerves. The first point, the peculiar histology of the terminations, suggests a different function from that of the motor endings of the long branches; the second, viz. the synapses with the efferent system, seems to indicate that the impulses in the short processes are carried from the periphery to the cells, i.e. for its axon.

I am aware that no direct evidence as to the course of the impulses can be brought forward, and, therefore, our conception
of these processes as dendrites is a hypothesis only, yet it seems to be more probable than any other.

Further, it may appear strange that the short arborescences springing from the axons are classified as dendrites like the processes originating from the cell-body. However, the presence of dendrites arising from the axon is known in Invertebrates and has been discussed recently in Hanström's work (1928). That in our case the proximal part of the axon is endowed with a particular function is suggested by the presence of the collaterals to the neuropile. In any case, as a peculiar feature of these neurons, we must take into consideration the presence of two kinds of dendrites, some arising from the cell-body, others from the axons, the latter at even a great distance from the cell.

Assuming then that the short arborescences are the dendrites which carry the impulses to the cells, we must search for the explanation of the function of their endings in the muscle-fibres themselves. We may imagine that the contraction of these fibres produces an excitation on the endings of the dendrites, and that resulting impulses are transmitted to the cell. Whatever kind of influence these impulses may exercise, whether they give rise to an excitation to be discharged in a following contraction of the muscles, or, on the contrary, have to inhibit some reaction in the cell during the diastolic period, at any rate, if our suggestion holds good, the impulses conveyed by the dendrites from the muscles would serve for the self-regulation of the rhythmical action of the neuromuscular apparatus of the heart.

The regulatory nerves (dorsal nerves) consist of fibres which, from the morphological point of view, were classified into two systems. The suggestion is obvious that one of these systems contains the inhibitory fibres whilst the other quickens the beat of the heart. However, to which of the two systems each of these regulating functions is to be ascribed I have but indirect indications. In the Stomatopoda I have found three separate pairs of nerves connecting the ganglionic trunk of the heart with the central nervous system. The most anterior pair carries inhibitory impulses, whereas the two posterior are
accelerator nerves. This fact is in accordance with the results of the investigations of Carlson, who had found the inhibitory nerves in Decapods originating in the infra-oesophageal ganglion in front of the roots of the accelerator fibres. Furthermore, in Stomatopoda the inhibitory fibres are of greater calibre than those of the accelerator fibres. All these data afforded us some basis for the suggestion that the thicker fibres in the dorsal nerves, i.e. what we have called the System I, have an inhibitory function. If that be the case, it would be directly shown that the inhibitory fibres are acting by synapses on the neurons of the local system. It may be recalled, further, that the terminal branches of these fibres are connected with each other by very numerous networks of fibrils. From this it may be concluded that this system acts as a whole—the impulses carried by the fibres being transmitted to a great number of terminal branches and from them transmitted to the neurons of the local system.

With regard to the system of the arterial valves and of the pericardium the following points may be of interest for physiology.

(1) The relations of the nerves of the valves to the nerves of the muscles of the pericardium.

(2) The absence of connexions between the system of the valves and the local system.

(3) The absence of connexion between the nerves of the anterior median valve on the one hand and the system of the nerves of the remaining five valves on the other.

I am not unaware that this statement, like similar assertions in general about the absence of nerve-fibres, has but relative value. Strictly speaking, it would be more correct to say everywhere that the connexions ‘could not be found’. In investigations of the nervous system the cases are not rare when a successful preparation reveals at once a striking abundance of nervous elements in places where, even using special methods, nothing had been seen of them before. However, it must be pointed out that, in the cases under discussion, the absence of the nerve-fibres has a very high degree of probability owing to the fact that numerous preparations with well-stained nerves have been carefully examined as to this point.

These remarks may excuse the writer from repeating these restrictions when similar questions are under consideration.
The junction into one system of the nerves of the valves and those of the pericardium seems to be easily conceivable at first sight, having regard to the fact that the function of the muscles both of the valves and of the pericardium is antagonistic to that of the heart. When the latter is in systole the valves guarding the arteries must be open, while in the diastolic period they are closed and their muscles contracted. One might think that the muscles of the pericardium contract equally at each diastole and so the blood from the pericardial cavity is pressed into the heart. But this is not the case as has been already observed by Plateau (1880). Mangold (1925) states that although the pericardium is endowed with contractile properties the rhythm of its contractions is much slower than that of the heart. Observing this phenomenon in Cancer pagurus this writer found that one of these, as he called them, 'fluctuations of the tonus of the pericardium' falls from 27 to 80 beats of the heart. Thus we see that the same system of segmental nerves supplies the muscles of the valves and of the pericardium, working at a totally different rhythm. On the other hand the muscles of the valves, and those of the heart which contract, although alternately, at the same rhythm, do not show any connexion of their nervous apparatus. It is not impossible that this connexion goes by the long route of the central nervous system, but I venture to suggest the following explanation. Suppose the muscles of the valves to be in a tonic contraction as well as the muscles of the pericardium, both under the influence of impulses carried by the common system of the segmental nerves. Suppose further that the tonic contraction of the muscles in the valves may be relaxed in systole in response to some stimulus acting on the valves and produced by the blood itself. It may be that it is the pressure of the blood forcing its way, or, perhaps, there are some substances liberated in systole the action of which can relax the apparatus closing the valves. In any case the rhythmic sequence of the action of the valves and of the heart might be co-ordinated in this way without direct nervous connexions of the respective muscular apparatus. Admitting this interpretation the independence of the fibres supplying the valve of the anterior median artery would be of no decisive significance for the relaxation of
its muscles and the synchronous working with the valves of other arteries.

SUMMARY

The results of our investigations may be summarized as follows:

(1) In the heart of the Decapod Crustacea three systems of nervous elements can be distinguished, viz. (a) a local system of neurons which are distributed in the heart itself; (b) a system of fibres connecting the heart with the central nervous system; and (c) a system of nerves which supply the valves of the arteries arising from the heart as well as the muscles of the pericardium.

(2) The local nervous system consists of a nervous trunk situated in the dorsal wall of the heart near to its inner surface from which branches to the muscle-fibres of the heart are distributed. The main trunk is generally called the ganglionic trunk from the presence of nerve-cells in it. The cells are of two kinds: large and small. Their number was found to be constant, and comprises in Cancer pagurus, Maia squinado, and Homarus vulgaris—the species which could be best investigated as to this point—nine elements, viz. five large and four small cells. It seems that in other species of marine Decapods the number of cells in the hearts, if not the same, does not at any rate vary much. Potamobius astacus, however, has not less than sixteen elements (eight large, and eight, maybe, nine or ten, small ones). The cells are multipolar in shape. Their long processes—the axons—after sending out shorter ramifications run in regular courses, giving off long branches to all the muscles of the heart including those of the ostia, but excluding the muscle-fibres of the arterial valves. The short processes, which I regard as dendrites, spring from the cell-bodies and from the proximal parts of the axons. The endings of the dendrites which ramify in the muscle-bundles differ in appearance from the terminations of the long branches springing from the axons. The small cells possess similar processes, i.e. dendrites and axons. The latter could not be traced well.
In the main or ganglionic trunk which in different species has different shapes, the following elements are present: (a) large and small cells, the arrangement of which varies in different species, but in all cases the small cells are situated in the posterior part of the trunk; (b) the axons of the large and small cells and a part of their branches; (c) the fibres of the dorsal nerves; (d) the neuropile-like networks of fibrils where the synapses between the efferent fibres and the neurons of the local system take place. These neuropiles form several more compact masses in Brachyura whilst in Macrura they are more diffusely scattered in the ganglionic trunk.

(3) The fibres connecting the heart with the central nervous system take their origin in the infra-oesophageal ganglion and travel in the nerves running on the thoracic muscles. As separate bundles, one on each side, they turn towards the dorsal surface of the heart; hence the term nervi cardiaci dorsales is proposed; the other term—regulator nerves—indicates their physiological character. In their further course these nerves pierce the heart-wall and reach the local nervous system. The fibres of the dorsal nerves are of various diameters. The thicker, which in the description have been called System I, run throughout the ganglionic trunk and break up therein in many richly arborizing branches which at many places resemble in appearance the neuropile-like networks of fibrils. They are the fields of conjunction of all the fibres of System I with each other, as well as with the neurons of the local system. From the latter the following parts are in close relation with the fibrils of System I: (a) the collaterals of the axons entering the neuropile; (b) the dendrites; (c) the cell-bodies surrounded by a network of fibrils of the dorsal nerves; these basketworks, however, could not be seen in all the species investigated, and occur on the large cells only. Some branches of System I were found leaving the ganglionic trunk, but their destination is uncertain.

The remaining fibres of the dorsal nerves which, it may be assumed, do not belong to the System I are of smaller but not equal diameter. Some take their course to the muscles without entering the ganglionic trunk, others travel in the latter, but their distribution could not be made out.
INNERVATION OF HEART OF CRUSTACEA

(4) The third system of nerves, which enter into relationship with the heart by innervating the valves situated at the origin of the main arterial trunks, contains the following elements:

(a) Nervi segmentales cordis, which number, as was found in Astacus, four on each side, branch from the thoracic nerves and pass on the ventral side of the pericardium towards the middle line. Here they join into—according to the species—one or two bundles, which take a longitudinal course. From these bundles branches are given off to the valves of five arteries, viz. arteriae antennales, arteriae hepaticae, and aorta posterior, and to the muscles of the ventral pericardial plate. The latter receive also branches springing directly from the segmental nerves. The system of the segmental nerves of the heart is connected with the nerves of the dorsal abdominal artery which in its turn receives segmental nerves originating in the abdominal ganglia and ending in the valves of the arteries arising from the vessel named.

(b) The nervus cardiacus anterior arises from the stomatogastric nerve and runs alongside the median anterior artery. The territory of the terminal branches of this nerve, known as 'nerf cardiaque' of Lemoine, has been found to be confined entirely to the valve of the median anterior vessel (aorta anterior s. arteria ophthalmica). No connexion with the nerves of other valves could be ascertained.

(5) Besides the three nervous systems enumerated which are in relation with the heart itself, several nerve branches running from the thoracic nerves penetrate the pericardial cavity. They break up here in the neuropile-like networks situated on the so-called ligaments of the heart and on the connective tissue covering the dorsal wall of the heart.

(6) The probable function of all these elements is thought to be as follows: The local system is an 'autonomic' nervous apparatus from which the muscles of the heart receive impulses necessary for their regular contractions. The fact that the dendrites of the cells end in the muscles suggests that the rhythmical discharges in the nerve-cells are under the influence
of the rhythmical action of the muscles. Thus, there may be secured a reciprocal regulation of the process in two parts of the neuromuscular apparatus of the heart.

The dorsal nerves convey to the heart the inhibitory and accelerator fibres. Some evidence seems to indicate that the thicker fibres which have been found giving synapses with the neurons of the local system are endowed with the inhibitory function.

The nerves of the arterial valves may be considered as carrying impulses which hold the muscle-fibres in contraction during the diastolic period of the heart.

The nerves in the pericardial cavity, ending in fine networks, have evidently some sensory function.

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EXPLANATION OF PLATES 13, 14, AND 15.

Plate 13.

Fig. 1.—Maia squinado. Large anterior cell. ax, axon.

Fig. 2.—Maia squinado. Part of larger neuropile. nd, fibre of the dorsal nerve; ax, axon of a large cell. In this preparation the axon deviates from the usual course and owing to this accidental position its collaterals to the neuropile are distinctly seen.

Fig. 3.—Cancer pagurus. Large cell with the pericellular network and accessory fibres (ac); ax, axon.

Fig. 4.—Cancer pagurus. Branching of two arborescences of a large cell in the same muscle bundle. ac, accessory fibres; ax, axon.

Fig. 5.—Maia squinado. Two small cells. ax, their axons; col, collaterals to the small neuropiles.

Fig. 6.—Maia squinado. Small cell. ax, axon; nd, two fibres of the dorsal nerves. These fibres give off collaterals to the neuropiles and branches which accompany the dendrites.

Fig. 7.—Palinurus vulgaris. Dorsal nerve entering the heart at the point indicated by the line a-a. The nerves are represented as if the heart-wall were totally transparent. S II, fibre of System II branching on
the inner surface of the heart; np, nerves on the exterior surface of the heart in the pericardial cavity, breaking up in a dense 'punctate substance'.

**Plate 14.**

**Microphotographs.**

**Fig. 8.**—*Maia squinado.* Anterior part of the ganglionic trunk. The three anterior cells are distinctly seen.

**Fig. 9.**—*Palinurus vulgaris.* Anterior part of the ganglionic trunk. The anterior cells and one situated farther back are distinguishable (gc).

**Fig. 10.**—*Munida rugosa.* Ganglionic trunk. gc, ganglion cells.

**Fig. 11.**—*Maia squinado.* Posterior part of the ganglionic trunk. Two large and four small cells are seen. The position of one of the large cells which lies forwards from the bifurcation of the trunk is not the typical one.

**Fig. 12.**—*Cancer pagurus.* Anterior bifurcation of the ganglionic trunk. gc, large cell with a thick dendrite running laterally; the ramifications of this dendrite which lie deeper in the muscles could not be represented; ax, ax, axons of the large lateral cells; nd, fibres of the dorsal nerves (cf. Text-fig. 18); a, thick fibre running forwards belonging to axon a, of the diagram, Text-fig. 8, but in the preparation represented in the microphotograph this fibre runs nearer to the median line than in the diagram.

**Fig. 13.**—*Cancer pagurus.* Posterior part of the ganglionic trunk. Four small cells deeply stained, with several projections. gc, large cell weakly stained, with several fibres surrounding the cell-body; nd, fibre of the dorsal nerve.

**Fig. 14.**—*Homarus vulgaris.* Short arborescence originating with two branches in the neighbourhood of the anterior bifurcation (bif) of the ganglionic trunk. gc, large cell insufficiently stained.

**Fig. 15.**—*Homarus vulgaris.* Dendrite of the large cell ramifying in several thick branches.

**Plate 15.**

**Microphotographs.**

**Fig. 16.**—*Palinurus vulgaris.* Branching of the axon (ax) of a large cell running down the ganglionic trunk; the respective cell is not included in this figure; nd, fibre of the dorsal nerve.

**Fig. 17.**—*Palinurus vulgaris.* Dendrites arising from the axon of small cells.

**Figs. 18, 19.**—*Cancer pagurus.* Parts of the circular trunks at the point of branching of the antero-lateral and lateral nerves; five axons of the circular trunk are distinctly seen (cf. Text-figs. 4 and 8). 

**Fig. 20.**—*Palinurus vulgaris.* Two large cells surrounded by thin fibres originating in the dorsal nerves. One of the cells, lying deeper, could not be sharply focused.
Fig. 21.—*Palinurus vulgaris*. Ramifications of two fibres of the dorsal nerves (*nd*) entering the ganglionic trunk. *d, b*, short branches arising from these fibres and running laterally from the ganglionic trunk; their formation of several thin fibres is well seen (especially in *d*).

Fig. 22.—*Palinurus vulgaris*. A fragment of the fasciculus longitudinalis pericardii (cf. Text-fig. 2).

Fig. 23.—Same preparation as fig. 22. Ramification of the nerves in the pericardial muscles (cf. Text-fig. 2).