

RECEPTOR ELEMENTS IN THE MUSCLES OF *LEANDER SERRATUS*

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(Plates I and II, and Text-figs. 1-4)

In continuation of the studies on receptor elements in the Crustacea the common prawn, *Leander serratus*, has been investigated by the methylene-blue method applied in the same way as described in an earlier publication (Alexandrowicz, 1951). It has been found that there are in *Leander* receptors of the same kind as in those crustaceans previously investigated, some of which exhibit features not yet observed before. As in other crustaceans they are similarly situated on the dorsal side of the body, but since a knowledge of the disposition of the dorsal muscles in the thorax and the abdomen is necessary for locating them, some data about the topography of the muscles are first given.

TOPOGRAPHY OF THE DORSAL MUSCLES

The disposition of the muscles as they come to view when exposed from the dorsal side by removal of the carapace and terga is shown in Text-fig. 1. On the left side a part only of the carapace has been removed, and the muscles are left *in situ*. On the right the muscle flanking the heart, which is the first head of the lateral thoracico-abdominal muscle, has been partly removed and the epimeral plate turned with its median surface uppermost. In this way the muscles inserting into this plate become exposed, and on such preparations the receptor elements of the thorax can be examined. It must, however, be borne in mind that in their normal position the muscles follow the curvature of the body and the epimeral plate lies in the dorso-ventral plane.

On pulling aside the posterior part of the first head of the lateral thoracico-abdominal muscle one can see its second head—a flat muscle spreading fanwise with its bundles inserting into the epidermal plate.

In the second large mass of muscles passing from the thorax to the dorsal side of the abdomen three units, called the 1st, 2nd and 3rd dorsal thoracico-abdominal muscles, can be distinguished. All three have their anterior attachments on the epimeral plate. The first dorsal thoracico-abdominal muscle inserts posteriorly into the anterior edge of the first abdominal segment. The second consists of two portions which run side by side anteriorly but separate posteriorly. One portion passes over into the abdomen and fuses end to end with the supplementary extensor muscle of the first abdominal segment; the

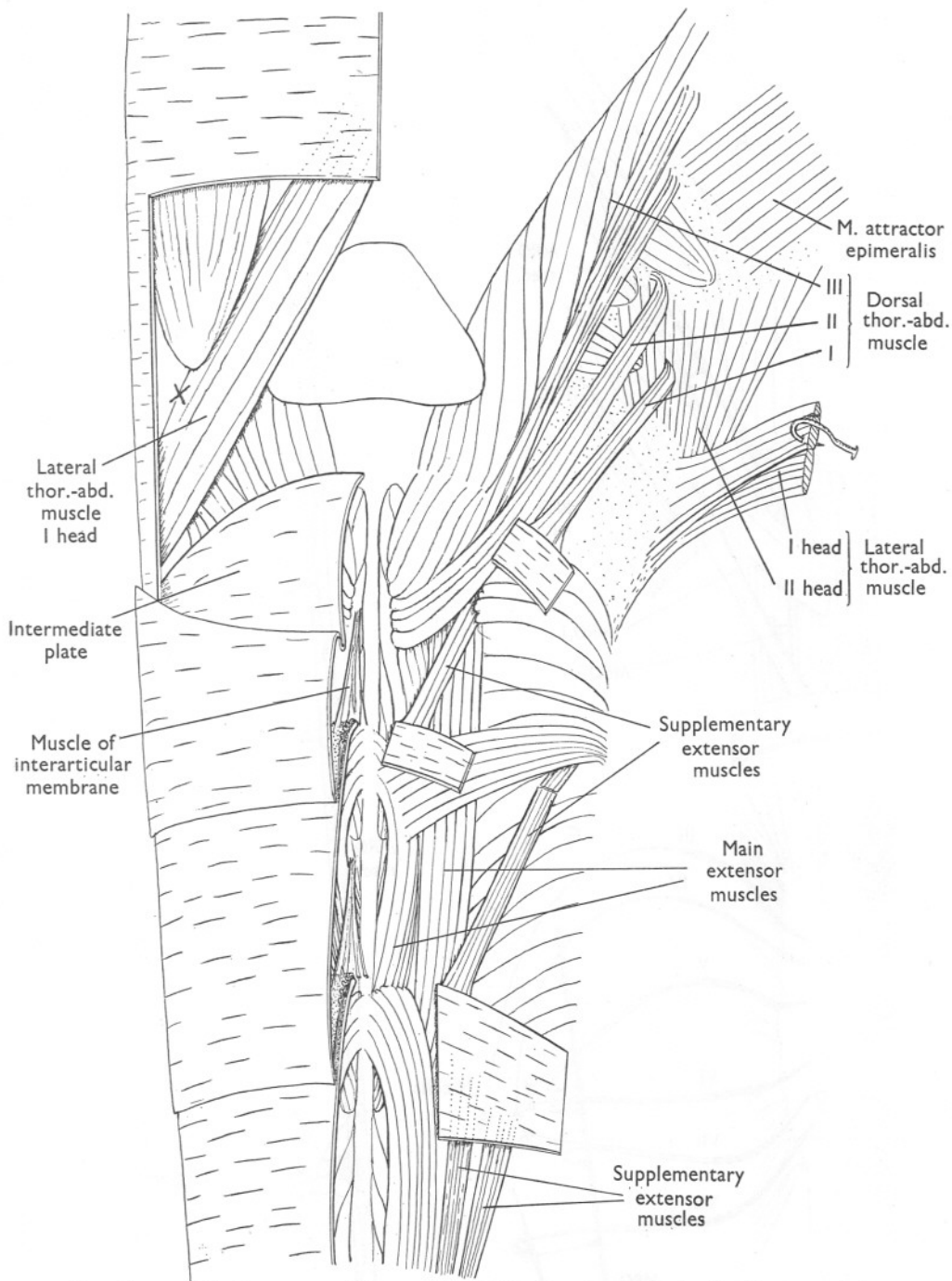
second portion passes under the intermediate plate and helps to form a bulky muscle filling up the concavity of this plate (Text-figs. 1, 2).¹ The 3rd dorsal thoracico-abdominal muscle, the stoutest of all, consists of three portions with separate attachments on the epimeral plate. They pass posteriorly under the intermediate plate, but a part of the stoutest portion is interrupted by a constriction at the anterior edge of this plate. The arrangement of the muscles situated under the intermediate plate is complicated, since it is here that the fibres of various parts of the thoracico-abdominal muscles and also of the extensor muscles of the abdomen meet. The anterior border of the latter is marked by a tendinous intersection which can be seen when the overlying fibres of the thoracic muscles are pulled aside (Text-fig. 2A).

The terms designating the muscles are the same as those used in the work on *Homarus* and *Palimurus* (Alexandrowicz, 1952*a*) and follow, with some minor additions, the nomenclature of Schmidt (1915). It should be emphasized that although there is similarity in the general plan of the musculature of the *Macrura* there are also differences, and it cannot be claimed that all the muscle units to which the same name has been applied correspond in fact to each other. Besides, the above description is a simplified one and many details in the drawings had to be omitted.

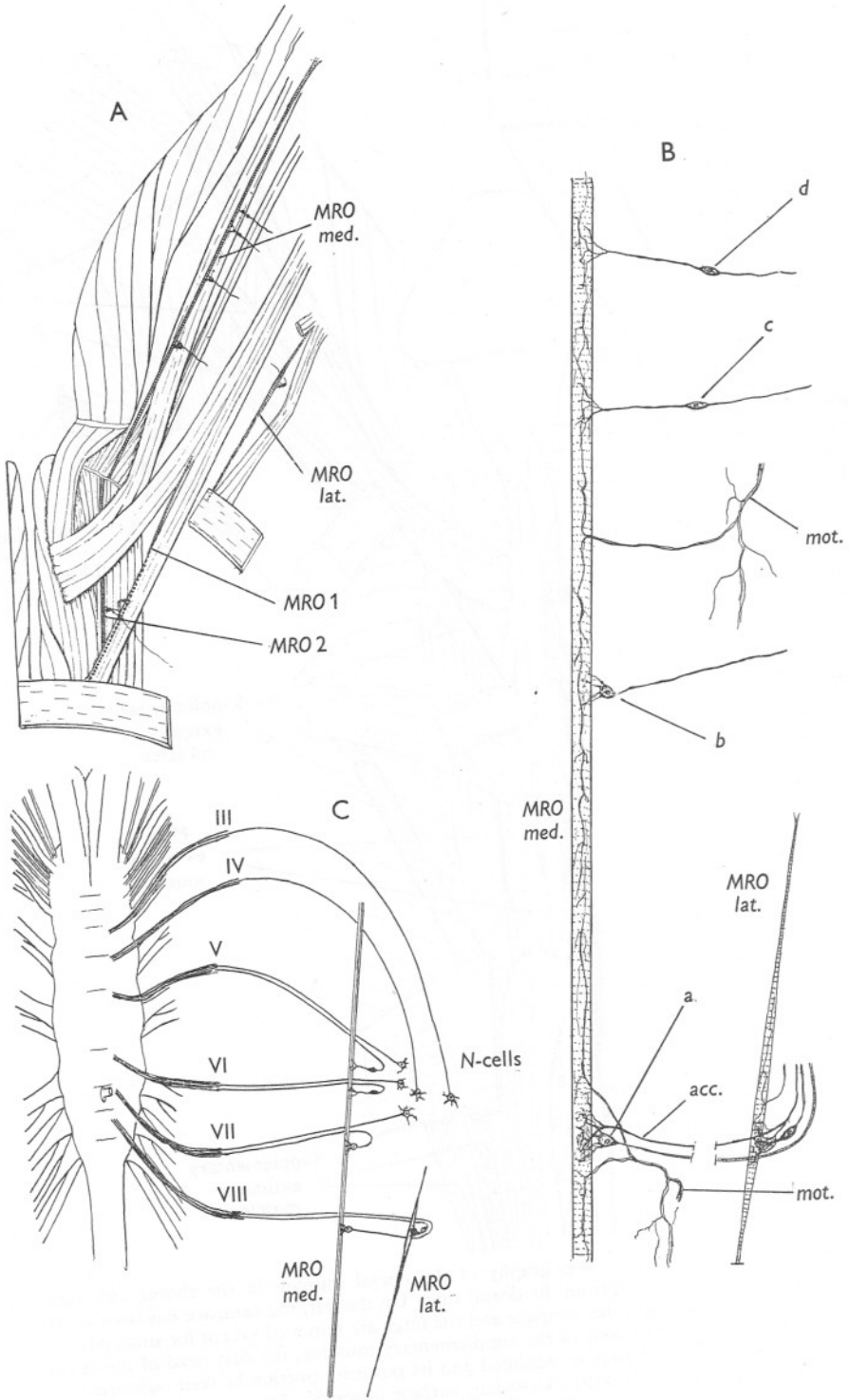
In the abdomen the muscles whose situation should be known when considering the receptor organs are the extensors. Two sets of these muscles which will be called the main and the supplementary extensors can be distinguished. The main extensors, which make up nearly all the mass of this musculature, have their bundles arranged in various ways. Those situated nearer the median line of the body are twisted around each other, while those in the lateral portion take a straighter course. The relations of the bundles of these portions, their courses and modes of attachment are very complicated and cannot be entered upon here.

The term 'supplementary extensors' is proposed for designation of superficially situated flat muscles with parallel or slightly diverging fibres which are never twisted. Posteriorly, in all five segments, they are attached to the anterior edge of the next segment, but they exhibit differences in their length and anterior insertions. In the first segment this muscle is ribbon-shaped and runs forwards and outwards to continue, as aforesaid, with the thoracico-abdominal muscle. In the second segment its shape and direction are the same, but it ends near the anterior border of the segment. In the following

¹ The text-books, even the most comprehensive, skip over this region, and although its chitinous covering, as in *Leander*, forms a conspicuous part of the skeleton it appears not to have a generally adopted name. The term 'intermediate plate' has been used by Calman (1904). Patwardhan (1937), in his monograph of *Palaemon*, calls it in the explanation of his fig. 1 'arthrodial membrane between the thorax and the first segment of the abdomen' and in the text says: 'The posterior half of the inter-tergal membrane connecting the cephalothorax with the tergum is calcified and rigid...' I am grateful to Dr Marie V. Lebour for pointing out to me these two sources of information.



Text-fig. 1. *Leander serratus*. Topography of the dorsal muscles in the thorax and three abdominal segments seen from the dorsal side. On the left, the carapace has been partly sectioned. On the right, the carapace and the terga are removed except for small parts of the latter with the insertions of the supplementary muscles; the first head of the lateral thoracico-abdominal muscle is sectioned and its posterior portion hooked outwards; the epimeral plate is turned with its median surface upwards. The cross on the left side marks the position of an N-cell.



Text-fig. 2.

segments the muscles become gradually shorter, wider, and divide into two or three portions with slightly diverging fibres. They insert into the tergum at a distance from its anterior border which is gradually greater in the subsequent segments (Text-fig. 3). It is to be noted that the histological structure of various units of the dorsal musculature is not the same, viz. the supplementary abdominal extensors and the 1st and 2nd thoracico-abdominal muscles have a more coarse cross-striation.

The term supplementary muscles, used here for facilitating the description, can be misleading as it may imply a subordinate role. It is true that these muscles are weak, but considering their different structure there is a ground for assuming that they must have a special function. Moreover, as similar differences have been observed in other crustaceans (*Macrura*, *Stomatopoda*, *Amphipoda*), it can be inferred that these animals have two systems of the extensor muscles presumably one for slow and the other for fast contractions. It is also for this reason that a special term seems to be appropriate.

RECEPTOR ELEMENTS

Two categories of receptors in the muscles of *Leander* can be distinguished.

(1) Muscle receptor organs (*MRO*) consisting of nerve cells connected with special receptor muscles (*RM*). As in other crustaceans previously investigated—(*Homarus vulgaris*, *Palinurus vulgaris*, *Pagurus striatus*, *P. calidus*, *Squilla mantis* (Alexandrowicz, 1951, 1952*a, b*, 1954), *Cambarus clarkii* (Wiersma, Furshpan & Florey 1953), they are of two sorts (*MRO*₁, *MRO*₂).

(2) Receptor cells, called *N*-cells, which end in ordinary muscles and have been found, as in *Homarus* and *Palinurus*, in certain thoracic muscles.

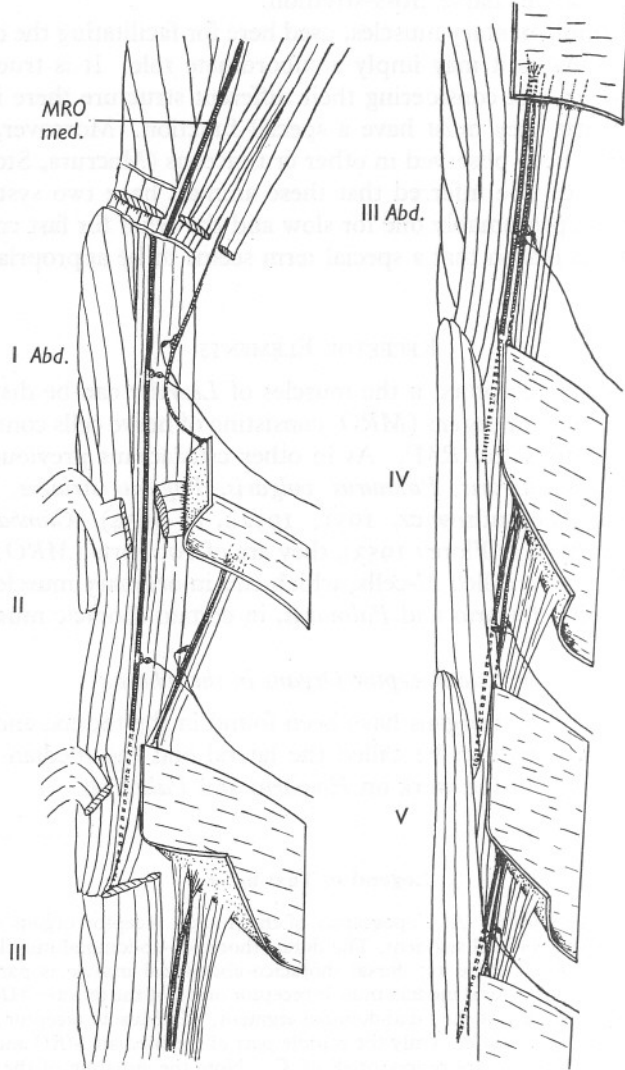
Muscle Receptor Organs in the Thorax

Two muscle receptor organs have been found in the thorax, and according to their situation they can be called the lateral and the median *MRO*, the same terms as used in the work on *Homarus* and *Palinurus*.

Legend to Text-fig. 2

Text-fig. 2. *Leander serratus*. A, Topography of the muscle receptor organs in the thorax and in the first abdominal segment. The dorsal thoracico-abdominal muscles are spread apart (cf. Text-fig. 1); the 1st dorsal thoracico-abdominal muscle is partly removed. *MRO lat.*, *med.*, lateral and median muscle receptor organ of the thorax; *MRO*₁, *MRO*₂, muscle receptor organs of the 1st abdominal segment. B, Muscle receptor organs of the thorax (semi-diagrammatic). Only the middle part of the median *MRO* and the anterior part of the lateral *MRO* are represented (cf. C). Note the situation of the nerve cells *a* and *b* close to the muscle and of the cells *c* and *d* at a distance from it. *mot.*, motor fibres; *acc.*, accessory nerve. C, Diagram showing the connexions of the thoracic receptor cells with the suboesophageal ganglion. III–VIII, nerve trunks of the 3rd–8th segment carrying axons of the receptor cells of the *MRO* and of the *N*-cells.

The lateral *MRO* lies between the bundles of the 1st dorsal thoraco-abdominal muscle (Text-fig. 2A). Its muscle component has in its middle part the shape of a spindle with its thickest part (c. 35μ) lying nearer to the anterior end. This spindle thins out in both directions to a fine thread, only c. 10μ thick. Both its attachments take place near to those of the 1st dorsal



Text-fig. 3. *Leander serratus*. Topography of the muscle receptor organs in five (I-V) abdominal segments. Note the varying length and shape of the supplementary extensor muscles (removed in the first segment), the gradual shortening of the receptor muscles in the 3rd-5th segment, and the fusion of the muscles of the *MRO* 2 in the 1st and 2nd segments. Parts of receptor muscles covered by muscle fibres are drawn in dotted lines.

thoraco-abdominal muscle, but the receptor muscle, although it is so thin and runs between the other muscle fibres, can be traced as an individual unit.

The nerve cell of this *MRO* is bipolar with dendritic processes starting with a common root (Pl. I, fig. 2). They expand in the thicker part of the muscle in dense arborizations (not seen in the photograph). The axon joins the nerve trunk belonging to the 8th thoracic segment. The situation of this receptor is very unfavourable, both for staining and observation. To see its muscle it is necessary to pull aside the muscle fibres covering it; the nerve cell is hidden from view by the nerve fibres curving round the thoraco-abdominal muscle. Moreover, the same nerve trunk conveys some deviating fibres of the pericardial organs which at this point break up in fine branches arranged as small glomeruli. To see the cell as shown in the photograph all these elements have to be removed, but the operation is very delicate.

It is difficult to get a clear picture of the nerves supplying this receptor. There is certainly a motor fibre for the muscle and there are also fibres of the accessory innervation intermingling with the arborizations of the cell-dendrites, but whether they derive from one or two accessory nerves I am unable to say.

The median thoracic *MRO* can be found much more easily. In preparations with the median side of the epimeral plate exposed as in Text-fig. 1 it can be seen on the surface of the middle portion of the 3rd dorsal thoraco-abdominal muscle (Text-fig. 2A). Anteriorly it ends near the insertions of the adjacent muscle; running backwards it passes deeper under the bundles of the 3rd dorsal thoraco-abdominal muscle, and its posterior insertion into the connective tissue septum between the thoracic and abdominal extensors can be seen only after the superficial layer of the muscles in the region of the intermediate plate is pulled aside. The muscle of the median *MRO* is much thicker than that of the lateral one, measuring 50–60 μ in diameter. Nearing the anterior end it becomes thinner. There are a good many connective tissue fibres running longitudinally on the periphery of the muscle and between the bundles of the myofibrils. Towards the anterior end the connective fibres gradually predominate over the muscle elements.

Nerve Cells

Four nerve cells are connected with the median receptor muscle. Their positions as shown in Text-fig. 2B and C are the most frequent, but variations in the situation of the three anterior cells are common. In one preparation all three have been found lying close together (Pl. I, fig. 4).

There are certain differences in the appearance of the cells. The posterior one (Text-fig. 2Ba; Pl. I, fig. 1) is multipolar; it is situated close to the receptor muscle, sending into it dendrites spreading over an area the length of which is equal to approximately three diameters of the cell. The tuft of arborizations is well delimited on both sides. In this region the myofibrils of the muscle, at least most of them, are replaced by connective tissue fibres.

The next cell *b* is usually multipolar and very similar to cell *a*, but often shows variations in its shape; sometimes with all the dendrites arising with a common root it looks like the anterior cells *c* and *d*. The latter are bipolar with distal processes which are of such a length that the cells as a rule lie much farther from the muscle than the cells *a* and *b* (Pl. I, fig. 3). Here again variations are not uncommon, and one or the other cell can have a multipolar shape and lie close on the muscle.

The dendrites of the cell *b* show the pattern of arborizations similar to those of the cell *a*, but are often more irregularly delimited. The dendrites of the two anterior cells are less densely arranged, but can be much longer than in cell *a*. The expansions of the three cells presumably end on the connective fibres, but the picture is not clear as the myofibril bundles pass through these areas.

The variable appearance of the terminations of the three anterior cells may be partly due to the unevenness of the staining, but evidently also because they are affected by frequent irregularities. As we see later this feature can help us in understanding the nature of these elements.

The axons of the four cells are directed at first outwards and, after joining the nerve trunks running on the median side of the epimeral plate, turn ventrally to proceed towards the suboesophageal ganglion: the axon of the posterior cell on curving round the thoracico-abdominal muscle is joined by the axon of the lateral *MRO*, and both travel in the nerve trunk of the 8th thoracic segment. The three other axons belong most probably to the 5th-7th segments, as shown in Text-fig. 2C. Some uncertainties arise when tracing these axons on account of the anastomoses occurring between the nerve trunks of various segments in which they travel. Moreover, the axons of the cells *b* and *c* or *c* and *d* are sometimes to be seen running side by side; it can be assumed that such associations are accidental and that these fibres in their farther course part company.

The nerves carrying the axons of the receptor organs belong to the set of nerve trunks originating in the suboesophageal ganglion on its dorsal side. They include the motor nerves of the thoracic muscles, the various nerves of the heart, of the pericardial organs and also the axons of the *N*-cells (see below).

Nerves

The motor fibres for the median receptor muscle branch from the nerves of the adjacent muscles. One fibre approaches the receptor muscle near the posterior cell and another in front of it in the region between the two middle cells (Text-fig. 2B). Each of them gives off branches running in the muscle in both directions.

Only the posterior cell has an accessory innervation limited to one fibre, which can be qualified as the thick accessory nerve (Pl. I, fig. 1). The thin accessory nerve seems to be missing.

Muscle Receptor Organs of the Abdomen

In the abdomen, muscle receptor organs have been found in the 1st to 5th segments. In the 6th they are most probably missing, but as the particular arrangement of the muscles in this segment makes the dissection difficult there is no absolute certainty as to this point. In the first two segments the two receptor units of one side (*MRO*₁ and *MRO*₂) are separated from each other, whereas in the 3rd-5th segments they lie close together.

The muscle receptor of the *MRO*₁ of the first segment (*RM*₁) has its forward insertion in the region of the intermediate plate between the bundles of the 2nd dorsal thoracico-abdominal muscle (Text-fig. 2A). From this point it runs obliquely backwards and inwards close to the supplementary extensor passing on its ventral side near its inner edge. Its posterior attachment is on the anterior border of the tergum of the 2nd segment. This *RM*₁, like the lateral thoracic *RM*, has a spindle-shaped middle part continuing in both directions with thin threads. The diameter of this thin part at the mid-point between its anterior attachment and the nerve cell was found to be 8 μ .

The muscle of the second more medially situated receptor *RM*₂ inserts anteriorly quite near the posterior end of the median thoracic *MRO* into the septum separating the thoracic and abdominal extensors (Text-fig. 3). In its backwards course, which is almost parallel to the median line of the body, it lies on the lateral portion of the main extensor muscle. At the border between the 1st segment and the 2nd segment it fuses end to end with the *RM*₂ of the 2nd segment, so that actually there is one receptor muscle running through the first two segments and passing into the anterior part of the third segment where it ends among the bundles of the main extensor muscle. Its total length in middle-sized specimens is about 2 cm, and the diameter which does not change much at various levels is about 50 μ . The position of this *RM* is superficial in these regions, where the muscle bundles on which it is lying are not covered by other muscles. In order to see it in its whole length these overlying muscles must be removed (Text-fig. 3). It is somewhat difficult to isolate the receptor muscle in the region between the two segments, and it is possible that the connective tissue fibres accompanying the *RM*₂ have here some points of attachment, but the continuity of the muscle can be ascertained.

The *RM*₁ of the second segment resembles that of the first segment in its dimensions and direction of its course. It lies on the supplementary muscle near its median margin, and its insertions are near to those of this muscle (Text-fig. 3).

In the 3rd-5th segments the two *MRO* units are situated near to each other, and the anterior attachments of both *RM* are at the same level (Pl. II, fig. 7). Posteriorly each *RM*₁ inserts into the anterior edge of the tergum of the following segment, whereas the *RM*₂ runs farther backwards and passing

deeper into the layer of the main extensor muscle ends between the bundles of the latter. The length of both *RM* decreases from the 3rd to 5th segment and so does the calibre of the *RM*₂. The *RM*₁ retains about the same thickness in its middle part and does not taper so much as in the first segments. Already in the 3rd segment the differences between the two *RM* are not so great as in the first two segments, and in the 5th segment the two muscles are almost of the same calibre. In the diagrammatic drawings (Text-fig. 3) the diameters of the *RM* are out of scale. Their true proportions can best be understood from the photographs (Pl. II, figs. 7, 8) made from the same preparation of the *MRO* of the 3rd segment. The represented parts of the muscles added together include only about half of their total length.

In all segments the receptor muscles are accompanied by connective tissue fibres running longitudinally; even in the thinnest parts of the *RM*₁ the elements of both the muscle and connective tissue are present. Connective tissue also replaces all or almost all the myofibrils of *RM*₂ in the area of expansion of the cell dendrites. In *RM*₁ a good deal of myofibrils can be seen passing over this area. Some difference in cross-striation of the muscles as recorded previously in the large *Macrura* and *Stomatopoda* can be observed, viz. the *RM*₁ has a coarser and *RM*₂ a finer cross-striation.

Nerve cells

The nerve cells in the abdominal *MRO* are situated laterally to the muscles, with exception of the cells of the *MRO*₁ in the 1st and 2nd segments, in which they lie either directly above the muscles or medially to them. The particular features of the cells of one pair of *MRO* can be better seen in the posterior segments where both receptors lie close to each other. Here they exhibit great resemblance to the pictures observed in *Homarus* (Pl. I, fig. 5). Cell 1 (of the *MRO*₁), which is always situated in front of cell 2, has wider extending processes than the latter in which these processes and all their ramifications are closer to each other. Consequently, the areas of the respective muscles in which the arborizations of the cells are interlaced with the end-branches of the accessory nerves differ markedly in size and shape (Pl. I, fig. 6).

In Pl. I, fig. 5, representing the receptors of the 5th segment, cell 1 is larger of the two. In the 1st-4th segments the cells are about the same size.

The cells are surrounded by membranaceous connective tissue. There is possibly a cavity separating the cells from this capsule as in large *Macrura* and *Stomatopoda*, but it is not distinct enough. Fine nerve fibrils wind round cell 2 forming a so-called basket-work. Similar fine fibres, but not so numerous, can sometimes be noticed on the periphery of cell 1.

Nerves

The pattern of the motor innervation is the usual one, i.e. some of the motor fibres run down alongside the axons of the cells and others branching from the motor nerves of the adjacent muscles reach the *RM* at points lying farther from the cells.

There are many other fibres approaching the cells and entering into relations with their dendrites (Pl. I, fig. 6; Pl. II, fig. 9). Most of them can be traced to their origin from one fibre of stouter calibre—the thick accessory nerve which is conveyed by the same trunk running on the surface of the dorsal muscles into which pass the axons of the receptor cells. In this trunk run also finer fibres which can be regarded as thin accessory nerves.

The thick accessory nerve gives off branches entering into relations with the dendrites of both receptor cells; whether it also supplies both receptor muscles or only the *RM I* is not clear. As to the thin accessory nerve it can be assumed that its branches reach the terminations of both cells, but their distribution is not clear. In general, the methylene-blue preparations with *Leander* tissues give less distinct pictures than with the large *Macrura*. It is therefore not to be expected that such points as appeared dubious in the larger species could be elucidated with this less suitable material.

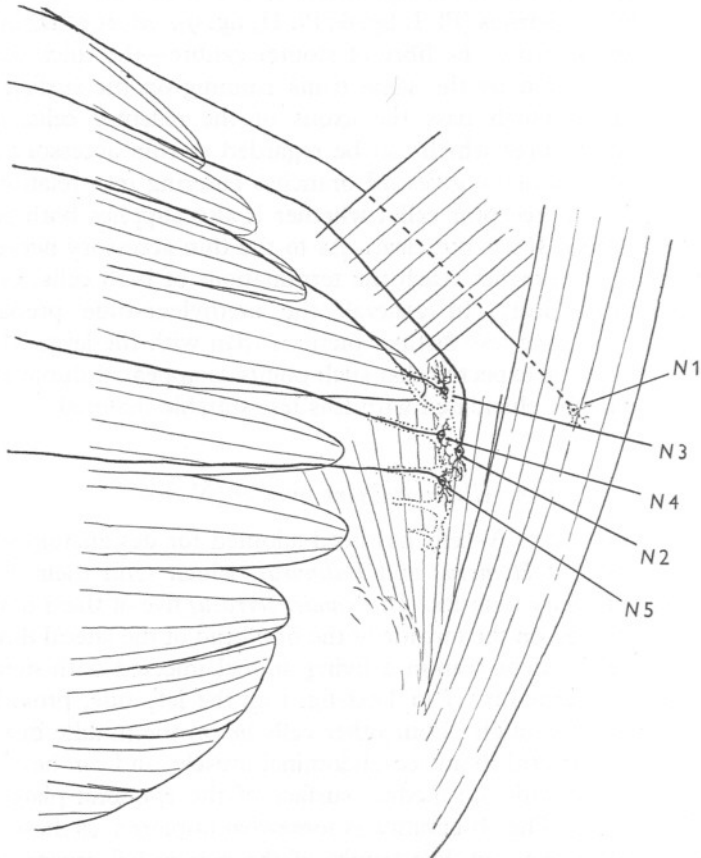
Receptor cells in ordinary muscles (N-cells)

The conventional term *N-cells* has been adopted for designation of nerve cells first described in *Homarus* and *Palinurus*, which send their dendritic expansions into ordinary muscles. In *Leander serratus* five of them have been found. One is situated on the outside of the first head of the lateral thoracico-abdominal muscle; it can be seen in a living animal injected with methylene blue at the point indicated by *X* in Text-fig. 1 on the left side, provided the cuticle is transparent enough. Four other cells lie on the middle bundles of the 2nd head of the lateral thoracico-abdominal muscle, and can be observed only on preparations with the median surface of the epimeral plate turned upwards (Text-fig. 4). The observation is somewhat impaired, as these *N-cells* are situated between the arch-like trunks of the pericardial organs and the muscles and therefore are covered by the former. As there is no connexion between the pericardial organs and the nerve cells it is possible to remove the overlying parts of them without injuring the cells and their processes.

The *N-cells* are about the same size as the nerve cells of the *MRO* or even larger than some of them. They are therefore comparatively larger than in *Homarus* and *Palinurus*, in which their size is always smaller than in *MRO*. The dendrites arising from different points of the cell body penetrate between the bundles of the muscles over a larger area than in the *MRO*. The muscles in these regions do not show any particular changes. The photographs

(Pl. II, figs. 10, 11) give an idea of the general appearance and various forms of the *N*-cells, but cannot show the processes running deeper into the muscles which are out of focus.

Whether the endings of these processes are on the muscle tissue or on connective fibres is difficult to discern, especially as the muscles in crustaceans are not composed of such units as the muscle fibre of vertebrate histology,



Text-fig. 4. *Leander serratus*. Topography of the *N*-cells on the lateral thoraco-abdominal muscle viewed from the inside (cf. Text-fig. 1). Cell *N*1 situated on the outside of the first head of the muscle is seen by transparency. The proximal course of the axons of the *N*-cells is shown in Text-fig. 2C.

but consist of bundles of myofibrils anastomosing with one another. Accordingly the connective tissue separating the muscle mass into fasciculi and enveloping the myofibril bundles does not form such regular tubular sheaths as the endomysium of the vertebrate muscle.

In the description of *N*-cells in *Homarus* more probability has been given to the assumption that their processes end on connective fibres. A corroboration

tive evidence is now afforded by the fact that the dendrites of the most anterior cell *N*₃ (Text-fig. 4) can be seen branching on a strip of tissue continuing with the muscle but in which no myofibrils can be noticed.

The axons of the *N*-cells in their course towards the suboesophageal ganglion join each a nervous trunk of a different segment (Text-fig. 2c). The axon of the cell *N*₁ situated on the outer side of the lateral thoracico-abdominal muscle enters a branch of the nerve of the 3rd segment, passing on the lateral side of the m. attractor epimeralis. The axons of the four remaining cells run in the trunks of the 4th-7th segments. The cell *N*₂ belonging to the 4th segment is situated behind the cell *N*₃ of the 5th segment. Its axon crossing m. attractor epimeralis on its inner surface near to its ventral attachment can be easily found in every preparation, as it stains readily even while its cell is pale or invisible.

The axons of the cells *N*₃₋₅ run in the trunks of the 5th-7th segments, which are surrounded by the neuropiles of the pericardial organs. As stated in the paper describing these structures (Alexandrowicz, 1953) no relation between the *N*-cells and the pericardial organs has been found.

DISCUSSION

It will be noted from the above description that the structure and arrangement of receptor elements in the muscles of *Leander*, although similar to that of the large *Macrura*, have certain peculiar features. One of them is the extraordinary thinness to which one receptor muscle, the *RM*₁, can be reduced. In the 1st abdominal segment the ratio of its diameter in the anterior part (8μ) to the total length of the muscle would be approximately 1:1000. It is, further, interesting that although both receptor muscles vary in their dimensions in different segments these variations are by far greater in *RM*₁. Hence it may be concluded that this muscle needs finer adjustments to the mechanism of movements in each of the segments, presumably conditioned by the differences in the arrangement of their extensor muscles.

The receptors of the second set, the *MRO*₂, show two unusual features: the fusion of the muscles of the 1st and 2nd abdominal segments and the occurrence of four cells connecting with one muscle in the thorax. The fusion of the receptor muscles has not been observed, either in the Decapoda or in the Stomatopoda. In some other crustaceans, however, on which some investigations are being made, a fusion of the muscles has been found. Thus in the thorax of *Ligia oceanica* (Isopoda) one receptor muscle runs through two segments, but the nerve cells are in one of them only; in *Praunus flexuosus* (Mysidacea) the muscles of both *MRO* pass through three thoracic segments, and in each of them two nerve cells are present. The functional meaning of such fusions of the muscles is difficult to conceive.

The median receptor organ in the thorax, which obviously belongs to the

same set as *MRO* 2 in the abdomen, appears as an anomaly not only because four cells connect with one muscle, but also because one of them has the accessory innervation which the others have not. However, anomalies in the anatomy of the *MRO* in the thorax can be easily explained as resulting from the retrogression of these organs in the segments which have become fused and have lost their motility in the course of the phylogenetic evolution of the Crustacea. As pointed out previously (Alexandrowicz, 1954, p. 105), during this process some *MRO* can disappear and in others certain components can be missing. According to this conception only the last thoracic segment has in *Leander* retained both muscle receptor organs, but in all probability they possess only one of the two accessory nerves. The three anterior cells of the median *MRO* can be regarded as the remnants of receptor organs of the 5th-7th thoracic segments, probably their *MRO* 2. They send their dendrites into the common muscle, that is perhaps made up of fused muscles of several segments, but have lost all their accessory innervation. The irregularities in the shape and position of these cells corroborate the assumption of their being elements of retrograding organs.

The receptor elements of the second category, the *N*-cells, have been found in *Leander* in the same number, five, as in *Homarus* and *Palinurus*. This does not necessarily mean that they are all exactly the same set of homologous elements, because there is no certainty that in each of these animals all *N*-cells have been found. Besides, the arrangement of the cells and the muscles is different, and the homology of the latter has yet to be established.

Examination of the *N*-cells in *Leander* has not helped towards understanding their function. Some features, such as the concentration of four cells on one small strip of muscle, make their role even more enigmatic. In a previous paper (Alexandrowicz, 1952*a*), when surveying the different types of receptor elements, it has been suggested that the *N*-cells might represent a more primitive type from which those with special muscles have developed. However, it is equally conceivable that, when highly specialized muscle receptors are becoming redundant, the reversed process may occur in the course of which their own muscles disappear and the nerve cells enter into relation with the ordinary muscles. In that case the *N*-cells might be the remnants of the retrograding receptor organs, presumably the *MRO* 1. The connexions of their axons with the 3rd-7th thoracic segments would fit into this picture. On the other hand, however, there is nothing in their appearance which would indicate that they are decadent elements. The cells are comparatively large, shapely, and their processes are well developed. In trying to solve the problem of the *N*-cells it would be of much help to know whether they are only in the thorax or whether they occur in other parts of the body also. The present investigation, in which thoracic and abdominal muscles of *c.* 150 specimens were examined, makes the first alternative more probable, but the possibility that some nerve cells have not been detected is still to be reckoned with.

SUMMARY

In *Leander serratus* muscle receptor organs have been found in the thorax and in the 1st–5th segments of the abdomen. In the abdomen they are represented, as in other crustaceans, by two units on each side consisting of a thin muscle connected with nerve cell and supplied by motor and accessory nerves. The two muscles (*RM1* and *RM2*) of each pair of receptor organs keep separated in the first two abdominal segments, whereas in the 3rd–5th they run close together. The muscles *RM2* of the 1st and 2nd segments are fused end to end, forming one muscle unit running through the segments and connected in each of them with the receptor cell.

In the thorax two muscle receptor organs, a lateral and a median, are present. The former has the usual components, i.e. one muscle and one nerve cell; the median consists of one muscle and four nerve cells. The axons of the posterior cell of the median receptor and that of the lateral receptor run towards the suboesophageal ganglion in a nerve trunk of the 8th thoracic segment; those of the three anterior cells join the trunks of the 5th–7th segments. It is suggested that these three cells are the remnants of muscle receptor organs which have been reduced following the fusion of the thoracic segments and loss of their motility.

The receptor elements of the second category, the *N*-cells, with the dendrites ending in ordinary muscles, have been found, five in number, in connexion with the lateral thoracico-abdominal muscle. Their axons run into the suboesophageal ganglion with the nerve trunks of the 3rd–7th thoracic segments.

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EXPLANATION OF PLATES I AND II

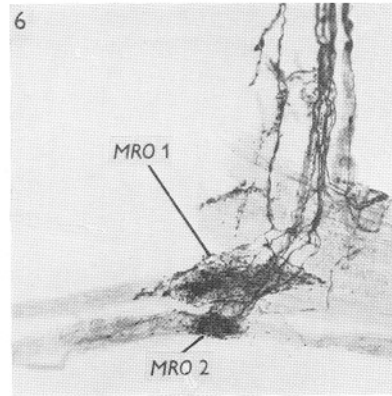
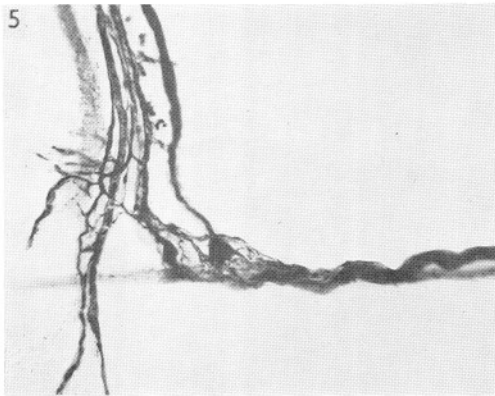
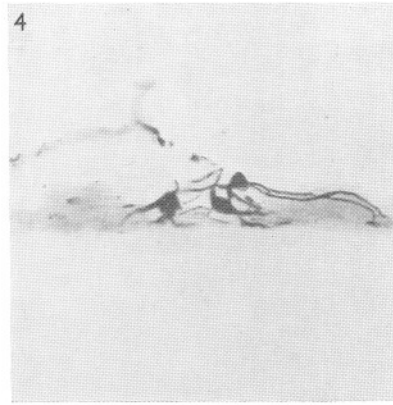
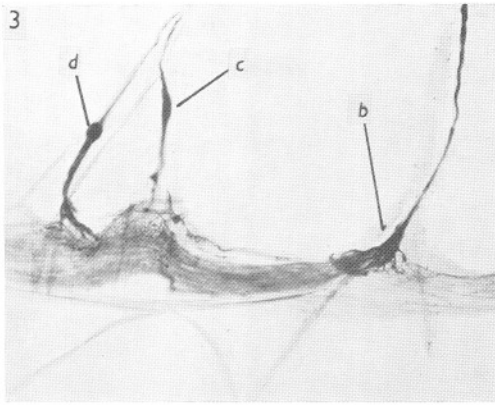
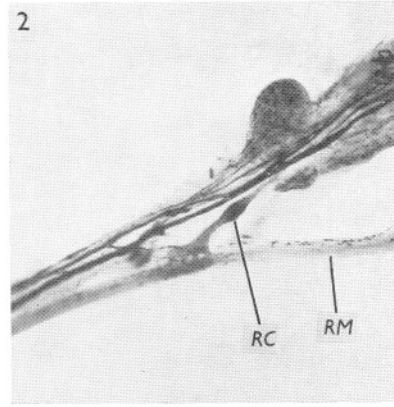
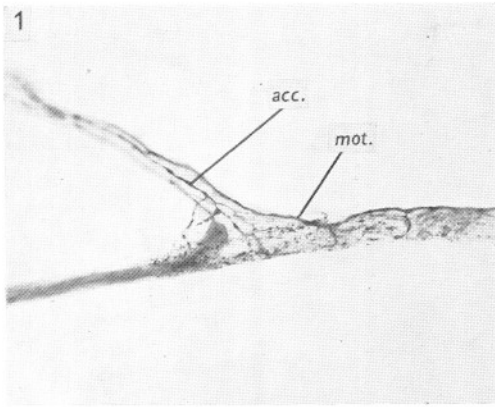
All photomicrographs were made from preparations of *Leander serratus* stained with methylene blue, fixed in ammonium molybdate and mounted in xylol-dammar.

PLATE I. The scale at the bottom applies to all figures.

- Fig. 1. Part of the median thoracic muscle receptor organ with its posterior nerve cell. *mot*, motor fibre; *acc*, accessory nerve.
- Fig. 2. Middle part of the lateral thoracic receptor organ. *RC*, receptor cell, *RM*, receptor muscle. The outlines of the dendritic arborizations are blurred by a diffuse staining.
- Fig. 3. Three anterior cells (*b*, *c*, *d*, cf. Text-fig. 2B) of the right median thoracic *MRO*.
- Fig. 4. Three anterior nerve cells of the median thoracic *MRO* bunched together and showing irregularly arranged processes.
- Fig. 5. Muscle receptor organs of the 5th abdominal segment (left side). The nerve cell of the *MRO* I is larger and is situated anteriorly.
- Fig. 6. Muscle receptor organs of the 5th abdominal segment (right side). Note the differences in size and shape of the networks formed by the cell dendrites and the accessory nerves. The nerve cells are faintly stained and are invisible in the photograph.

PLATE II. The scale at the bottom applies to figs. 9-11.

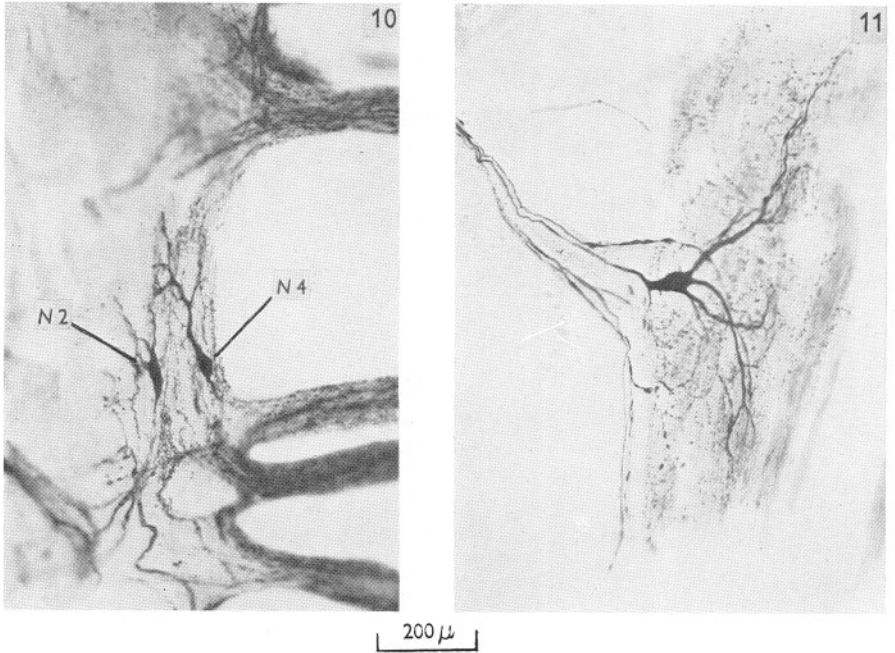
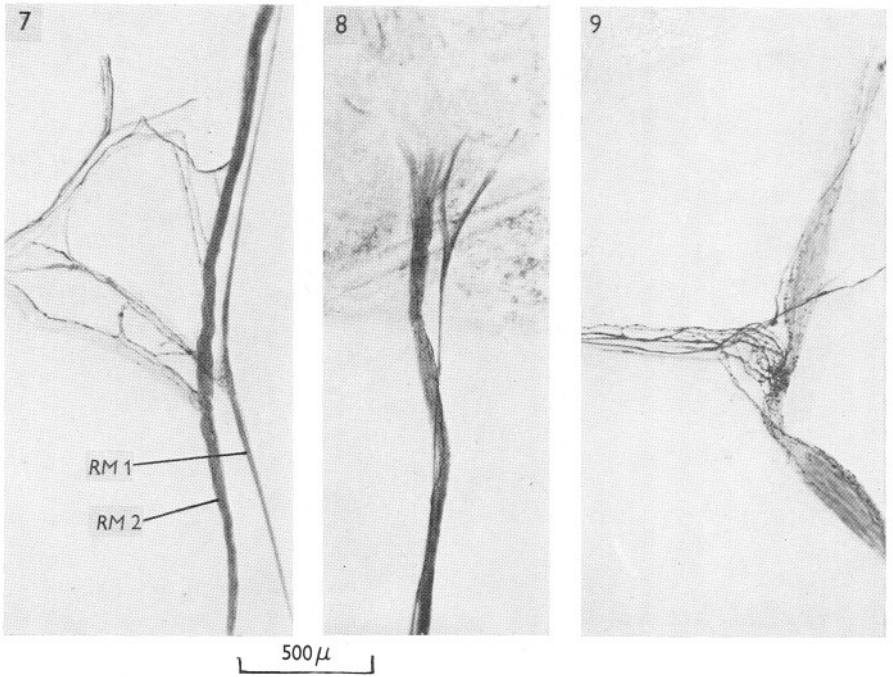
- Fig. 7. Middle quarter of the *MRO* of the 3rd abdominal segment of the left side. The receptor muscles became displaced during the mounting of the preparation: in the animal body the *RM* I lies dorsal and to the side of the *RM* 2; it passes on its median side in the anterior quarter as seen in fig. 8.
- Fig. 8. Same preparation as in fig. 7. Anterior quarter of the *MRO* of the 3rd segment with the attachment of the receptor muscles.
- Fig. 9. Motor and accessory nerves of the *MRO* of the 3rd segment. The kink in the muscle and its thickenings are artifacts.
- Fig. 10. Two *N*-cells (*N* 2 and *N* 4, Text-fig. 4). The overlying arch-like parts of the pericardial organs are almost completely removed.
- Fig. 11. *N*-cell situated on the outside of the first head of the lateral thoraco-abdominal muscle (*N* 1, Text-fig. 4).



200 μ

Figs. 1-6.

(Facing p. 144)



Figs. 7-II.