THE FINE STRUCTURE OF CRUSTACEAN PROPRIOCEPTORS. II. THE THORACICO-COXAL ORGANS IN *CARCINUS*, *PAGURUS* AND *ASTACUS*

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(*Communicated by M. Abercrombie, F.R.S.—Received* 26 *June* 1964)

[Plates 35 to 40]

ERRATA: In Part I of this work, *Phil. Trans. B*, 1962, **245**, on p. 293, lines 26–27, 'integumental scolopophores' should read 'subintegumental scolopophores'. On p. 315 the letters '*CP*' were missing from the end of the first line.

CONTENTS

There is a complex of proprioceptor organs spanning the thoracico-coxal joints of the walking legs of decapod crustacea. The muscular receptor is a specialized portion of the promotor muscle of the leg, associated with sensory fibres which are the dendrites of neuron-like sensory cells. Similar sensory fibres enter strands of connective tissue which are attached distally with the levator and depressor muscles of the basipodite (innervated elastic strands). In macrurans, but not in crabs, there is in addition a thoracico-coxal chordotonal organ. The fine structure of these proprioceptors is described, in *Carcinus*, *Pagurus* and *Astacus*.

In *Carcinus* and in *Pagurus* the dendrites of all the sensory fibres are associated with specialized strings of connective tissue, within larger connective tissue strands. Fine processes of the dendrites (dendrite fingers) penetrate these connective tissue strings (vacuolated strings) and run up and down them for a certain distance, within the extracellular connective tissue substance, which is amorphous connective tissue containing bundles of collagen fibres. Elsewhere the dendrites are surrounded by sheath cells. The connective tissue of the strands consists mostly of collagen, except proximally in the muscular receptor, where amorphous connective tissue is more plentiful. Blood channels penetrate the strands in places. Appearances which seem to be connected with the formation of the amorphous connective tissue are described.

In *Carcinus* and in *Pagurus* three sensory fibres are associated with the muscular receptor; these are referred to as *T*, *S* and *P*. The dendrites of *T* are associated with vacuolated connective tissue strings which attach directly to the proximal ends of the fibres of the proprioceptor muscle. The *S* dendrites pass into strands of connective tissue flanking the muscle; dendrite fingers of *P*, which is a smaller nerve fibre, enter some of the vacuolated strings which are associated with the *S*

Vol. 248. B. 752. (Price 16*s*. 6*d*.; U.S. $2.45) 54 [Published 18 February 1965

dendrites. The elastic strands are innervated each by one or more sensory fibres, with dendrites again associated with vacuolated connective tissue strings.

In *Astacus* two sensory fibres send irregularly branched dendrites into a strand of connective tissue proximal to the proprioceptor muscle. No specialized connective tissue strings can be distinguished, but there are unsheathed dendrite fingers penetrating the connective tissue in places. The chordotonal organ contains isodynal scolopidia, each with two bipolar sensory cells of similar fine structure.

A rough calculation of the surface area of the dendrite fingers of the *S* neuron of *Carcinus* has been made.

Introduction

The first part of this work (Whitear 1962) dealt with the structure of the chordotonal organs in the joints of the legs of *Carcinus maenas*; the present part is a study of the proprioceptors at the bases of the legs in decapods, which for the most part are not chordotonal

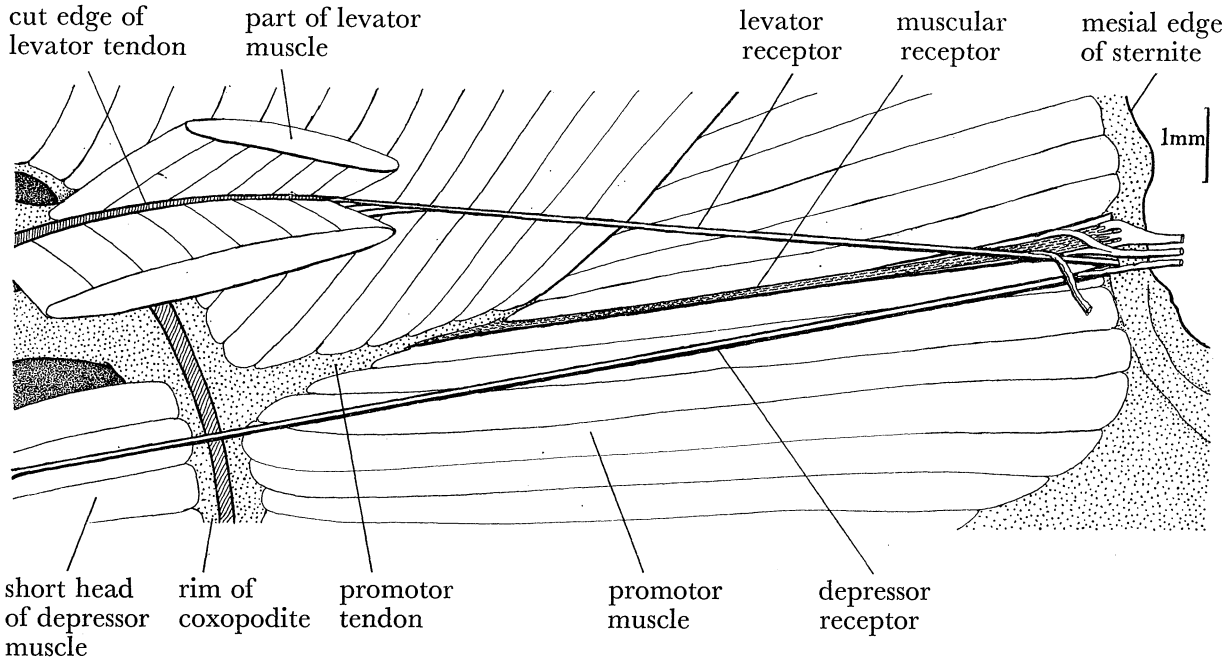

Figure 1. Posterior view of the proprioceptors at the base of the third peraeopod of *Carcinus maenas*. Much of the levator muscle has been cut away. The sensory nerves are shown cut short.

organs. These receptors were first described by Alexandrowicz & Whitear (1957); at the base of each peraeopod is a muscular receptor and a set of innervated elastic strands, and, in macrurans only, a chordotonal organ. The chordotonal organs are type I arthropod proprioceptors, according to the classification of Pringle (1961); they contain primary sensory nerve cells, which are complicated in their fine structure. By contrast, the sensory cells of the muscular receptors and of the innervated elastic strands, which belong to Pringle's category of type II arthropod proprioceptors, are neuron-like and appear to lack any special modification of internal structure.

In *Carcinus*, the muscular receptor is innervated by a motor nerve and by three sensory fibres (*T*, *S* and *P*) whose cell bodies lie in the thoracic ganglia, and have not been located. Figure 1 shows the disposition of this receptor and of the innervated elastic strands, in the segments of the non-chelate legs. In the chelipeds the arrangement is essentially similar but the organs attach to a skeletal rod instead of directly to the sternite.

The arrangement in *Pagurus* was described in detail by Alexandrowicz (1958) who used the nomenclature for the sensory fibres which is adopted here. The muscular receptors attach directly to the sternites, as in *Carcinus*, and are supplied by *T*, *S* and *P* fibres, but the proximal attachments of the innervated elastic strands are different.

In *Astacus*, mentioned briefly by Alexandrowicz & Whitear (1957), the thoracico-coxal proprioceptors are similar to those of *Homarus*, which were described in detail in that paper. The muscular receptor has two large sensory fibres with dendrites branching irregularly in the connective tissue proximal to the receptor muscle. The muscular receptor, and a chordotonal organ, are suspended from a rod arising from the endophragmal skeleton. The innervated elastic strands are bifurcated proximally; one limb of each is suspended from the rod mentioned above, the other from a ligament.

The fine structure of the dendrite endings is similar in *Carcinus* and in *Pagurus*, but in *Astacus* conditions are somewhat different, and are considered separately.

Material and methods

The thoracico-coxal proprioceptors were examined by electron microscopy in *Carcinus maenas* (L.), *Pagurus bernhardus* (L.) and *Astacus pallipes* Lereboullet. Adult males were used whenever possible. The animals were dissected from above and behind to expose the organs. In *Carcinus*, the organs of peraeopods IV and V are the most easily accessible, and were mainly used, though peraeopod III was used occasionally. In *Pagurus* the muscular receptors of the second peraeopod segment are by far the most accessible, and were used exclusively. The innervated elastic strand of the depressor muscle was obtained by dissecting the coxa from behind, in peraeopods II and III. In *Astacus* the organs of peraeopods II, III and IV were used.

In all cases cold buffered 2% osmium tetroxide was dropped on the organs *in situ* as soon as they were exposed. This made them more visible. They were dissected out without delay, attached to a portion of sternite or other skeleton, from which any muscles or other unwanted structures had been removed. The preparations were left about 3 h in cold fixative; this was made up, for the marine animals, of equal parts of the buffered 2% osmium tetroxide and sea water. For *Astacus*, Ringer's solution was used instead of sea water. After washing in distilled water the preparations were extended in a watch glass, blotted gently, and flooded with absolute alcohol. At some convenient stage the attached skeleton was either removed or trimmed to a minimum. During dehydration the organ was bathed for an hour or 50 min in 1% phosphotungstic acid in absolute alcohol. Specimens were embedded in Araldite epoxy-resin. Sections were cut on a Porter–Blum microtome with a glass knife. Chloroform vapour was used to flatten the sections. They were examined on either carbon or celloidin films in a Siemen's Elmiskop I.

Dendrite connexions in *Carcinus* and in *Pagurus*

In *Carcinus* and in *Pagurus*, examination in the electron microscope showed that all the sensory fibres concerned had similar relationships to the connective tissue. The dendrites have an intimate relation to strings of connective tissue, which are specialized in structure, but not in substance. The strings appear to be made of the same elements as is the rest of

the animal's connective tissue, that is, of collagen mixed with amorphous connective tissue substance, both secreted extracellularly (see Whitear 1962, and the discussion of the formation of amorphous connective tissue, below). These strings of connective tissue appear vacuolated in transverse section, and will therefore be referred to as *vacuolated strings*.

Between the ganglion and the proprioceptor each fibre is encased in several layers of sheath cells, which are also present over much of the dendrite surface even within the connective tissue of the organ. Most of the mitochondria lie peripherally in the dendrites, whose surface is in some places complicated by the intrusion of processes from the adjacent sheath cells. Where the dendrite is related to a vacuolated connective tissue string, however, a sheath is absent. Each vacuolated string is encased in, and presumably secreted by, a connective tissue cell (*string cell*), which in transverse section is seen as a number of lobules around the string. The cell membrane of this cell lies immediately next to the substance of the string, which is extracellular. There may be more than one string cell along the length of a string.

The cell membrane of the dendrite is separated from the cell membrane of the string cell by the usual 200 Å gap. The dendrite sends processes between the vacuolated strings and has lobules on the far side of them, which can be seen in light microscope preparations. In places the string cells are interrupted, to allow the dendrite processes to penetrate up to the string itself. Here finer processes (*dendrite fingers*) actually enter the substance of the string. The apparent vacuoles of the string are in reality filled by these dendrite fingers.

The arrangement is shown in the stereogram, figure 2. The dendrite fingers are too fine to contain any mitochondria. In fixed material they are about 0·1 μm in diameter, in *Carcinus* somewhat more, in *Pagurus* somewhat less. As they may taper this is a rough figure only. The dendrite fingers pass into the string for a certain distance more or less transversely, then turn and run longitudinally in one or both directions for a considerable distance. In longitudinal sections it was not uncommon to find a dendrite finger 3 μm long, and some appeared to extend for as much as 7 μm. They may be longer, for it would not be expected to cut so slender a structure in uninterrupted longitudinal section for any great distance. On the other hand, the number of dendrite fingers counted in serial sections, which were not very far apart, varied, so that it is unlikely that they are more than a few microns long.

Figure 8, plate 35, shows two vacuolated strings of the *Carcinus S* fibre, with string cell cytoplasm, and a dendrite lobule penetrating between them. Figure 9, plate 35, is a higher power picture of the same material showing dendrite fingers entering the string. Figure 10, plate 35, is similar, but from a *Carcinus T* dendrite, and shows that the cell membrane of the dendrite appears thicker than that of the string cell. A similar thick membrane has been reported from other large nerve fibres, for instance, by Hama (1961) in crayfish giant axons, so that this is not a peculiarity of sensory fibre membranes.

Figure 11, plate 35, shows a longitudinal section of dendrite fingers of the *T* fibre of *Pagurus*. In this section five dendrite fingers (arrowed) enter the vacuolated string over a distance of 2 μm.

In some specimens the gap outside the cell membrane of the dendrite fingers looked no bigger than the interstices of the connective tissue, so that there appeared to be direct

contact. In other specimens (especially of *Pagurus*) a gap of about 200 Å was seen outside the dendrite finger membrane. These appearances occur in figures 9 and 10, respectively. Of course it is not known what the effect of fixation and preparation may have been. Occasionally, collagen fibres were in close proximity to the dendrite fingers, but usually

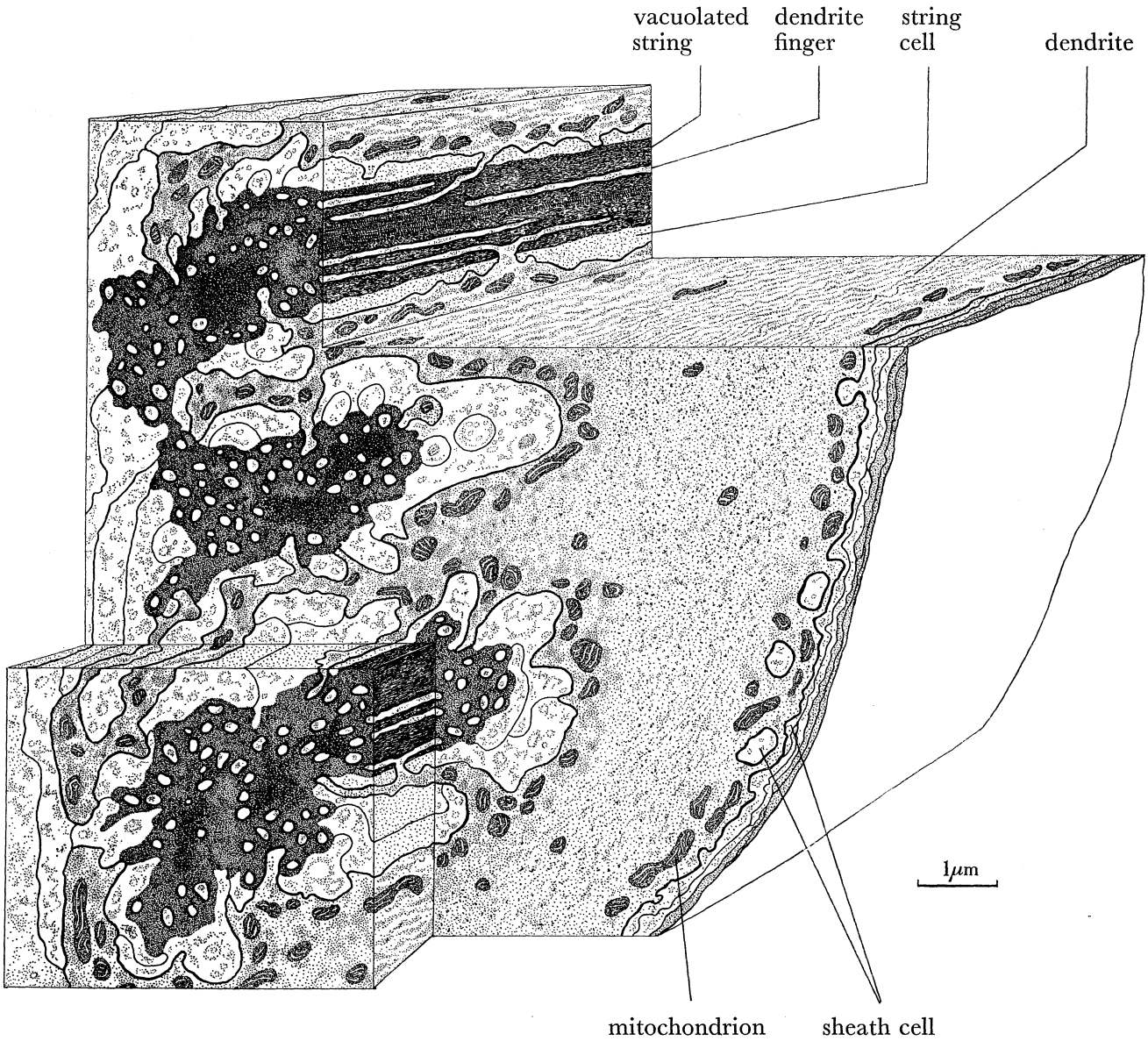

FIGURE 2. Stereogram to show the relationship of the dendrites of the sensory fibres to the connective tissue. Based on *Carcinus*, but conditions in *Pagurus* are similar.

they are surrounded by amorphous connective tissue. The collagen fibres are not scattered throughout the vacuolated string but occur in bundles; they can be seen in figure 8, plate 35 and figure 12, plate 36, in transverse section, and in figure 11 in longitudinal section, when they show cross-striations. Figure 12 is a transverse section of a *Carcinus S* fibre string near its distal end. Only three dendrite fingers remain, which happen to be adjacent to collagen fibres over part of their surface. The nucleus is that of the string cell.

Formation of the amorphous connective tissue

In insects, the connective tissue is usually described as consisting of collagen and connective tissue matrix (Osborne 1963). The term, amorphous connective tissue, is used here, rather than connective tissue matrix, because it is not entirely clear that the two substances are identical. However, they appear to have considerable resemblances in crustacea and in insects.

In crustacea, the amorphous connective tissue may form quite large and solid-looking masses, which is not to say that it is necessarily solid rather than a viscous fluid in life. In *Carcinus* and in *Pagurus* structures are occasionally encountered, which were called *rosette cells* from their appearance in transverse section (figure 13, plate 36). Longitudinal and oblique sections suggest that they are concerned with the secretion of the amorphous connective tissue. A mass of this substance appears at one side of figure 13.

Rosette cells were found most often in the outer layers of the 'tendon' region, at the proximal end of the muscular receptor, where amorphous connective tissue is most abundant. They have also been seen in the elastic strands of the chordotonal organs and elsewhere in the connective tissue. In transverse sections, a cell with a complicated configuration encloses the rosette, which is apparently secreted external to the cell membrane. There are projections from the cell into the central secreted mass, which account for its complicated configuration, but not every mass of extracellular material contains a cell process. The resemblance to a basement membrane will be immediately obvious from figure 13, in which a few processes are indicated. There may in some cases be differences in the apparent density of the secreted material in different layers.

It appears from oblique sections, as in figure 14, plate 36, that the cell pays out the secreted material at one end, or rather, that the cell moves, leaving secreted material behind. This then becomes agglomerated into more solid-looking masses; a layered structure is sometimes discernable well outside the cell. Most of the masses of this type of connective tissue substance, however, look amorphous and homogeneous, as in figure 13, with a granular rather than a fibrillar structure in both longitudinal and transverse sections. Some masses were more electron-dense than others.

Wigglesworth (1956) described amoebocytes in *Rhodnius*, with characteristic inclusions, which seemed to contribute to the formation of basement membrane and extracellular connective tissue sheaths. Blood cells with electron-dense inclusions are commonly met with in crustacean material, both on the outer surfaces of organs and insinuated within them. No appearances have been seen which suggest that these blood cells contribute to the connective tissue. The resemblance of the amorphous connective tissue, when it is formed within rosette cells, to basement membrane, has already been commented on. There is a possibility, in electronmicrographs of crustacean material, of confusing a blood-filled tissue space with amorphous connective tissue, as the blood plasma can look surprisingly dense; the morphological relations, however, usually make it possible to distinguish one from the other.

Rosettes have not been seen in association with the vacuolated strings, which would perhaps not be expected when the strings are fully formed. There is nothing in the appearance of the extracellular material of the string, nor in that of the string cell, to

suggest that the vacuolated strings are made of any substance different from the ordinary connective tissue. As the collagen bundles are central in the string, it seems likely that the cells secrete collagen, and then amorphous connective tissue. Where the strings join the general connective tissue, there is often a laminated appearance.

How the dendrite fingers come to be enclosed in the strings is a matter of supposition. There are a certain number of what appear to be dendrite fingers, on the periphery of each string, which are bounded externally only by the string cell, as in figure 9, plate 35 (arrowed). The secretion of further connective tissue substance by the string cell would result in the enclosure of these dendrite fingers within the string.

The arrangement of the dendrites of the muscular receptor in *Carcinus*

The dispositions of the vacuolated connective tissue strings and of the dendrites of the muscular receptor of *Carcinus* are shown diagrammatically in figure 3. The organ is drawn as if much shorter than it actually is. Figures 4, 5 and 6 are drawings made from electron-micrographs of transverse sections at approximately the levels indicated in figure 3.

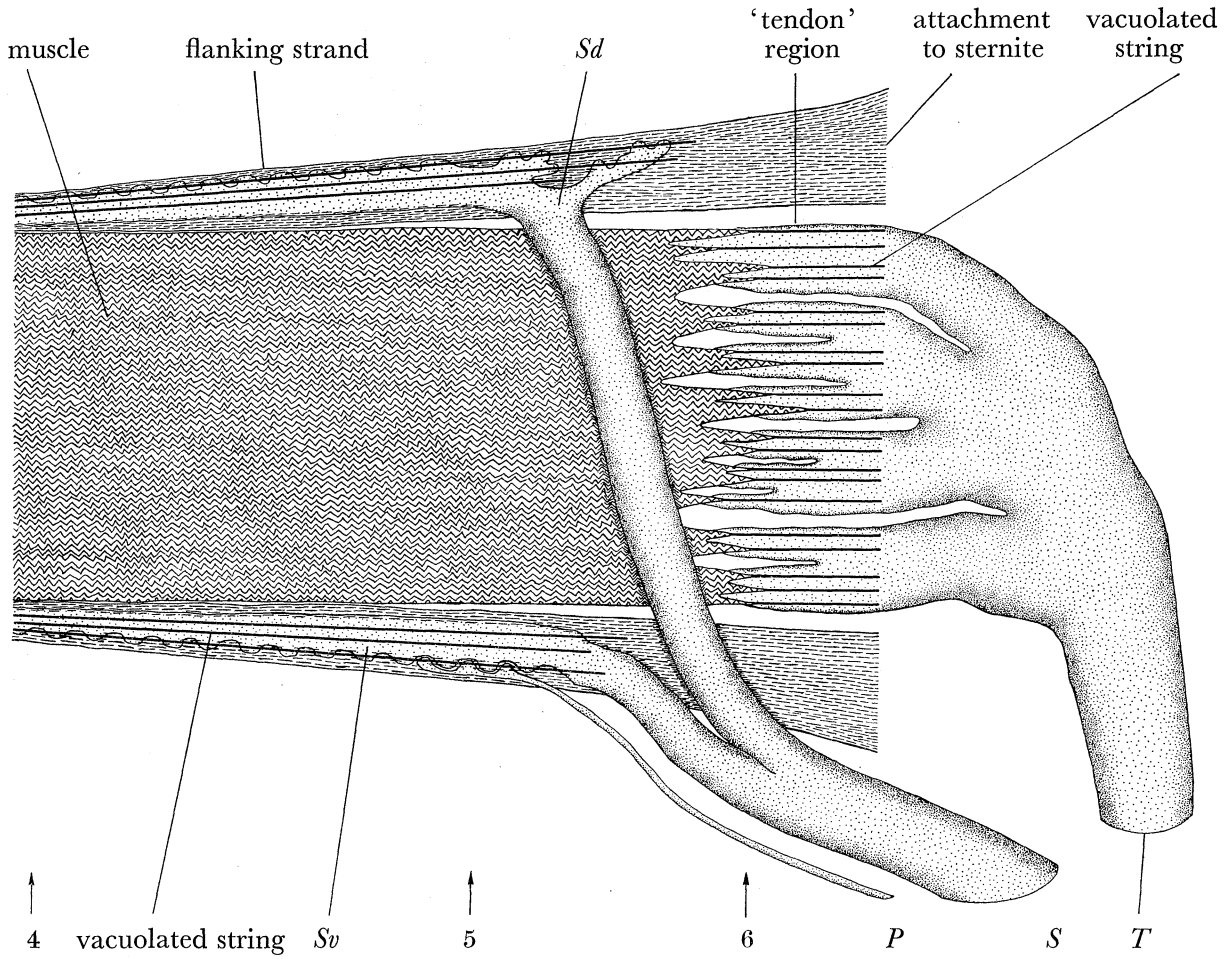

Figure 3. Diagram of the proximal end of the muscular receptor in *Carcinus*, to show the sensory fibres and their relationship to vacuolated connective tissue strings. The general connective tissue of the 'tendon' region is omitted. Not to scale, and shortened. The arrows mark the levels of the sections of figures 4, 5 and 6.

The muscle is ensheathed in connective tissue, which forms flanking strands of appreciable thickness dorsally and ventrally. The main element of the connective tissue here is collagen. Proximally the flanking strands are separated from the muscle, distally they

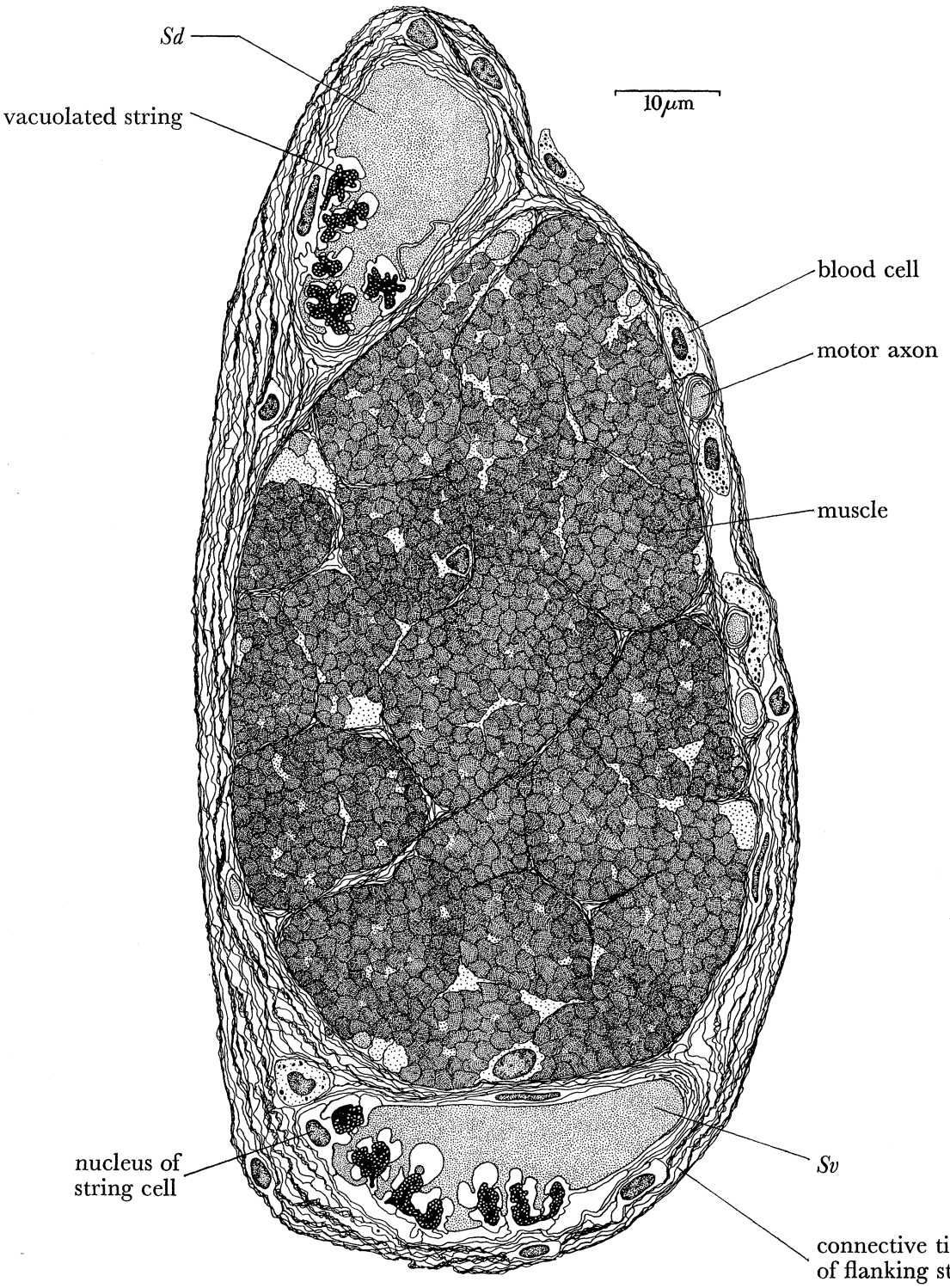

FIGURE 4. Drawing, taken from electronmicrographs, of a transverse section of the muscular receptor of *Carcinus*, showing the *Sd* and *Sv* dendrites and their vacuolated strings. Level of section indicated in figure 3. Anterior to the left.

are attached to it. Distally the organ attaches to the promotor tendon of the coxopodite (figure 1). Proximally it is attached to the back of the sternite, near the mesial edge; here the connective tissue of the proprioceptor organ merges into the hypoderm of the sternite.

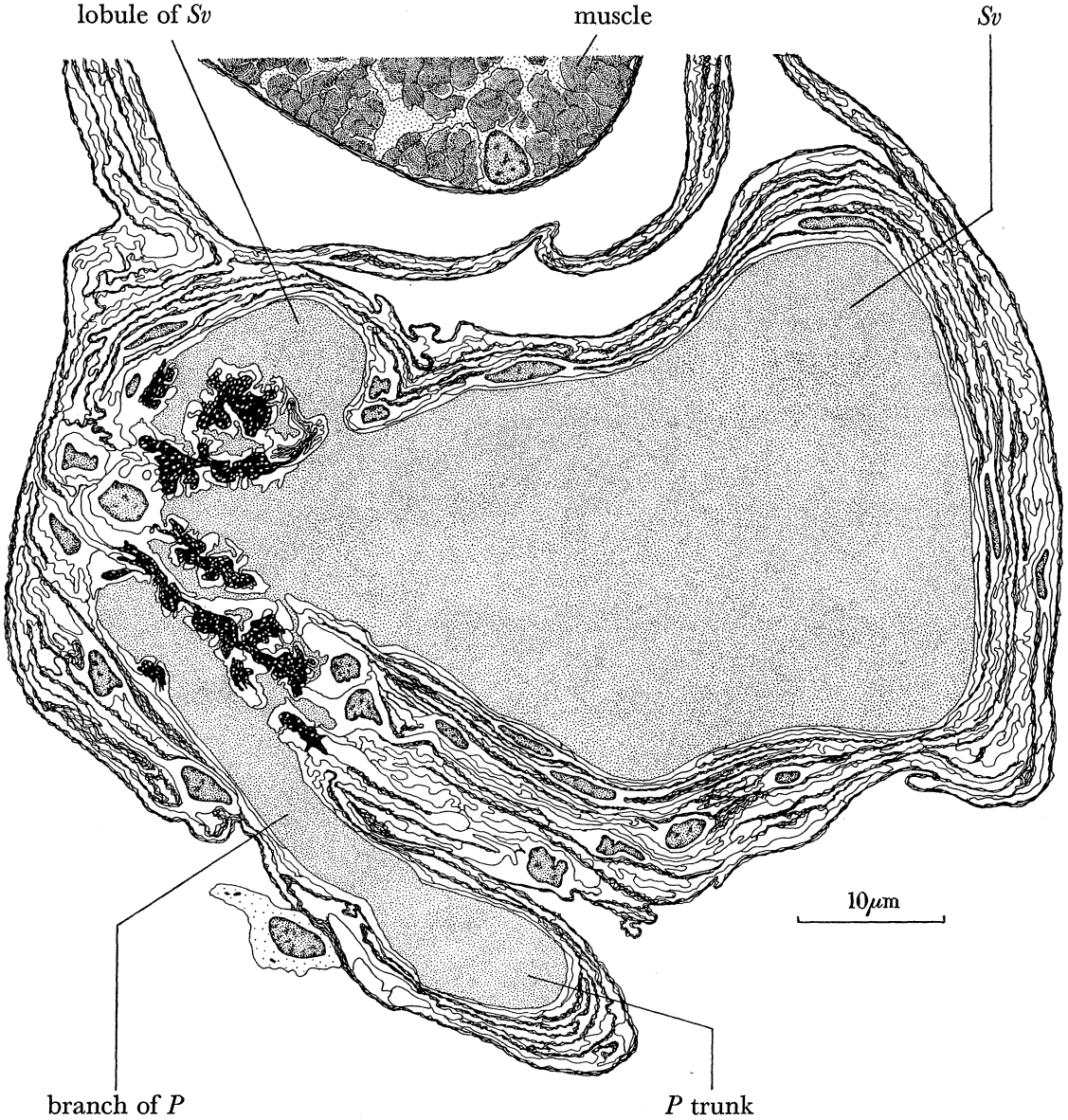

FIGURE 5. Drawing, taken from electronmicrographs, of a transverse section of the *Sv* and *P* dendrites of the *Carcinus* muscular receptor, at the level indicated in figure 3. Anterior to the left.

The sensory nerve fibres of the muscular receptor were called the *T*, *S* and *P* fibres by Alexandrowicz (1958). The *S* fibre is bifurcated, and its branches, *Sd* and *Sv*, run in the dorsal and ventral flanking strands, respectively. The *Sd* branch passes up posterior to the organ near the base of the muscle. Where the branches are enclosed within the connective tissue they are lobulated, and associated with vacuolated strings. The vacuolated strings are situated towards the anterior side of the flanking strands, and mostly on the side away from the muscle. Figure 4 shows the muscle and the *S* dendrites, at a level where the flanking strands are continuous with the muscle sheath. Figure 15, plate 37, is a

low-power electronmicrograph of *Sd* at the same level. The dendrites may be either rounded, or slightly flattened. Proximally, both *Sd* and *Sv* contain about eight vacuolated strings, but where the flanking strand is joined to the muscle there are fewer, and not all of these reach to the extreme distal end of the dendrite. In some specimens the dendrite extended a little beyond any of the vacuolated strings. The strings are not entirely separate from one another, as each is lobulated and has occasional connexions with adjacent strings; they form a loose network. Proximally and distally they merge into the general connective tissue of the flanking strands.

The *P* fibre is markedly smaller than the *S* and *T* fibres, but otherwise similar in appearance; it enters the proximal region of the ventral flanking strand. Figure 5 shows the lobulated *Sv* dendrite and the *P* fibre, with a branch. At this level the flanking strand is separated from the muscle, though it is continuous with the outer sheath of the organ. The *P* fibre branches become associated with some of the same vacuolated strings as is the *Sv* dendrite. There is no actual contact between the dendrites of *S* and *P*, they merely send dendrite fingers into opposite sides of the same vacuolated strings. Figure 16, plate 37, is an electronmicrograph from the same series of sections from which figure 5 was made; it shows dendrite fingers from both fibres entering a single vacuolated string. It seems inescapable that *P* must be stimulated by the same mechanism as *S*, though the area of contact of its dendrite fingers with the connective tissue is very much smaller.

The trunk of the *T* fibre is of about the same thickness as the trunk of the *S* fibre, but near the sternite it thickens and divides irregularly into a number of branches, which are associated with the proximal end of the muscular receptor, the so-called 'tendon' region. Throughout the length of the muscle itself, the various muscle fibres are separated more or less by sheaths of connective tissue. Proximally the fibres (or bundles of fibrils, in electronmicrographs) become more distinct, and each is attached proximally to vacuolated connective tissue strings. The vacuolated strings attach indirectly to the sternite, by way of connective tissue and hypoderm.

The branches of the *T* fibre are associated with these vacuolated strings. The tips of *T* dendrites are seen near the proximal end of each muscle fibre. At such a level the sheath of a muscle fibre may still be distinct, enclosing some muscle fibrils, dendrite branches, the vacuolated strings and the string cells. Such a complex appears in figure 6, but as not all the parts of the muscle end at exactly the same level, this section also includes muscle fibres, and large dendrite branches enwrapping vacuolated strings that are attached to muscle fibres more distally. The spaces not occupied by muscle or nerve are filled by connective tissue cells and by masses of amorphous connective tissue. It was the presence of this connective tissue which led Alexandrowicz & Whitear (1957) to call this the 'tendon' region. Collagen is not so plentiful here as in the flanking strands and in the innervated elastic strands.

Figure 17, plate 38, is of a longitudinal section of the tendon region, showing *T* dendrites and the attachment of a vacuolated string to a muscle fibre. Figure 18, plate 38, is of a transverse section across the junction of a muscle fibre and vacuolated strings. The muscle fibrils appear to attach directly to the connective tissue strings at points where a dense area is usually discernible (arrowed in the figure). Dendrite fingers are already present at this level.

Proximally, the minor branches of the *T* fibre merge into larger ones, each of which is, therefore, associated with a number of vacuolated strings, intruded into the dendrite. The vacuolated strings eventually become excluded from the nerve, on the anterior side,

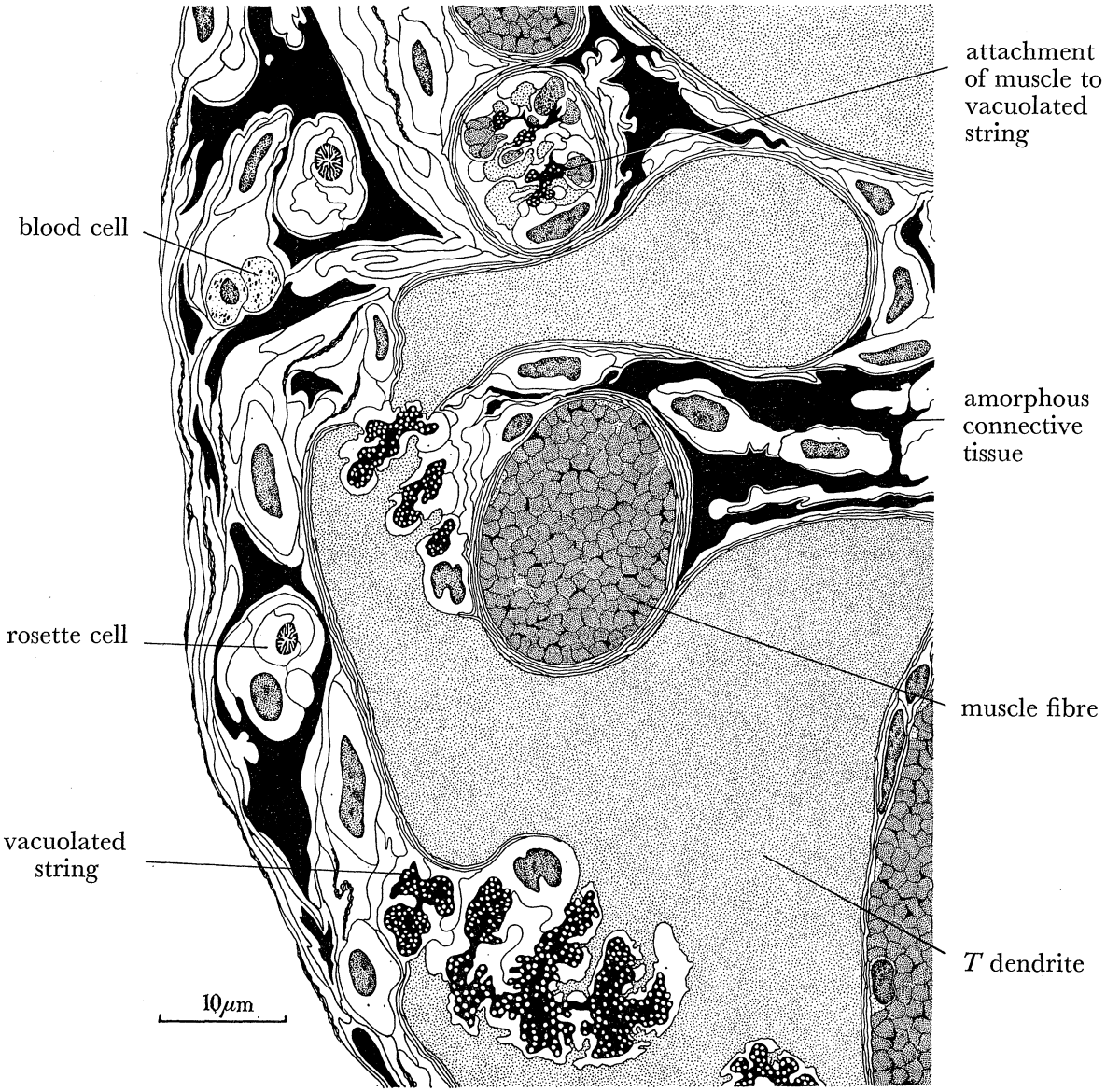

FIGURE 6. Drawing, taken from electronmicrographs, of a transverse section of part of the 'tendon' region of the *Carcinus* muscular receptor, showing branches of the *T* dendrites, vacuolated strings, and the proximal ends of muscle fibres. Level indicated in figure 3, anterior to the left.

where they merge into the connective tissue. The connective tissue attaches to the hypodermis, in a region of interdigitating cell processes with many attachment plaques. The hypodermal cells here can be recognized by the masses of tubules, 200 to 300 Å in diameter, which pack their cytoplasm. The underlying chitin of the sternite shows some minute striations with a periodicity of about 400 to 500 Å, and also dense streaks, some of which cross the boundary into the hypodermal cells.

It will be clear from the above description that the *T* fibre vacuolated strings are in series with the muscle, while the *S* fibre vacuolated strings are in parallel with it.

Blood spaces penetrate the connective tissue sheaths of the organ at various places, notably near the proximal end of the muscle.

In the nerve trunks between the sternites and the thoracic ganglia, each proprioceptor nerve fibre is enclosed in a sheath of cells. Other pieces of connective tissue may be present, but the fibres are not bound up together, or, if at all, only loosely. It is common to find the *S* and *T* fibres much flattened in sections; this is probably due to shrinkage of the nerve during fixation or preparation. The apparent diameter of the *T* trunk is about 40 μm, but it may be thicker near the sternite. The trunk of *S* is about the same size, and where it bifurcates into *Sd* and *Sv* branches each is about 30 μm in diameter. The diameter of *P* is 7 to 10 μm. The sheaths of these fibres have an inner layer of closely packed sheath cells, from 2 to 5 μm thick, and looser outer layers which may bring the total thickness of the sheath up to 10 μm.

The motor nerve to the muscle has not been specially investigated. Numerous axons may be found associated with the muscle, as in figure 4, and sections of fibres containing plentiful synaptic vesicles were not uncommon in the muscle.

The muscular receptor dendrites in *Pagurus*

The morphology of the muscular receptors in hermit crabs is not quite the same in different segments. That of the second peraeopod is most easily accessible, and it was the only one used for electron microscopy, as the chances of good fixation were better. A sketch of this organ is shown in figure 7 (inset). In *Pagurus*, *T*, *S* and *P* fibres are present, with the same general arrangement as in *Carcinus*, but the *S* and *P* fibres branch more extensively and *P* is distributed with both main branches of *S*. In peraeopod II the flanking strands, proximally, are not distinct as they are in *Carcinus*. The nerve bundle containing the *T*, *S* and *P* fibres approaches the organ from behind. *T* separates from the bundle, runs mesially, branches, and then turns back on itself as it enters the 'tendon' region, proximal to the muscle. At about the point where *T* diverges, *P* begins to branch, runs towards the muscle, and sends its branches into the connective tissue, which is mainly on the anterior side of the organ. Small branches of *S* accompany the *P* branches. The main *S* fibre bifurcates and passes distally. The two large dendrites separate and pass to opposite sides of the muscle, giving off branches as they go. These minor branches correspond to the lobules of the *S* dendrites in *Carcinus*. The distribution of *P* is more proximal than the main distribution of *S*, but there is overlap. There may be differences in the details of nerve distribution in different specimens.

Figure 7 is a section through the proximal part of the muscle, at the level indicated in the sketch. The large *S* branches are posterior to the muscle and have branches passing into the connective tissue above and below the muscle. Anterior to the muscle are numerous small dendrites associated with vacuolated strings. Some of these branches belong to *S*, and some to *P*, but there is no way of distinguishing between them. The vacuolated strings are usually rather flattened and strap-like in *Pagurus*, and contain proportionally more collagen than do those of *Carcinus*, so that they do not stand out as well from the general connective tissue.

The branches of *S* and *P* in *Pagurus* are both longer and more numerous than they are in *Carcinus*. It was not possible to make reconstructions accurate enough to be quite certain that the two fibres do send dendrite fingers into at least some vacuolated strings in common. In any particular section some dendrites are found which are not in contact with any

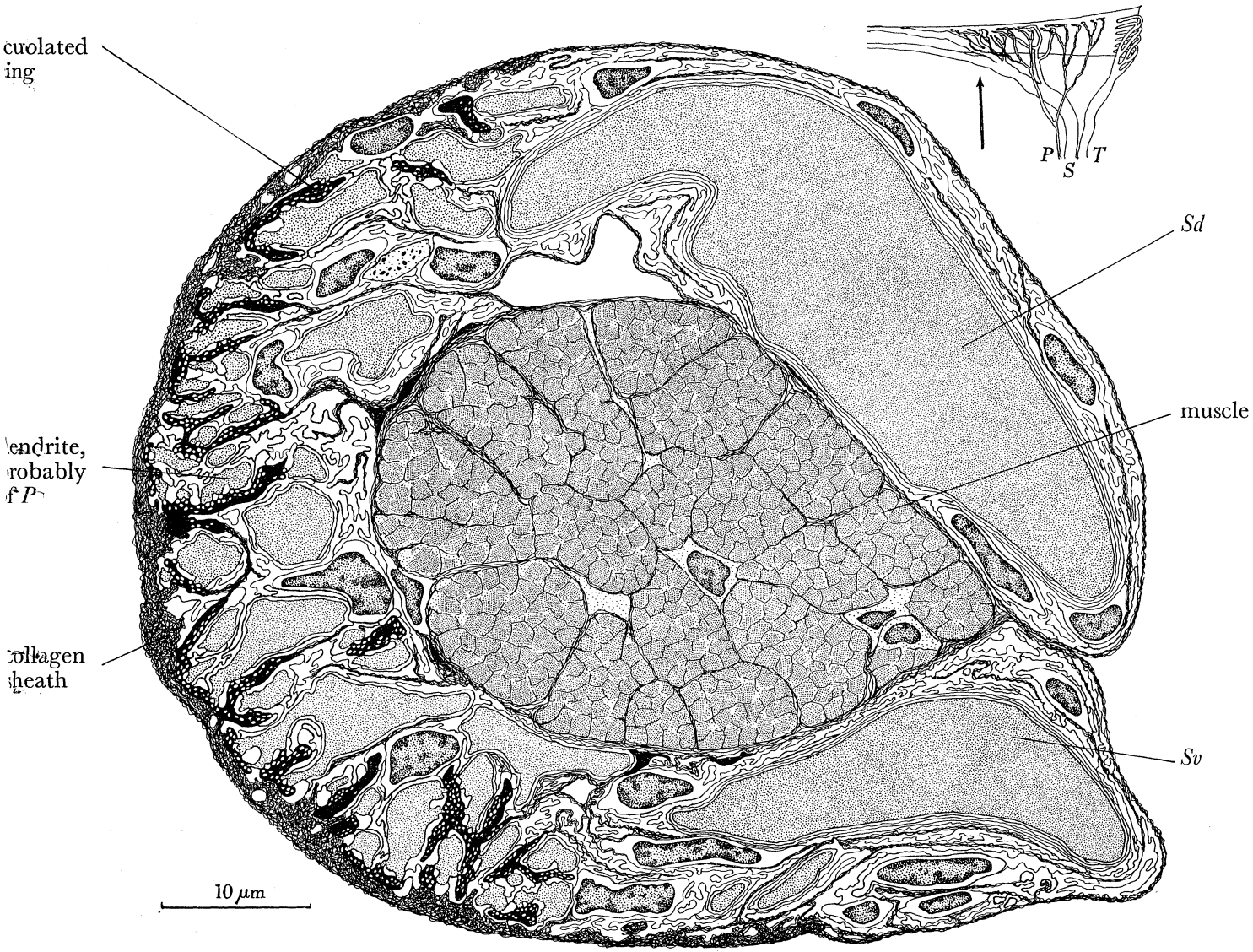

FIGURE 7. Drawing, taken from electronmicrographs, of a transverse section of the muscular receptor of *Pagurus*, at the level indicated in the sketch, inset. Anterior to the left.

vacuolated string. However, there is no appearance to suggest that the branches of the two fibres do not intermingle, and the probability is that they do have vacuolated strings in common.

Alexandrowicz (1958) reported that one or more fine fibres ran with the *T* fibre in *Pagurus*. Electronmicrographs of the *T* fibre approaching the organ showed some small fibres, with very few mitochondria, which might have belonged to a separate nerve, but could equally well have been branches of *T*. A small fibre was also seen crossing in front

of the base of the muscle, but there was no indication of its nature. In the 'tendon' region itself it was even less possible to tell whether all the branches seen did or did not belong to the *T* fibre. Profiles which might have represented a small nerve fibre were seen; one appears in figure 19, plate 39, which is a general view of *T* branches and vacuolated strings. No specialized endings were found, such as might have been expected if the fine fibre were inhibitory (Peterson & Pepe (1961) found the inhibitory endings of the crayfish abdominal stretch receptor packed with vesicles), but on the other hand it would be quite possible to miss such endings even if they were present. The question of the existence and distribution of a fine fibre remains open.

The general relationship of the *T* dendrites to the vacuolated strings, and of the vacuolated strings to the muscle, appears similar in *Pagurus* to that in *Carcinus*. There are more, and smaller, branches of *T*. Figure 19 is of a section of the 'tendon' region, proximally. Figure 11, plate 35, is of a longitudinal section of one of these vacuolated strings.

The innervated elastic strands in *Carcinus* and in *Pagurus*

The innervated elastic strands are named the levator and depressor receptors, for the muscles with which they associate distally. Their position in *Carcinus* is shown in figure 1. In this animal the depressor strand is noticeably thicker than that of the levator receptor. In fresh material they have a characteristic glistening appearance. Both strands originate on the sternite immediately ventral to the base of the muscular receptor. Usually, the base of the depressor strand is a little more distal than that of the levator, and is ventral to it, but there are individual variations; the base of the levator strand has been seen to fray out and to pass on either side of the nerve to the depressor receptor. This fibre, the only one to the depressor receptor, is 15 to 20 μm in diameter, and runs with the nerve to the muscular receptor. It enters the depressor strand near its base, and becomes associated with vacuolated strings in exactly the same way as are the dendrites of the muscular receptor. The longest vacuolated string reaches very nearly to the base of the strand.

Near its base the *Carcinus* depressor receptor is strap-like, and in fixed material measures about 70 μm dorso-ventrally, and about 30 μm in the antero-posterior direction. Its substance is made up of connective tissue cells and of bundles of collagen fibres, and it is penetrated by blood channels. The dendrite lies against the posterior side in the middle, and is lobulated; four or five vacuolated strings lie more or less in the middle of the strand. More distally the strand and the dendrite taper. Not far beyond the level of the base of the muscle in the muscular receptor, the depressor strand measures 40 by 23 μm and the dendrite about 10 μm or less; there may be up to eight vacuolated strings but they are smaller than in the proximal region. The depressor dendrite does not extend a great way down the strand, probably no further than do the *S* dendrites of the muscular receptor. At the extreme end of the dendrite the strand measures 30 by 20 μm, and may still be penetrated by blood channels. The ends of the vacuolated strings can still be identified in the middle of the strand, but contain very few, or no, dendrite fingers. A few lobules of dendrite, poor in mitochondria, lie among them. The more distal parts of the strand consist only of connective tissue, mainly bundles of collagen fibres.

The *Carcinus* levator strand is thinner and receives two fibres, which approach separately from the main proprioceptor bundle and enter the levator strand at a little distance from

its origin. Figure 20, plate 39, is a transverse section of the levator strand showing the entry of the more distal of the two fibres. Here the strand itself is about 10 μm in diameter; four vacuolated strings lie anterior to the dendrite. More distally the strand tapers a little, to a diameter of about 8 μm; the dendrite has lobules on the far side of the strings but lies mainly posterior to them. The end of the distal levator dendrite is about opposite the extreme ends of the vacuolated strings of *Sv*, in fixed material. The second levator fibre has its distribution mainly proximal to its point of entry to the strand, but does not extend so far proximal as do the vacuolated strings of the depressor strand.

In *Pagurus* the depressor receptor originates on the border of the coxopodite instead of in the thorax, and the levator receptor originates partly near the muscular receptor, but has a larger strand attaching to the endophragmal skeleton elsewhere. Only the depressor dendrite was examined by electron microscopy. Two nerve fibres enter it at some distance from its base and are distributed both up and down the strand. The presence of vacuolated strings was confirmed. Two of these are shown in figure 21, plate 39, and illustrate the usual *Pagurus* type of vacuolated string with a good deal of collagen in it.

The organs in *Astacus*

In *Astacus* the arrangement of the proprioceptors at the bases of the legs is essentially the same as that in *Homarus*; details will be found in Alexandrowicz & Whitear (1957). A receptor rod, suspended in a wrapping of connective tissue, arises from the endophragmal skeleton in each leg segment. A muscular receptor and a chordotonal organ extend from the anterior rim of the coxa to the connective tissue of the rod, the chordotonal organ being attached near the tip of the rod, the muscular organ a little further down. There are also two innervated elastic strands, associated distally with the levator and depressor muscles of the leg, respectively. Proximally each innervated elastic strand has two attachments, one to the receptor rod and the other to a ligament which is slung across the base of the leg; nerve fibres enter each of these attachments.

In electronmicrographs the muscle of the muscular receptor is seen to consist of rather few fibres, scattered in connective tissue. Proximally a considerable length of connective tissue is interposed between the muscle and the rod. To this region are distributed the richly branched dendrites of two sensory fibres, one of which also sends a branch down the side of the muscle for some distance. In electronmicrographs the trunks of these nerves have much the same appearance as in crabs, with the trivial difference that where there is interdigitation of dendrite and sheath cell, the dendrite sends processes into the sheath cell rather than the other way round.

The branches of the two fibres intermingle and cannot be distinguished from one another in sections of the strand. The branches may be anything from 10 μm to less than 0·5 μm in diameter. A thin layer of sheath cell is interposed between dendrite and extracellular connective tissue, which consists, as usual, of a mixture of bundles of collagen fibres and amorphous substance. In the nerve trunks, rather few mitochondria are arranged peripherally. In the dendrites within the strand there are more mitochondria, most of which are also situated peripherally. The number of mitochondria seen in any particular section of a dendrite depends on how near its surface the section runs.

Large and small branches of the dendrites are scattered through the connective tissue of the strand. No discrete 'strings' of connective tissue can be distinguished in *Astacus*. Nevertheless, the connective tissue does, in places, contain quite numerous dendrite fingers, of about 0·1 μm in diameter, or a little less. These fine processes of the dendrites are not ensheathed, but are in intimate relationship to the extracellular connective tissue, just as are the dendrite fingers in the vacuolated strings of *Carcinus* and of *Pagurus*; there is again a hint of a small gap outside the membrane of the dendrite finger. Such a process is seen leaving a dendrite in figure 22, plate 40. Unfortunately the connective tissue is also penetrated by processes from connective tissue cells or sheath cells, so that it is difficult to be certain of the identity of dendrite fingers in transverse sections of the organ. Figures 23 and 24, plate 40, show dendrites and dendrite fingers in longitudinal section. There is no doubt about the identity of these structures. As in the other animals described, dendrite fingers in *Astacus* may run in either, or in both, longitudinal directions. Figure 25, plate 40, shows part of the anterior side of the strand in transverse section, with small dendrite branches, ensheathed, and structures which are believed to be dendrite fingers.

The dendrite passing distally down the side of the muscular receptor is lobulated, but no dendrite fingers were seen here.

Though fine nerve fibres may accompany the large sensory fibres of the muscular receptor, in electronmicrographs there was no way of identifying them, and no specialized endings, other than the dendrite fingers, were seen. Of course it is possible they were missed. It was quite common to find vesicular profiles in some of the dendrite branches (there are a few in figures 23 and 24) but as similar profiles appeared in the sheath cell cytoplasm it is doubtful if they had any particular significance.

The levator and depressor receptors each receive several nerve fibres. They were not investigated in detail. Sections cut near the confluence of the two proximal arms of the strand showed ensheathed and lobulated dendrites, but no dendrite fingers were seen.

The chordotonal organ (elastic receptor of Alexandrowicz & Whitear 1957) has a structure like that of the chordotonal organs of the legs of *Carcinus*, described in the first part of this work (Whitear 1962). All the scolopidia seen were isodynal, with two sensory cells of the ciliary type. Quite commonly one of the two distal processes was much more slender than the other, but otherwise the structure of the sensory cells, the scolopale, and the tube, was precisely as already described for *Carcinus*. A scolopale with ciliary segments is shown in figure 26, plate 40. Many of the nerve cell bodies and of the scolopales were situated in the strand proximal to the point of nerve entry, but their orientation was the same as that of the more distal scolopidia, with the tube distal to the scolopale.

Discussion

The best known 'type II' arthropod proprioceptors are the stretch receptors in the abdomen of macrurans, first described by Alexandrowicz (1951 and several subsequent papers). Pilgrim (1960) gives a list of the crustacean species in which this type of proprioceptor (muscle receptor organ or *MRO*) has been found. There has been a good deal of physiological and pharmacological study of these receptors in certain species, which is reviewed by Edwards (1960). The fine structure of the muscle receptor organ in two species of North American crayfish (*Orconectes virilis* and *Procambarus alleni*) has been investigated

by Peterson & Pepe (1961) and by Bodian & Bergman (1962), respectively. These authors describe the subdivision of the dendrite branches of the sensory neuron, until the finest branches are embedded in connective tissue. Bodian & Bergman state that even the smallest dendrite branches in their material were enclosed in sheath cells, so that they were not in contact with the extracellular connective tissue substance; as these branches also contained mitochondria, they cannot be as fine as the 'dendrite fingers' of this paper. Peterson & Pepe found that the finest divisions of their dendrite branches were 'twigs' from 0·05 to 0·3 μm in diameter; these twigs therefore are the same size as the dendrite fingers. They describe the twigs as being embedded in the connective tissue between the muscle fibres, but as they do not distinguish between 'connective tissue cells' and 'sheath cells', nor, in this connexion, between connective tissue cells and extracellular substance, it is not clear whether or not the dendrite twigs are ensheathed. In their figures of dendritic twigs there appears to be less connective tissue around them than is present around any of the dendrite fingers described in this paper, and some of them appear to be adjacent only to each other.

In insects, Osborne (1963) found that in the abdominal stretch receptor of a cockroach the finest divisions of the dendrites were embedded in connective tissue ground substance without the intervention of a sheath. These naked terminals were less than 0·2 μm in diameter, but did contain mitochondria. There were evidently not a great number of such dendrite endings; the neuron in insects is much smaller than it is in crustaceans. Similar naked dendrite endings occur in moths (Osborne, personal communication).

In the thoracico-coxal receptors of crustaceans the dendrite fingers are numerous, even in *Astacus*, and there is no doubt that they are surrounded by extracellular substance. The arrangement of the *S* fibre in *Carcinus* is simple enough to allow a very rough calculation of the surface areas involved. It must be emphasized that the measurements are not precise, indeed some of them are not direct measurements at all. The muscle contracts on fixation, and there is probably further shrinkage during the preparation for microscopy, so that the figures must be taken as minimal, and approximate.

It is difficult to arrive at a figure for the length of the vacuolated strings, or of the extent of the *Sd* and *Sv* dendrites within the flanking strands of the organ. The total length of the organ can be determined by direct measurement when it is *in situ*. In large male *Carcinus*, with carapaces 6 to 6·5 cm in breadth, the length of the organs of the middle legs was 8 to 9 mm, when the leg was held in an intermediate position. In fixed material it was not possible to gauge the extent of the dendrite branches within the flanking strands, accurately, but the length was estimated at about 2 mm. As these branches seemed usually to occupy from one-third to one-quarter the total length of the organ, the corresponding figure in life may be about 3 mm, in a fully grown crab. (When the leg is moved backwards, the organ would be stretched, and the dendrites longer.) As all measurements of diameter were made on fixed material, the figure of 2 mm will be taken, not only as the length of the dendrites within the strands, but also as the length of the vacuolated strings, though this would not necessarily be the same. Some of the strings are shorter, and the dendrite may extend distally a little way beyond any of them. All measurements of diameter, and the counts of the dendrite fingers, have been taken as round numbers.

The branches of *Sd* and *Sv* within the flanking strands can be treated as cones of length

2 mm, with bases 30 μm in diameter; the difference between the medial and peripheral lengths can be ignored. Their total surface area will then be

$$2\pi rl = 3{\cdot}14 \times 30 \times 2000 = 188400\ \mu m^2.$$

The actual surface will be larger because of the lobulation of the dendrite and because of interdigitation with the adjacent sheath cells, but there is no means of estimating how much should be allowed for this, as neither is regular.

The number of dendrite fingers in any particular section of *Sd* or *Sv* can be counted with some accuracy. The number will, however, not be the same even in sections not far apart, while the size of the vacuolated string varies along the length of the dendrite. About half way along the dendrite, where the flanking strands are bound to the muscle, 300 to 400 dendrite fingers were counted in *Sv*, while more proximally, in the region of the *P* branches, the number exceeded 700. Similar numbers were found in *Sd*, in one proximal section over 800. Far distally, beyond the end of some of the strings, the number of dendrite fingers in a section might be less than 20. Individual dendrite fingers do not exceed a few microns in length, but for the purpose of the calculation an average number for the middle region (350) will be assumed to run the whole length of the dendrite, in each branch; this will give a rough figure for the whole surface of the dendrite fingers. The diameters of the dendrite fingers are not constant, but will be taken as 0·1 μm.

Then each theoretical dendrite finger 0·1 μm in diameter and 2 mm long will have a surface area

$$\pi dl = 3{\cdot}14 \times 200\ \mu m^2$$

and the total surface of all the dendrite fingers of *S* will be

$$628 \times 700 = 439600\ \mu m^2.$$

This will be the area of dendrite membrane exposed to extracellular connective tissue substance, and which might be assumed to be the site of origin of the generator potential. It will be noticed that this is about twice the minimum area calculated for the part in apposition to sheath cells in the same region, which might be assumed to be the site of general metabolic exchange. Even if the figure for the sheathed area is doubled to allow for lobulation, it is still no larger than the unsheathed area.

It is not possible to make a similar calculation for the *T* fibre of *Carcinus*, because one cannot include all its branches in a single section, and so cannot know the total number of dendrite fingers, nor even of dendrite branches, which are in any case numerous and of various sizes. Similarly, in *Pagurus* the branches of all fibres are too numerous and too variable to allow of any calculation, while in *Astacus* it is not possible even to count the dendrite fingers. The general impression is that dendrite fingers are as numerous in *Pagurus* as in *Carcinus*, but scarcer in *Astacus*. The ensheathed surface must, however, be relatively greater in the much branched dendrites of *Pagurus* and *Astacus* than in the simpler bifurcated *S* fibre of *Carcinus*.

It would be rash to assume that the membrane of the dendrite fingers is the exclusive site of origin of the generator potential, particularly if the intimate association with the extracellular elements of the connective tissue is lacking in the abdominal muscle receptor

organs. Eyzaguirre & Kuffler (1955*a*, *b*) limited the site of stimulation of the *MRO* to the distal parts of the dendrites. The presence of dendrite fingers may, however, legitimately be regarded as a specialization connected with the stimulation of the sensory cell. The vacuolated strings must be stretched when the organ as a whole is stretched, and the lack of any cushioning of sheath cells around the dendrite fingers must ensure that this deformation is maximally transmitted to the dendrite membrane.

No published physiological studies of the thoracico-coxal proprioceptors have been seen. S. H. Ripley (personal communication) made recordings from the *T* fibre of *Carcinus* and found that it behaved like a dendrite. Alexandrowicz (1958) made suggestions as to the functions of the various fibres, based on a consideration of their anatomical connexions. Nothing in the present results contradicts his hypotheses, and indeed the discovery of the vacuolated strings and of their connexion with the muscle fibres rather emphasizes that the *T* fibre is stimulated by the muscle pulling on it directly. It is assumed that this happens when the leg moves forwards, as the muscle is a modified part of the promotor muscle. The electron microscope results also confirm that the proximal parts of the flanking strands, in crabs, are quite free of the muscle, so that the tension on the flanking strands can be independent of that on the *T* fibre vacuolated strings. It must be assumed that the muscle is normally under a certain tension, which could be reduced when the leg moves backwards. Such a movement would stretch the flanking strands and so the vacuolated strings of *S*, but slackening of the muscle could prevent increase of strain on the *T* fibre vacuolated strings. Alexandrowicz supposed that the *P* fibre also would be stimulated at the backward movement of the leg; this again is confirmed by the fact that *P* and *Sv* send dendrite fingers into the same vacuolated strings.

The connective tissue strands have been referred to as 'elastic' because their manipulation in fresh preparations makes it obvious that they are so. From the electronmicrographs it looks as if this elasticity must reside in the collagen, for bundles of collagen fibres are the main constituents of the strands, whether they are innervated by dendrites or belong to chordotonal organs. This question, however, needs further investigation. For instance, no comparison has been made of the mechanical properties and fine structure of the proprioceptor strands and of other connective tissue structures such as the suspensory ligament of the macrurans or the ligaments on the endopleurites of crabs.

It is a pleasure to acknowledge my indebtedness to Professor J. Z. Young, F.R.S., for the use of the facilities of his laboratory and for reading the manuscript, and also to Mr S. Waterman for photographic assistance.

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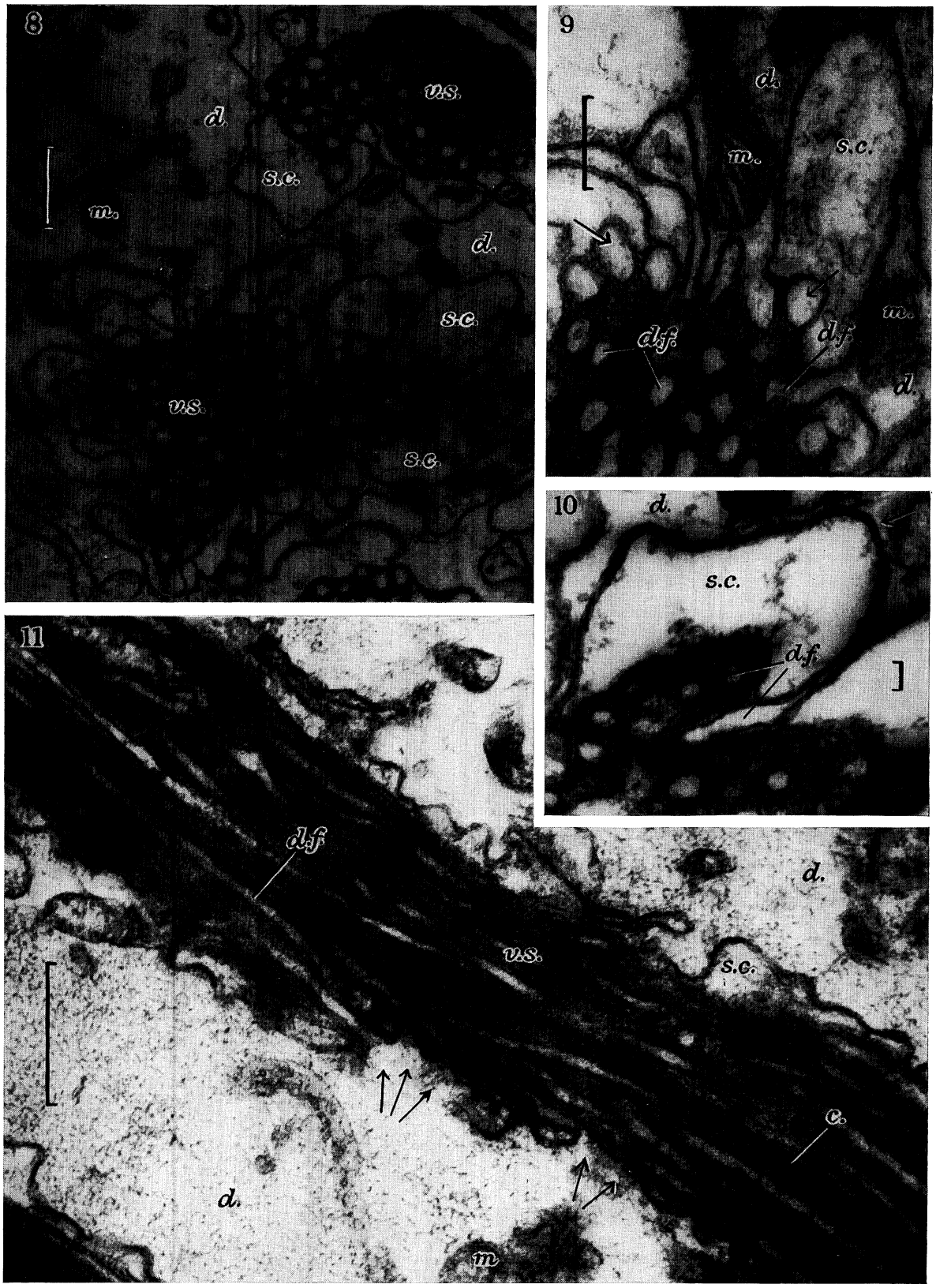
Key to the abbreviations in the plates

a.c.t.	amorphous connective tissue	*mus.*	muscle
c.	collagen fibres	*mus.c.*	cytoplasm of muscle cell
c.s.	ciliary segment	*n.*	nucleus
d.	dendrite	*r.c.*	rosette cell
d. (*P*), (*Sv*)	dendrites of the *P* and *S* fibres, respectively	*sc.*	scolopale
d.f.	dendrite finger	*s.c.*	string cell cytoplasm
f.n.	possible fine nerve fibre	*sh.*	sheath cell
m.	mitochondrion	*v.s.*	vacuolated string



Vacuolated strings

FIGURE 8. Transverse section of a dendrite lobule and vacuolated strings of the *S* fibre of *Carcinus*. Scale 1 μm.

FIGURE 9. As figure 8, scale 0·5 μm. The arrows indicate what are believed to be dendrite fingers on the periphery of the string.

FIGURE 10. Transverse section of a vacuolated string of the *T* fibre of *Carcinus*, showing the entry of a dendrite finger. The arrow indicates a point at which the dendrite membrane appears thicker than that of the string cell. Scale 0·1 μm.

FIGURE 11. Longitudinal section of a vacuolated string of the *T* fibre of *Pagurus*. The arrows indicate the points of entry of dendrite fingers. Scale 1 μm.

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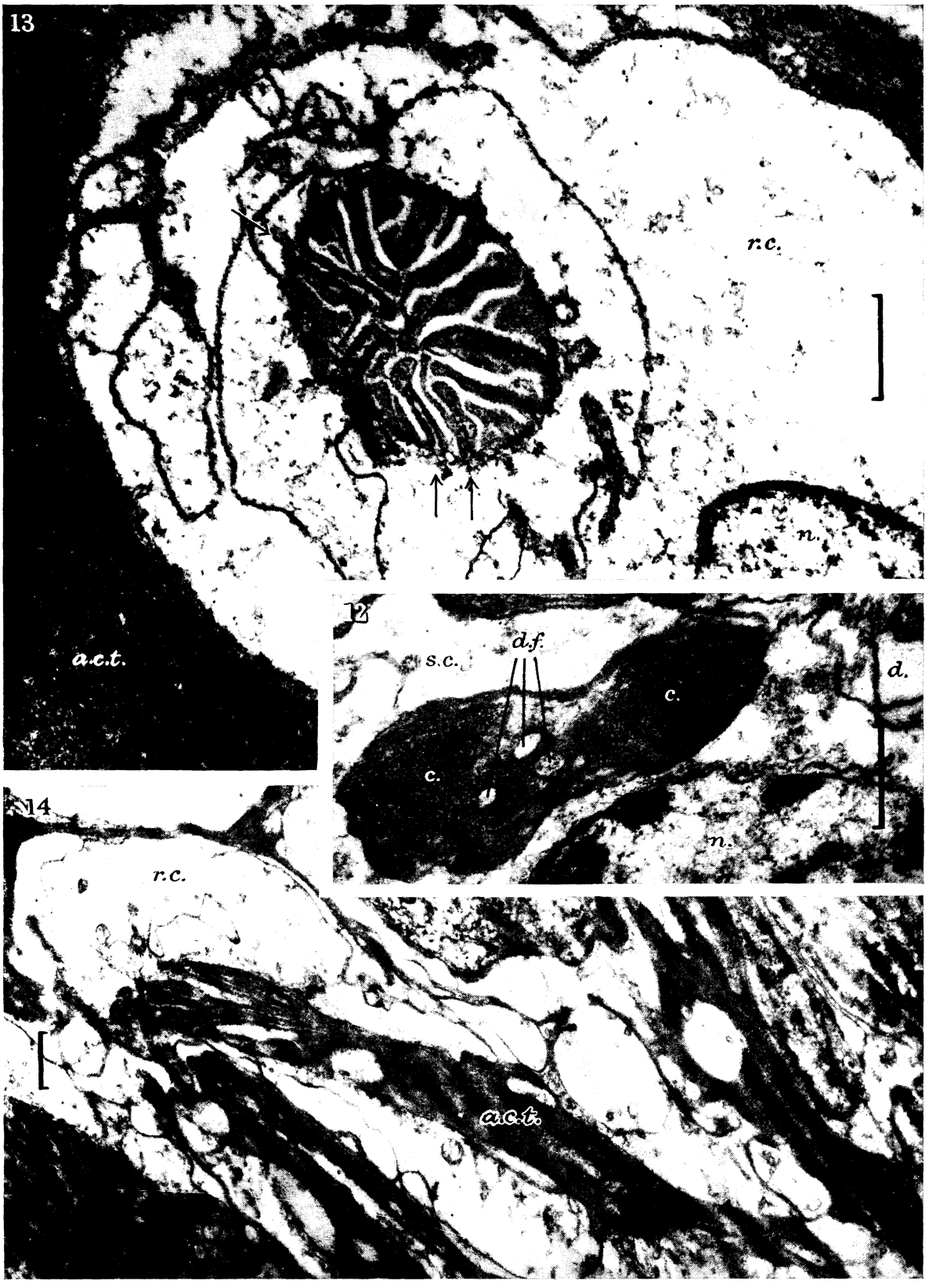
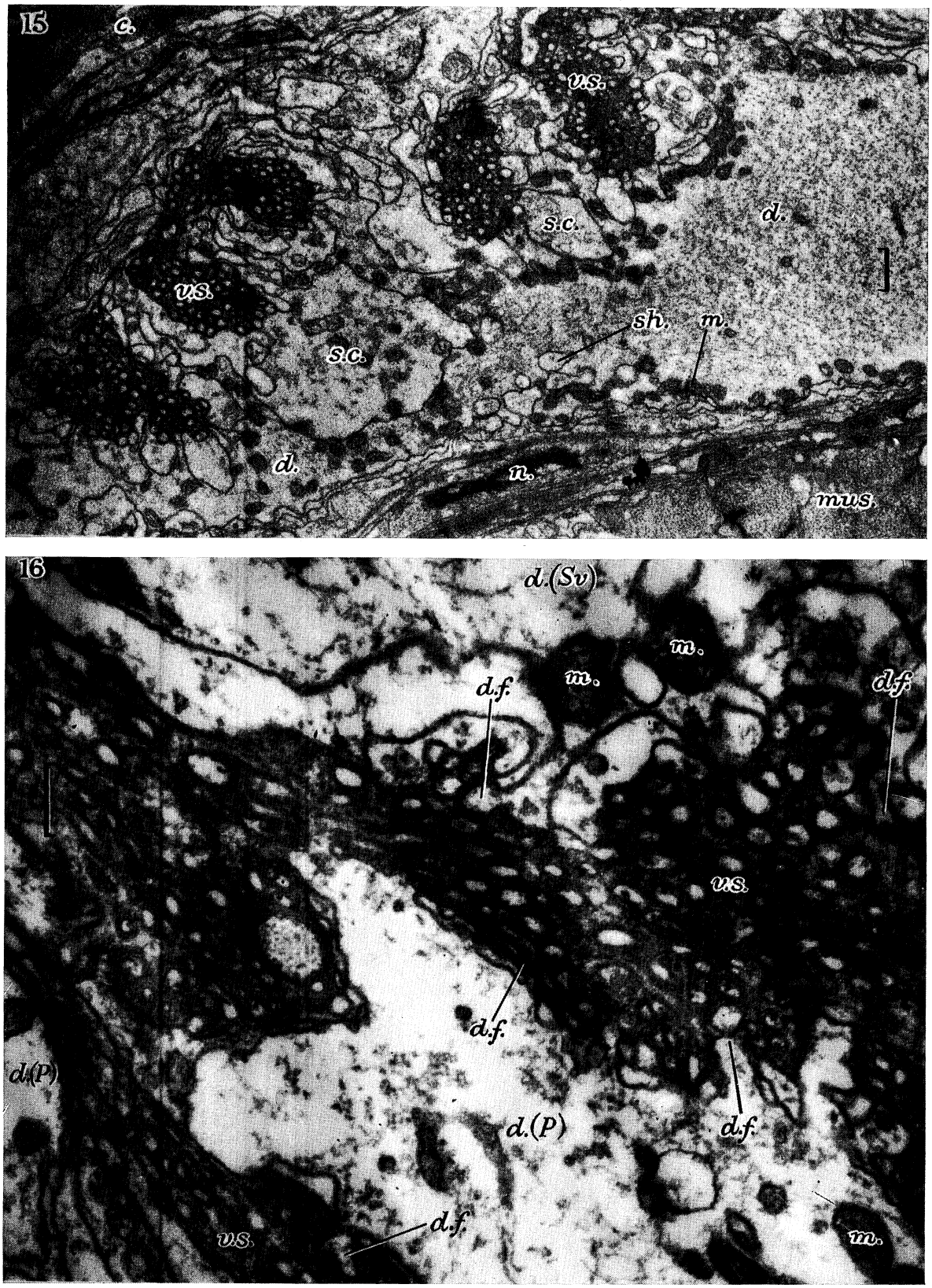


Connective tissue

FIGURE 12. Transverse section near the distal end of a vacuolated string of the *S* fibre of *Carcinus*, to show the connective tissue of the string. Scale 1 μm.

FIGURE 13. Transverse section of the 'tendon' region of *Carcinus*, with a rosette cell and amorphous connective tissue. The arrows indicate projections of the rosette cell membrane. Scale 1 μm.

FIGURE 14. Oblique section of a rosette cell in the same region. Another rosette is in the bottom left corner. Scale 1 μm.

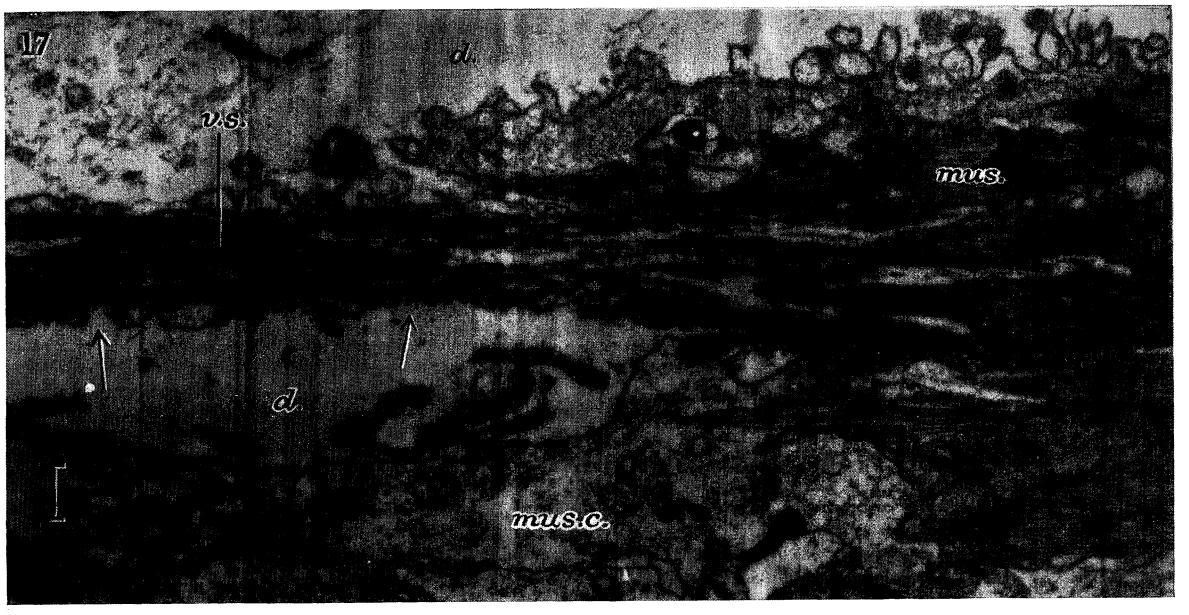


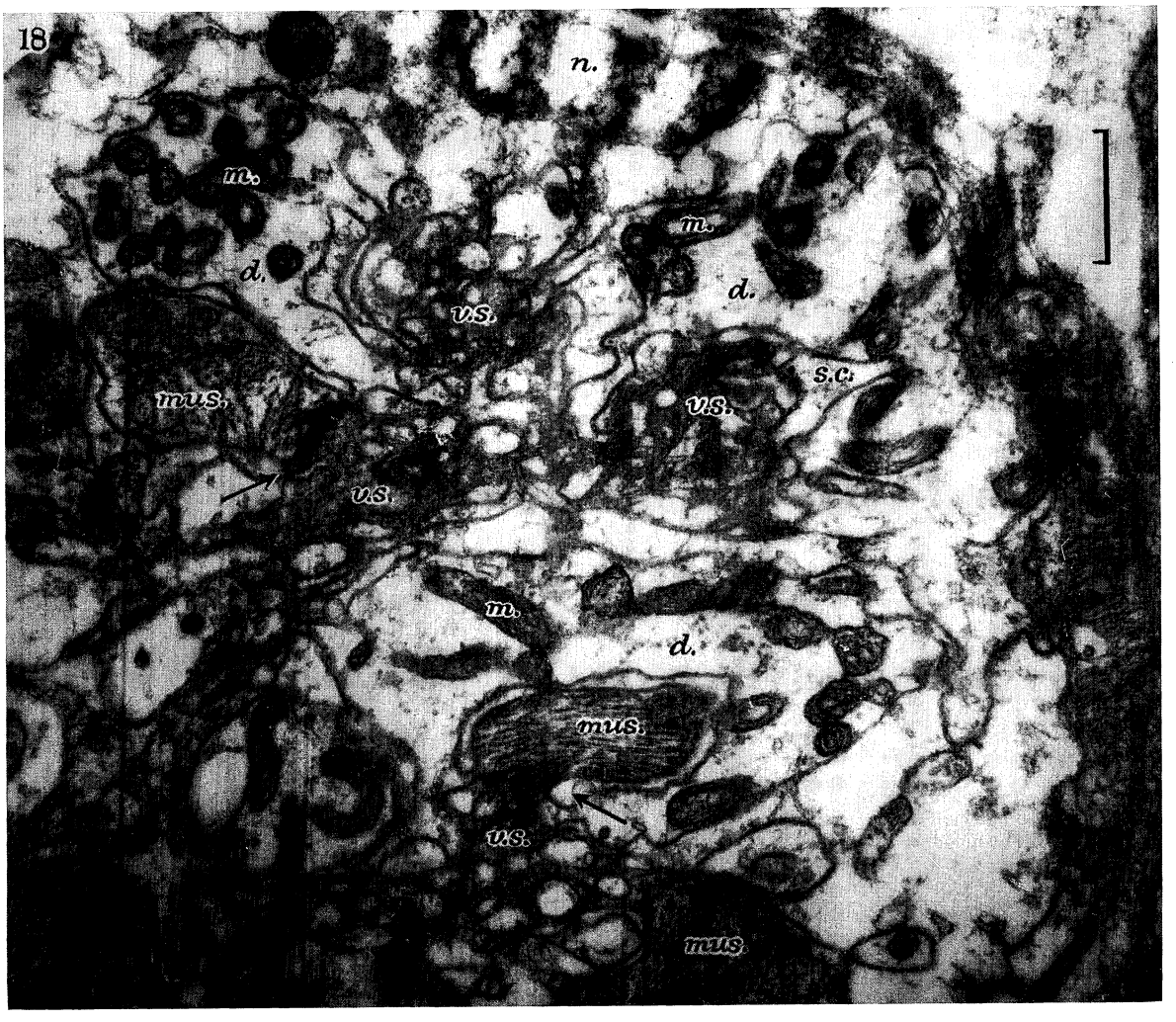
Dendrites of the *S* and *P* fibres in *Carcinus* muscular receptor

Anterior to the left

FIGURE 15. Transverse section of the *Sd* dendrite at a level where the flanking strand is bound to the muscle. Scale 1 μm.

FIGURE 16. Transverse section of the ventral flanking strand more proximally. Dendrite fingers enter the upper vacuolated string from both *Sv* and *P* fibres. Scale 0·5 μm.

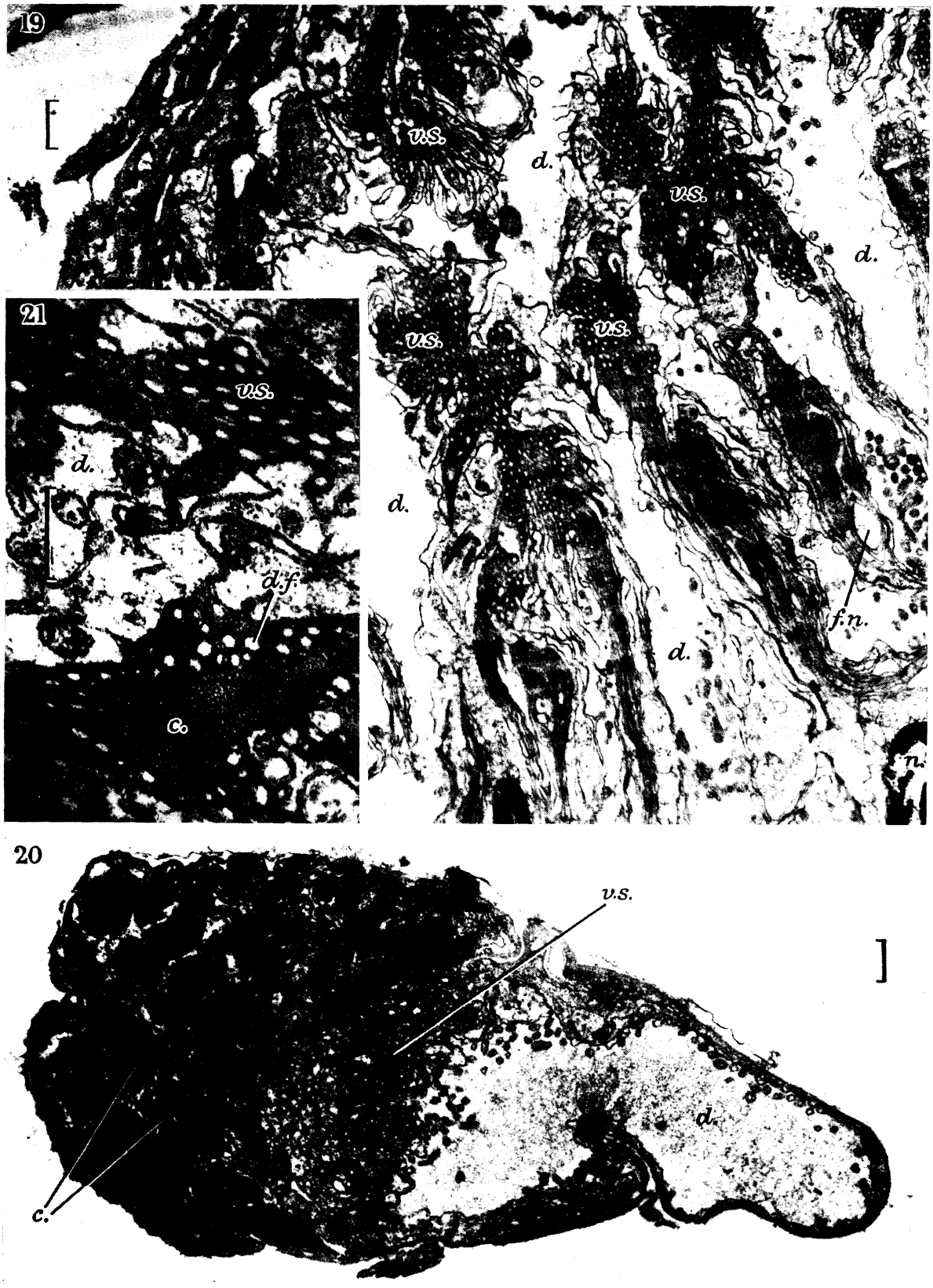




Connexion between the muscle and the vacuolated strings of the *T* fibre in *Carcinus* muscular receptor

FIGURE 17. Longitudinal section of a muscle/vacuolated string junction. Distal to the right. The arrows indicate the points of entry of dendrite fingers. Scale 1 μm.

FIGURE 18. Transverse section of a muscle/vacuolated string junction. The arrows indicate dark areas where the muscle fibre appears to be attached to the vacuolated string. Scale 1 μm.

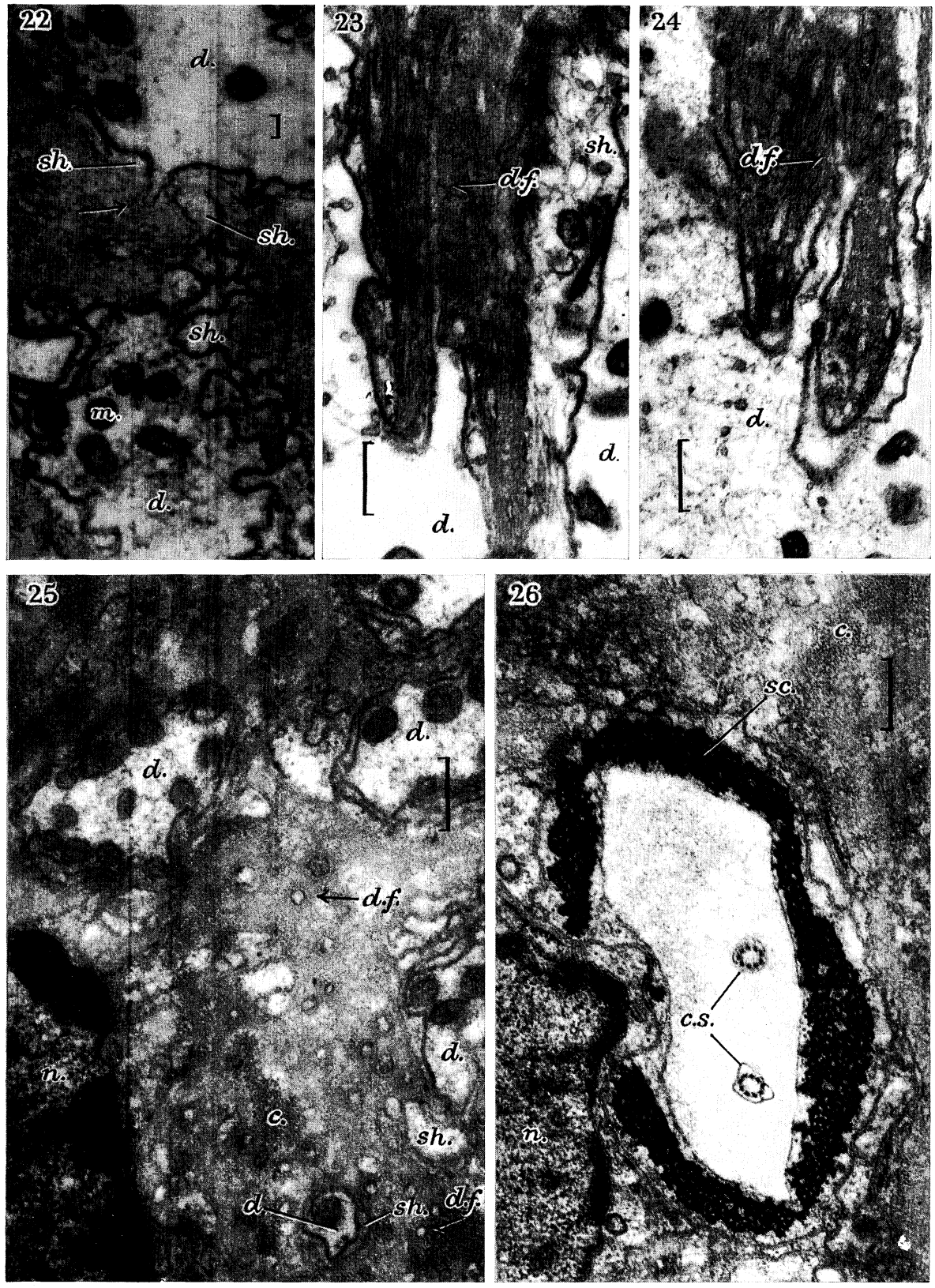


Anterior to the left, approximately

FIGURE 19. Transverse section of the 'tendon' region of *Pagurus* muscular receptor. Scale 1 μm.

FIGURE 20. Transverse section of the levator receptor of *Carcinus*, at the point of entry of the more distal fibre. Scale 1 μm.

FIGURE 21. Transverse section of vacuolated strings of the depressor receptor of *Pagurus*. Scale 0·5 μm.



Muscular receptor and chordotonal organ of *Astacus*

FIGURE 22. Transverse section of the 'tendon' region of the muscular receptor, showing a dendrite finger (arrowed) entering the connective tissue. Scale 0·1 μm.

FIGURE 23. Similar, but in longitudinal section. Scale 0·5 μm.

FIGURE 24. As figure 23, from the same section. Scale 0·5 μm.

FIGURE 25. Transverse section of the 'tendon' region of the muscular receptor, showing dendrite branches and what are believed to be dendrite fingers, in the connective tissue. Scale 0·5 μm.

FIGURE 26. Transverse section of the thoracico-coxal chordotonal organ, showing an isodynal scolopidium cut at the level of the ciliary segments. Scale 0·5 μm.

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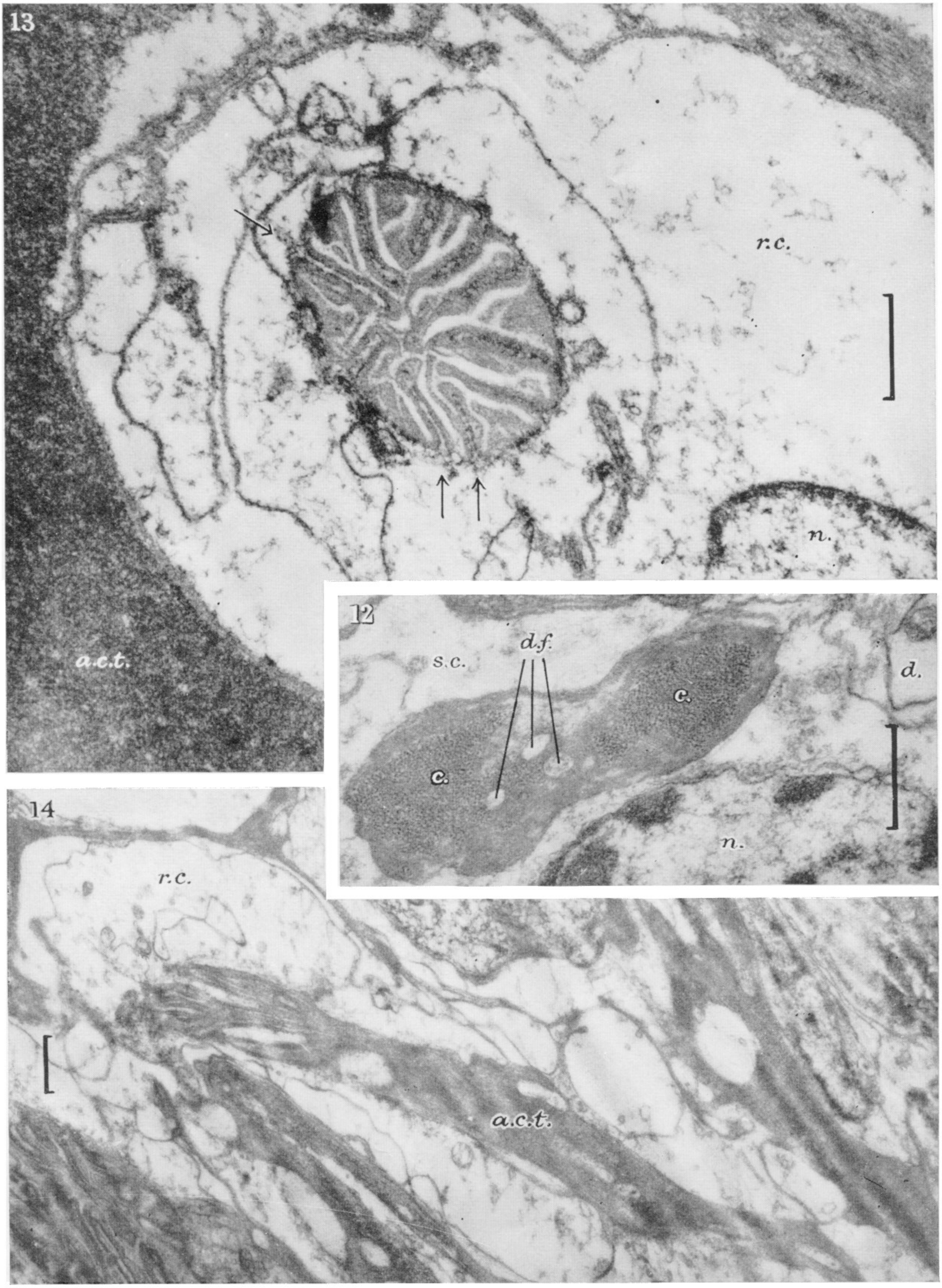

Connective tissue

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Dendrites of the *S* and *P* fibres in *Carcinus* muscular receptor

Anterior to the left

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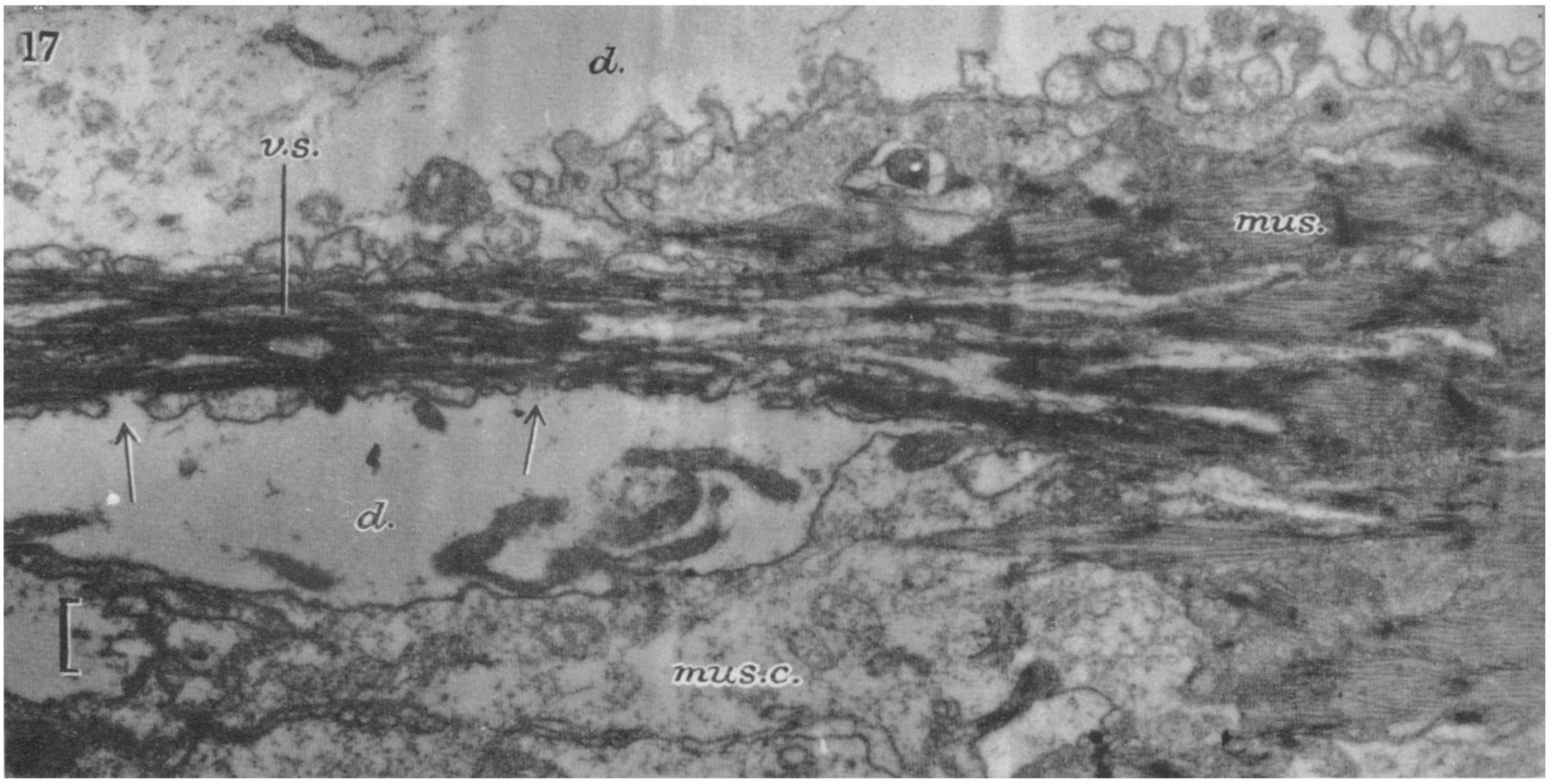

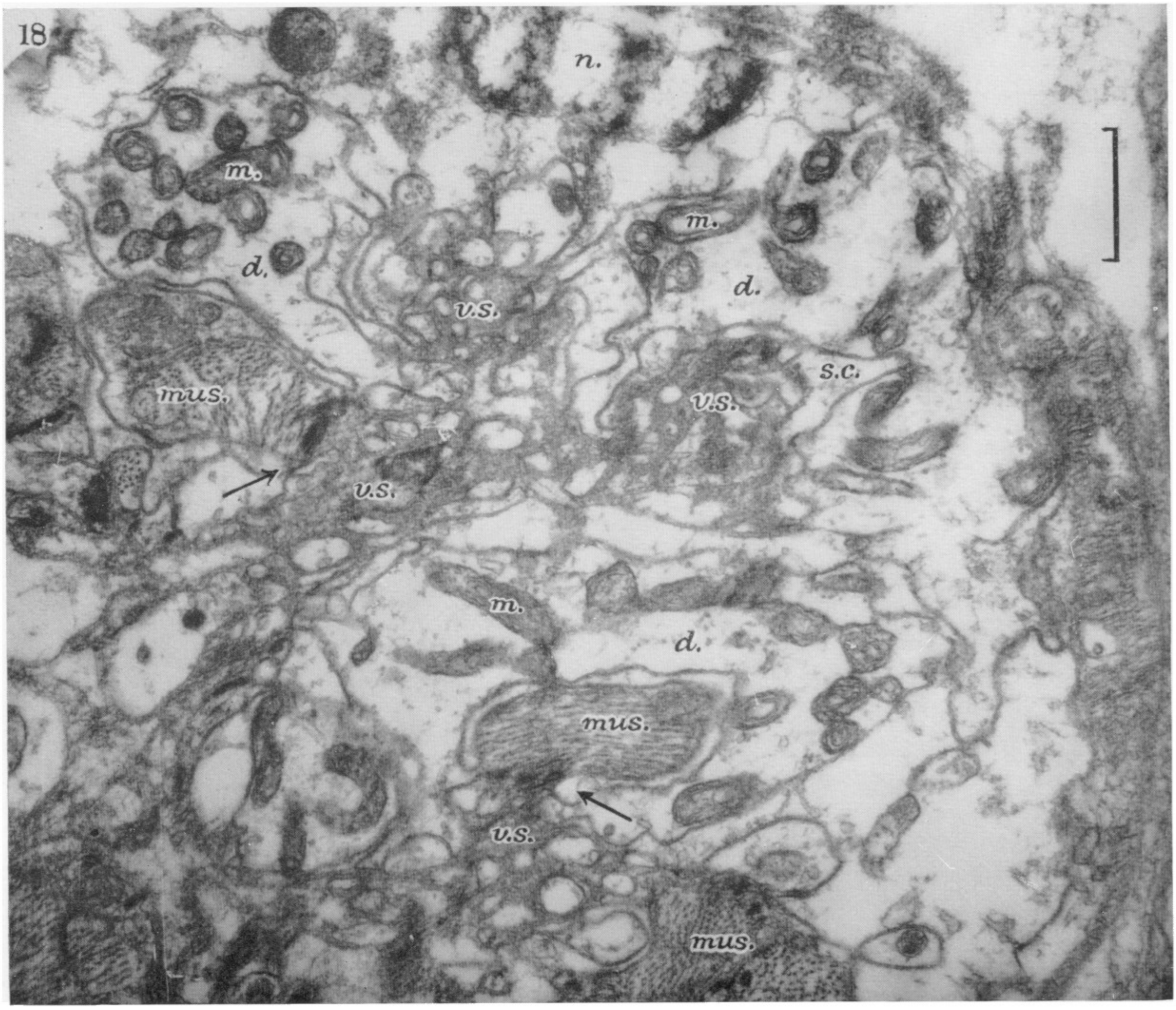

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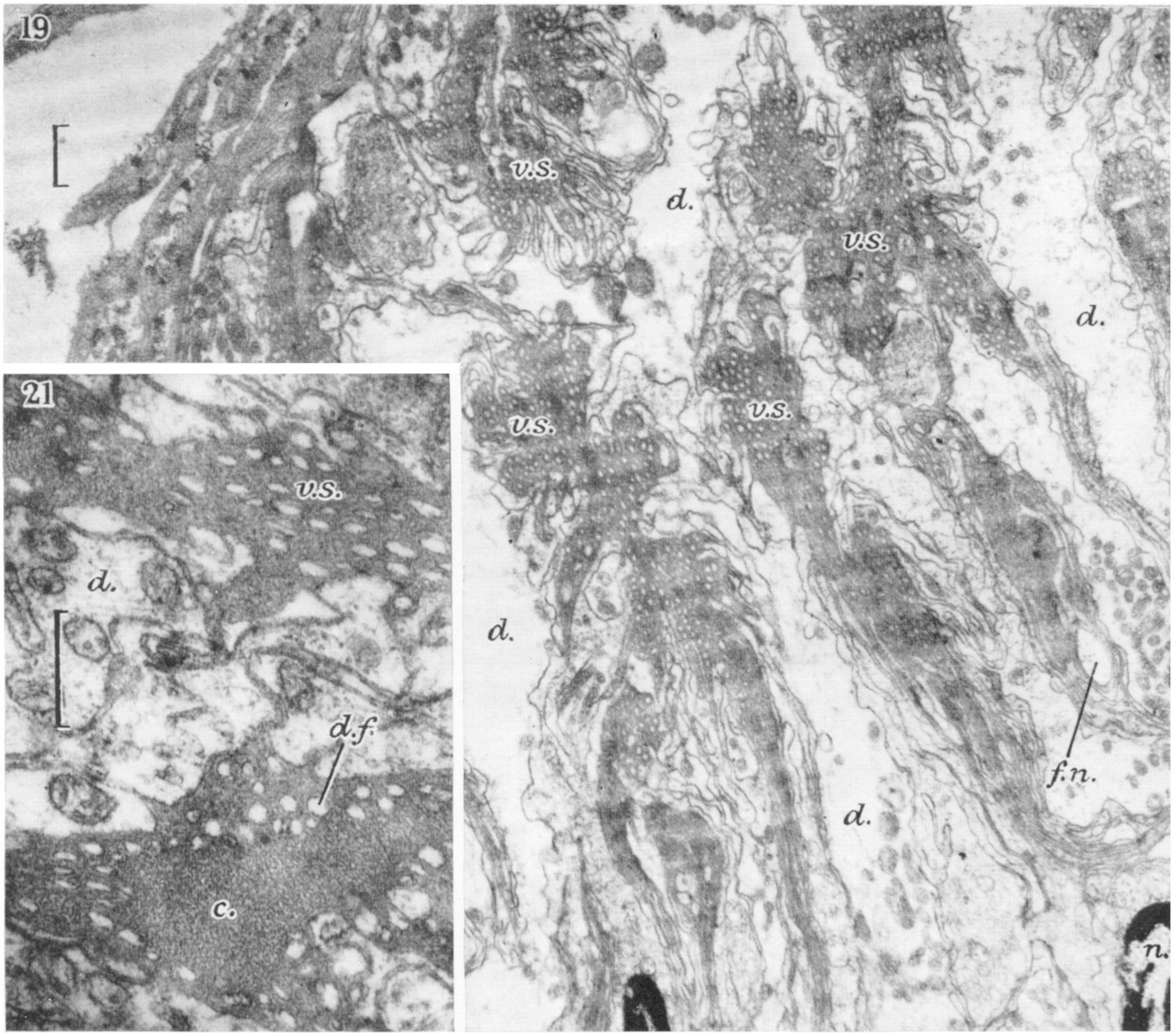
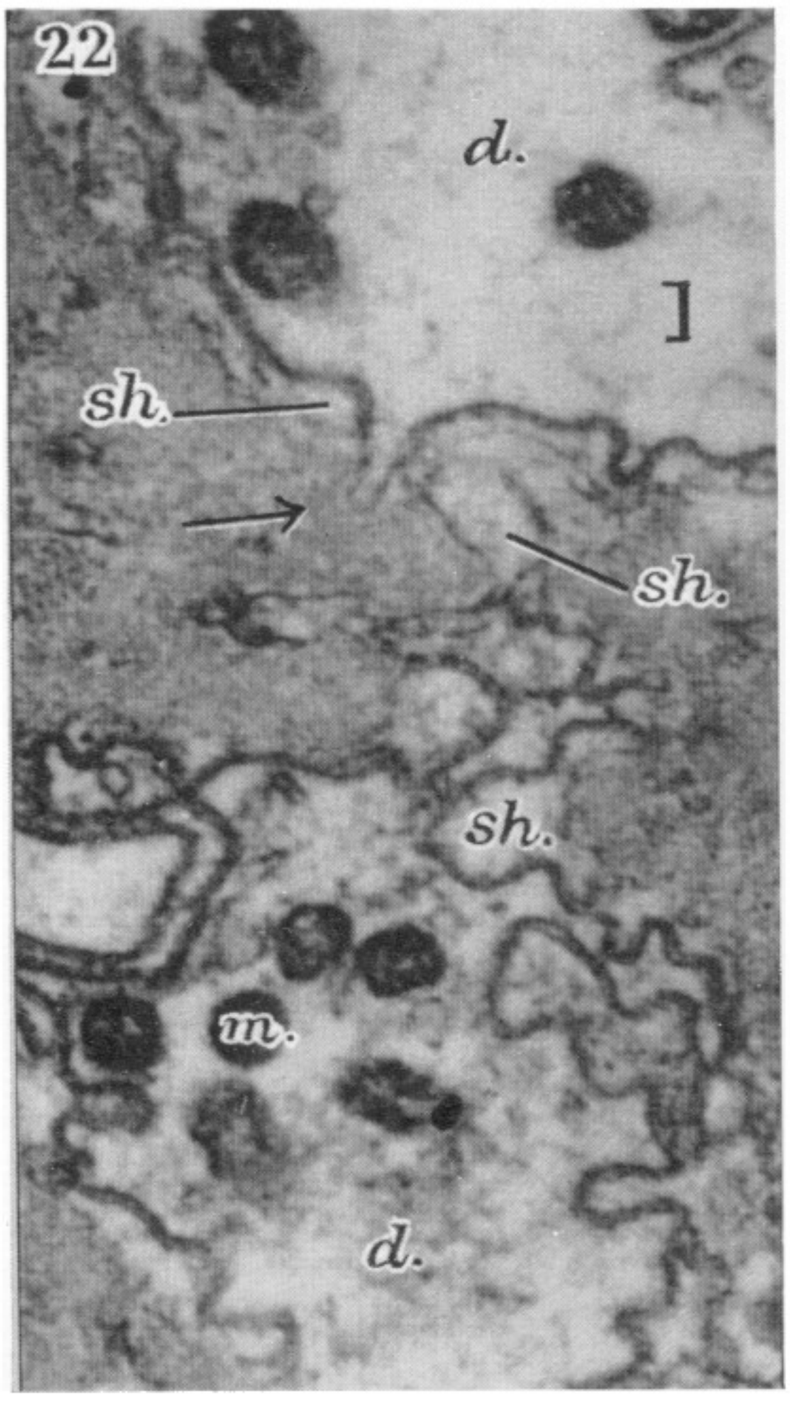


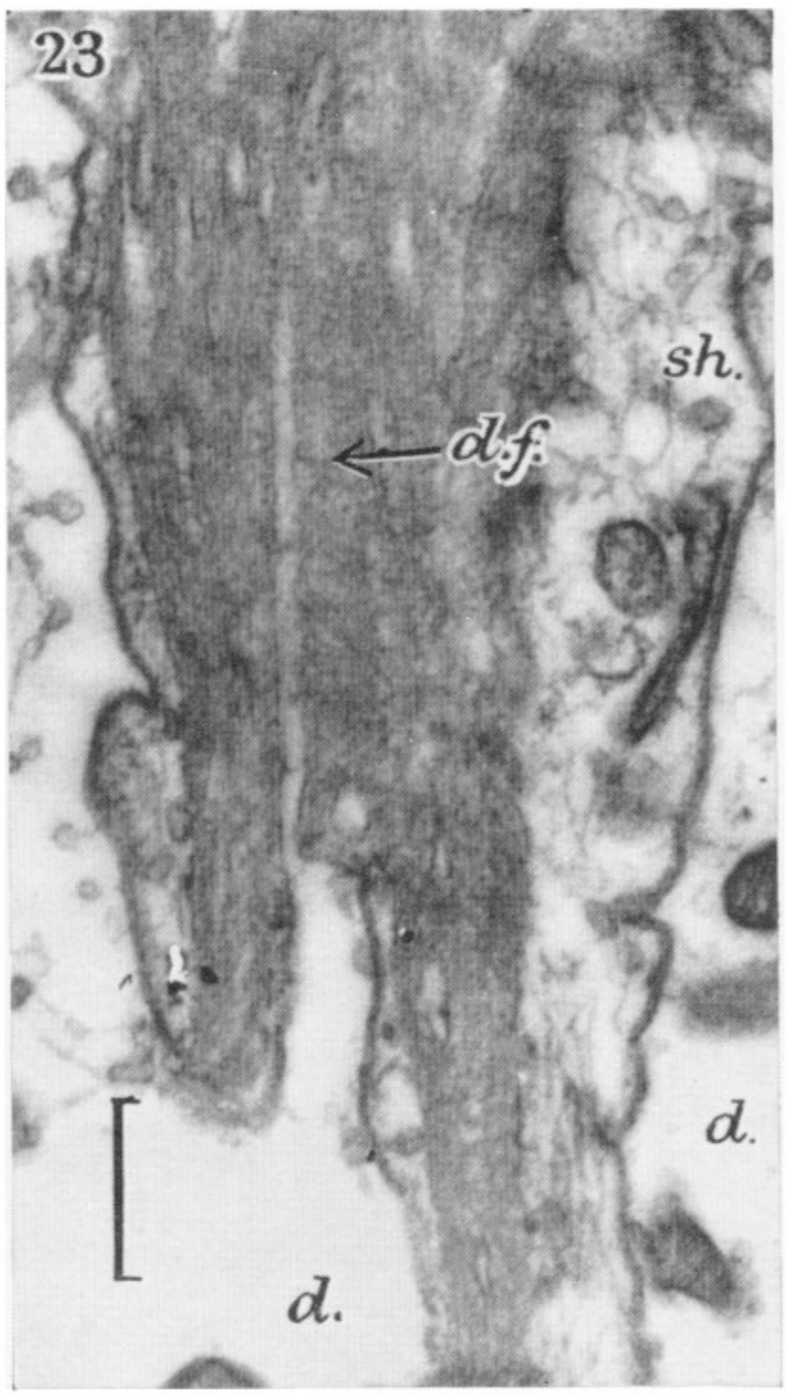
Anterior to the left, approximately

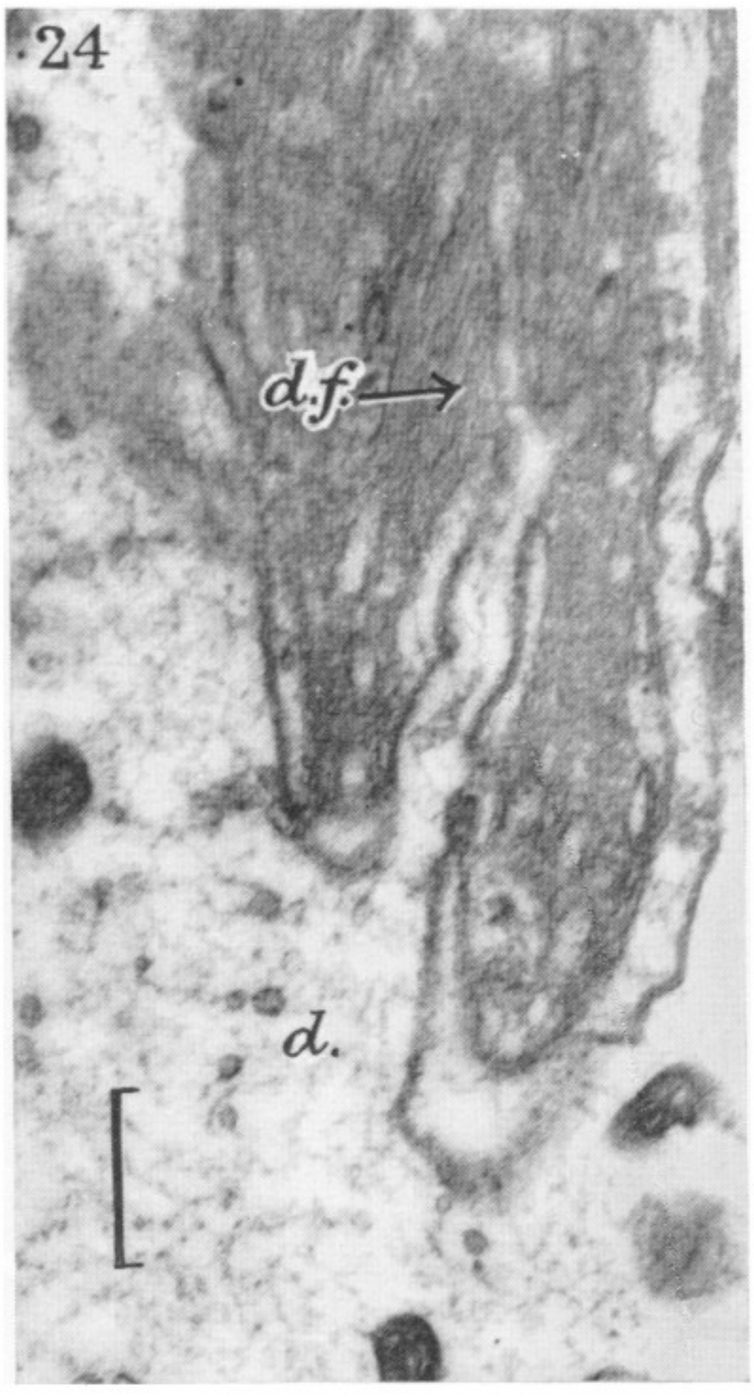
FIGURE 19. Transverse section of the 'tendon' region of *Pagurus* muscular receptor. Scale 1 μm.

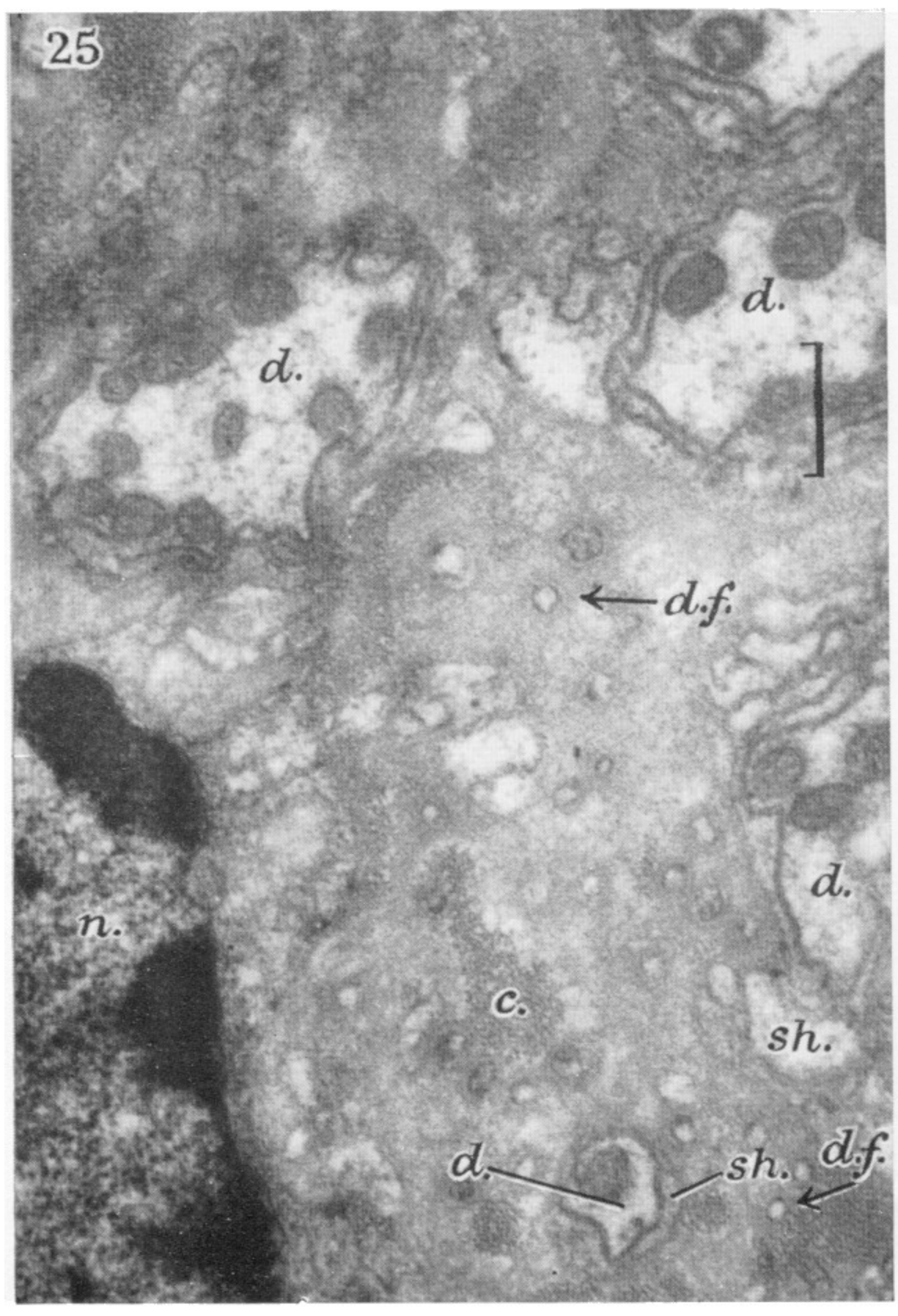
FIGURE 20. Transverse section of the levator receptor of *Carcinus*, at the point of entry of the more distal fibre. Scale 1 μm.

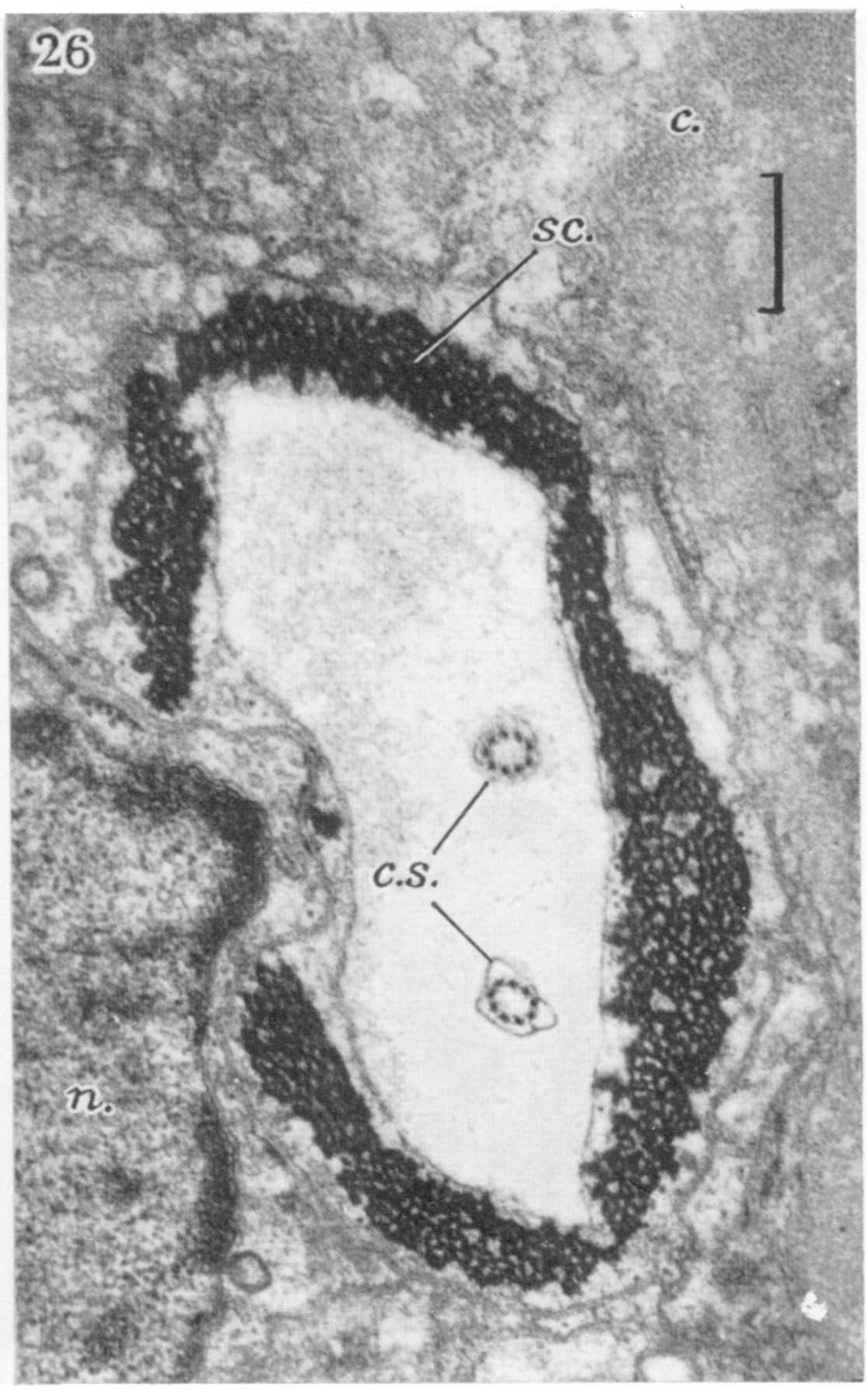
FIGURE 21. Transverse section of vacuolated strings of the depressor receptor of *Pagurus*. Scale 0·5 μm.











Muscular receptor and chordotonal organ of *Astacus*

FIGURE 22. Transverse section of the 'tendon' region of the muscular receptor, showing a dendrite finger (arrowed) entering the connective tissue. Scale 0·1 μm.

FIGURE 23. Similar, but in longitudinal section. Scale 0·5 μm.

FIGURE 24. As figure 23, from the same section. Scale 0·5 μm.

FIGURE 25. Transverse section of the 'tendon' region of the muscular receptor, showing dendrite branches and what are believed to be dendrite fingers, in the connective tissue. Scale 0·5 μm.

FIGURE 26. Transverse section of the thoracico-coxal chordotonal organ, showing an isodynal scolopidium cut at the level of the ciliary segments. Scale 0·5 μm.