THE STRUCTURE AND INNERVATION OF THE NUCLEAR BAG MUSCLE FIBRE SYSTEM AND THE NUCLEAR CHAIN MUSCLE FIBRE SYSTEM IN MAMMALIAN MUSCLE SPINDLES

By I. A. BOYD

Institute of Physiology, University of Glasgow

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CONTENTS

1. The structure and innervation of muscle spindles from normal, de-afferented and de-efferented muscles of the cat hind limb were studied. The spindles were either completely isolated by micro-dissection, or were serially sectioned transversely.

2. All spindles contain two distinct types of intrafusal muscle fibre, 'nuclear bag fibres' and 'nuclear chain fibres', which differ in structure and innervation.

3. Nuclear bag muscle fibres, usually two per spindle, are less than half the diameter of extrafusal fibres, and each contains numerous large nuclei packed together in the equatorial region of the spindle. Nuclear bag fibres practically never branch. The fibres contain numerous myofibrils uniformly distributed in cross-sections, and relatively little sarcoplasm; they atrophy very slowly after the ventral spinal roots are cut. Several small motor nerve fibres (γ_1 fibres) enter each spindle and terminate in a number of discrete motor end-plates on the nuclear bag muscle fibres. These γ_1 end-plates lie in a group at each spindle pole and long lengths of nuclear bag fibre are free of motor innervation.

4. Nuclear chain muscle fibres, usually four per spindle, are about half the length and diameter of nuclear bag fibres in spindles in the leg muscles. The nuclear chain fibres in spindles from the small muscles of the foot may, however, equal the nuclear bag fibres in length, and in diameter beyond the ends of the lymph space. Each nuclear chain fibre contains a single row of central nuclei in the equatorial region; the fibres occasionally branch, but often none of them do so. They contain fewer myofibrils per unit area, irregular in size and distribution, and relatively

more sarcoplasm, than nuclear bag fibres. Nuclear chain fibres atrophy nearly as rapidly as extrafusal fibres after the ventral roots are cut. A number of very fine motor nerve fibres (γ_2 fibres) enter each spindle and terminate in a network of fine axons and small nerve endings (the 'γ_2 network') situated on the nuclear chain muscle fibres in most regions other than the nuclear region.

5. All spindles receive both γ_1 and γ_2 innervation, γ_2 fibres forming slightly more than half of the total number of motor fibres which varies from seven in simple spindles in phasic muscles to twenty-five in the most complex spindles in tonic muscles. Both γ_1 and γ_2 fibres remain intact after dorsal root transection and degenerate following ventral root transection. The histological evidence supports the view that the γ_1 and γ_2 nerve fibres at the spindles are derived from two types of stem fibre, neither of which belongs to the α group.

6. Each spindle has one primary sensory nerve ending, supplied by one group I*a* afferent nerve fibre, and from zero to five secondary sensory nerve endings, each supplied by one group II afferent nerve fibre. The primary sensory terminations lie on both nuclear bag and nuclear chain muscle fibres. The secondary sensory terminations lie predominantly on the nuclear chain muscle fibres. In spindles with several secondary sensory endings, their terminations may lie on the same region of nuclear chain fibres as motor endings of the γ_2 network.

7. In general, spindles in tonic muscles have more secondary sensory endings and motor nerve fibres and endings than those in other muscles. Nuclear chain intrafusal fibres are probably functionally 'slower' than nuclear bag intrafusal fibres, while both types are 'slower' than extrafusal fibres. Both nuclear chain fibres and nuclear bag fibres, however, probably show a gradation in activity related to the nature of the muscle in which they lie.

The reader is advised to study figure 33 and its legend first, at the same time studying the plate figures to which reference is made in figure 33*b*, then to read the portions of the Results in italics consecutively followed by the Discussion, finally studying the detailed Results. Further details of many of the illustrations and tables are available for reference in the Archives of the Royal Society.

Introduction

The structures in skeletal muscle first described by Kölliker (1862) and named muscle spindles by Kühne (1863) have been the subject of many investigations since that time. The best descriptions of normal mammalian spindles are those of Sherrington (1894), who described the structure, Ruffini (1893, 1898) who described the innervation, and Barker (1948), who gave a detailed account of structure and innervation.

A number of workers attempted to differentiate the sensory from the motor innervation by degeneration experiments. The ventral spinal roots were cut by Onanoff (1890, dog) who observed degeneration of only a few spindle nerve fibres, by Sherrington (1894, cat) who showed that the large myelinated fibres from spindles remained intact, by Hinsey (1927, cat) who removed the lumbar sympathetic trunk in addition and found primary and secondary sensory endings intact in the spindles, and by Hines & Tower (1928, cat) who confirmed that the spiral 'equatorial ending' was sensory.

The dorsal spinal roots were cut by Onanoff (1890) who found few fibres left in the spindles, by Hinsey (1927) who removed the lumbar sympathetic trunk in addition and found intact small myelinated fibres and motor end-plates at the extremities of spindles, by Hines & Tower (1928) who found that a 'polar ending' unlike extrafusal motor end-plates remained intact, and by Cuajunco (1932, cat) who found small fibres with long lengths of unmyelinated axon cylinder and small end-plates.

Both ventral and dorsal roots together were cut by Boeke (1927, cat) who found degenerating motor endings in spindles shortly thereafter, by Hinsey (1927) who found no

nerve fibres left except groups of non-myelinated fibres associated with blood vessels in the spindle capsule, and by Hines & Tower (1928) who found no innervation left in the spindles at all.

The evidence in all these investigations is given in text descriptions and some good drawings, but photographic evidence is scanty and shows little detail. Barker (1948, rabbit) attempted to relate the nerve endings in normal spindles to the intrafusal muscle fibres on which they lie. He confirmed the findings of Ruffini (1898) that spindles had a primary ending and from zero to two secondary endings, and found intrafusal motor end-plates similar in form to extrafusal end-plates. He also stated that individual intrafusal fibres each contained a 'nuclear bag'.

Cooper & Daniel (1949) and Cooper, Daniel & Whitteridge (1955) found that the intrafusal fibres in muscle spindles in human extrinsic eye muscles had some central nuclei but never a nuclear bag, whereas those in eye muscle spindles from sheep and goats did have nuclear bags. Cooper & Daniel (1956) described spindles in the small muscles of the human hand; they contained intrafusal fibres some of which had a nuclear bag, while others had a myotube of central nuclei, in the equatorial region. Boyd (1956) stated that the intrafusal fibres in spindles in the tenuissimus muscle of the cat were of two distinct sizes, differing in length and diameter. The fact that intrafusal fibres vary greatly in diameter had been noted by earlier workers (Sherrington 1894; Huber & de Witt 1898; Cuajunco 1927). Boyd (1958*a*) said that the large fibres contained nuclear bags while the small fibres contained a chain of nuclei down the centre, and that they represented two distinct types of intrafusal fibre with differing innervation, which was extremely complex in normal spindles.

Coers & Durand (1956) studied the distribution of cholinesterase in spindles and on the basis of the fact that the only part of the spindle free of cholinesterase was the region of the primary (annulo-spiral) ending deduced that the secondary (flower-spray) endings, hitherto described as sensory, were probably motor in function.

The investigation of which a detailed report is given in this paper involved the study of the structure and innervation of spindles before and after degeneration of their afferent or efferent nerve fibres and nerve endings, and the presentation of the evidence as far as possible in photographic form with drawings to serve as keys to the photographs. In particular, it was an attempt to obtain answers to the following questions:

1. Do all, or only some, spindles from the limb muscles contain two distinct types of intrafusal muscle fibre?

2. Are the secondary endings adjacent to the primary ending sensory, as stated by earlier workers, or motor as suggested by Coers & Durand (1956)?

3. Is any of the extensive innervation further towards the spindle poles sensory, as suggested by Ruffini (1898)?

4. Does the inflow in afferent fibres arise in nerve endings on one or on both types of intrafusal muscle fibre?

5. Do the two types of intrafusal fibre have a separate motor innervation arising from different types of stem fibre, consistent with the concept, suggested by Boyd (1958*a*) on the basis of an examination of normal spindles, that the small muscle fibres are 'slow' fibres and the large muscle fibres are 'twitch' fibres?

Preliminary results have been published (Boyd 1959, 1960, 1961, 1962*a*). During this investigation relevant information about normal spindles (see Discussion) has been obtained by Barker and his associates (1959, 1960) and by Swett & Eldred (1960*a*, *b*).

Methods

Procedure for spinal root section

Cats were anaesthetized with pentobarbitone sodium (Nembutal) either by intravenous injection into a forelimb vein, or, in later experiments, by intraperitoneal injection. Under aseptic conditions spinal laminectomy was performed on one side between segments *L*4

Table 1. The extent of denervation which was achieved by the operations on the spinal roots

(*a*) Dorsal roots *L*5 to *S*2 cut

			checks on root section					
			1	2		3	4	
				compound a.p. on stim. of:				
cat no.	weight (kg)	degen. time (days)	T.S. spinal roots for gang. cells	D.R.	V.R.	extent of root section from plexus	muscle receptors	extent of de-afferentation
1	2·2	6	absent	—	—	—	absent	complete
2	2·3	4	present (*L*6 only)	—	—	—	degenerating	incomplete
3	2·8	4	absent	—	—	—	degenerating	complete
4	2·0	3	absent	—	—	—	degenerating	complete
5	2·5	6	present (*L*6 only)	—	—	—	present (absent from soleus)	incomplete (soleus complete)
6	2·4	5, 225	absent	absent	normal	complete	absent	complete
7	2·3	4, 110	absent	—	—	—	absent	complete
8	2·7	45	absent	absent	normal	complete	absent	complete
9	2·6	56	absent	absent	normal	complete	absent	complete
10	2·6	35	present (*L*5, *S*1)	present (*S*1 only)	normal	complete	present	incomplete
11	2·4	58	absent	absent	normal	complete	absent	complete

(*b*) Ventral roots *L*5 to *S*2 cut

			checks on root section					
			1	2		3	4	
				compound a.p. on stim. of:				
cat no.	weight (kg)	degen. time (days)	T.S. spinal roots—V.R. removal	V.R.	D.R.	extent of root section from plexus	extrafusal end-plates	extent of de-efferentation
12	2·0	5, 247	—	present (*L*5, 6, 7)	normal	*L*6, 7 incomplete	present	incomplete
13	2·4	5, 160	—	present (*L*6, 7)	normal	*L*5, 6 incomplete	present (a few)	incomplete
14	2·7	83	complete	absent	normal	complete	absent	complete
15	2·5	62	complete	absent	normal	complete	absent	complete
16	2·8	48	complete	—	—	complete	absent	complete

and *S*2, leaving the vertebral spines intact. Spinal roots *L*5 to *S*2 were exposed and the division between dorsal and ventral roots was located central to the dorsal root ganglion. In cats 1 to 11 (see table 1) the dorsal roots were transected central to the ganglia, which

were removed with as much of the dorsal roots distal to them as could be obtained without extensive damage to ventral root fibres (5 to 10 mm in all). The excised pieces were fixed in Bouin's fluid. In cats 1 to 5 the ganglia of $L6$ to $S2$ inclusive were removed; the ganglion of $L5$ was removed in addition in cats 6 to 11. In the ventral root section experiments (cats 12 to 16) a length of 5 to 10 mm of each ventral root underlying the dorsal root ganglion was removed and fixed in osmic acid. The animals were allowed to recover.

After degeneration times varying from 3 days to 8 months the cats were killed and the spindles from a variety of hind-limb muscles were examined. In cats 1 to 4 the hind limbs were perfused with methylene blue and then stained spindles were dissected from the tenuissimus muscle. In cats 4 to 16 a number of muscles were stained with gold chloride after removal from the animal, and whole spindles were isolated completely under a dissecting microscope. Many spindles from twenty other normal cats were also examined by one or other of these two methods.

Four or five days after the initial operation on cats 6, 7, 12 and 13 a second operation was performed in which the soleus muscle was removed and examined for spindles with nerves in the process of degeneration, and the animals were allowed to recover. Thus, there are two degeneration times in table 1 for these experiments.

Certain muscles from both the denervated and normal hind limbs of cats 6, 8 and 15 were fixed in 12% formalin and embedded in paraffin wax. Also, the hind limbs of two normal cats were perfused with Heidenhein's Susa fixative and some of the muscles were then removed and embedded in wax. Serial transverse sections of 6 or 10 μ thickness of all these muscles were cut and stained either with haemalum and eosin or by Masson's trichrome method.

Checks on the extent of denervation

It was important to know whether all the afferent nerve fibres (cats 1 to 11), or all the efferent nerve fibres (cats 12 to 16), were cut at the time of operation. If even a few fibres were left uncut then the sensory and motor innervations of the spindles could not be differentiated with certainty. With the gold chloride method, only a few spindles in each muscle were uniformly well impregnated, so there had to be no error in the de-afferentation or de-efferentation. This was particularly important because of the conflicting evidence on the nature of the 'flower-spray' endings of Ruffini (1898) and the 'diffuse ending' of Cooper (1960). A number of checks on the extent of denervation were carried out and the results for each experiment are given in table 1.

(1) *Sectioning of spinal roots*

After every operation in which the dorsal root ganglia were removed, the excised portions of each root were serially sectioned transversely and examined for ganglion cells. In every case, except in cats 2, 5 and 10, a length distal to the ganglion of at least 200 μ of each root containing no ganglion cells was excised in addition to the ganglion itself; the length of the excised portions clear of ganglion cells was usually 0·5 to 1·5 mm. It was difficult to remove all the ganglion cells in $L5$ and $L6$ because of the short length of the root in the spinal canal, and in cats 2, 5, 10 the excised portions of one or other of these roots contained cells at the peripheral end, as was the case in $S1$ in cat 10, also.

To make certain that this procedure was a satisfactory test for complete de-afferentation,

the remaining parts of each root were removed *post mortem* from cats 9, 10 and 11. Transverse sections through the remains of the spinal roots, at a level corresponding to the point of maximum diameter of the root ganglion, contained no cells, showing that the entire dorsal root had been removed. Serial transverse sections through the peripheral stump of the dorsal root, and the ventral root, confirmed that no ganglion cells were left in the root distal to the position of the ganglion in cats 9 and 11, and that the damage to the ventral roots was small, respectively.

In the experiments in which the ventral roots were cut, the excised parts were sectioned transversely and in all cases they appeared to be complete. This check proved inadequate, however, for other checks revealed that in cats 12 and 13 a complete small ventral root fasciculus had been left intact. In cats 14, 15 and 16, therefore, greater care was taken to find all the ventral root fasciculi at the time of operation. Also, the remaining parts of the spinal roots were removed *post mortem* and transverse sections at the level of the dorsal root ganglion confirmed that no part of any ventral root had been left uncut at the time of operation.

(2) *Compound action potentials in muscle nerves*

Cats 6 and 8 to 15 were allowed to survive after the operation for times sufficiently long for nerve fibres which were cut at the operation to degenerate completely. Then the animals were anaesthetized with Nembutal, the spinal canal was opened from $L4$ to $S2$, and all the ventral and dorsal roots on the operated and normal sides were cut centrally and placed on electrodes in a paraffin pool. The tenuissimus and soleus nerves were exposed in further paraffin pools over the back of each leg; the nerves were cut close to the muscles and were placed on recording electrodes. The compound action potential was recorded in each of these nerves in response to stimulation of dorsal roots $L5$ to $S2$ of the appropriate side, individually and together. The process was repeated for the ventral roots. In a small nerve like the nerve to the tenuissimus muscle an action potential in a single fibre of large diameter can be detected easily when recording is carried out from the whole nerve.

In cats 6, 8, 9 and 11, in which the dorsal roots were cut, no action potential (a.p.) was recorded when the dorsal roots on the operated side were stimulated. After all the limb muscles had been denervated to prevent twitching a potential of magnitude similar to that obtained on the normal side was recorded when ventral roots $L5$ to $S2$ on the operated side were stimulated together. This showed that damage to the ventral roots at the time of operation was small. In cat 10, a small a.p. was recorded when dorsal root $S1$ on the operated side was stimulated, showing that some large afferent fibres were intact in the nerve.

In cats 14 and 15, no twitching of any muscles occurred, and no a.p. was recorded in the nerves on the operated side, when the ventral roots were stimulated. The a.p. recorded when the dorsal roots were stimulated was similar to that obtained on the normal side. In cats 12 and 13, however, twitching of muscles did occur when the ventral roots on the operated side were stimulated, while potentials of some magnitude were recorded from the tenuissimus and soleus nerves when any one of ventral roots $L5$, $L6$, $L7$ in cat 12, and $L6$ and $L7$ in cat 13, was stimulated.

This method of checking the denervation was not used in cat 7, which died about 3 months after operation, and in cat 16 in which the hind limbs were perfused with formalin so that the muscle nerves were obtained in good condition for histological examination.

(3) *Dissection of lumbar plexus*

The complete lumbar plexus was dissected out from most animals *post mortem* and the roots examined. If large parts of the roots were not cut, this was detected, e.g. cats 12 and 13, but this method of checking was not satisfactory if only a small portion of root was left uncut, e.g. cat 10, in which de-afferentation appeared to be complete on visual examination of the plexus.

(4) *Nerve endings in muscle*

It was established by several previous workers that tendon organs and the primary (annulo-spiral) nerve endings in spindles are sensory. The presence of even one intact tendon organ or primary sensory ending in the muscles proved that de-afferentation was not complete. This proved to be an excellent test, since numerous well stained tendon organs are encountered during teasing of all normal muscles stained with gold chloride (except the tenuissimus muscle). The absence of end-plates on the extrafusal muscle fibres was a good test of successful de-efferentation since end-plates are numerous and stain readily in normal muscle.

The satisfactory nature of methods 1, 2 and 4 for checking the extent of denervation is shown by the fact that in any experiment in which some roots were incompletely cut, this was revealed by all of these tests (table 1). Results from cats 2, 10, 12 and 13 were used only to confirm those obtained from the other animals. In cat 5, the de-afferentation of the soleus muscle was considered to be complete since only a few ganglion cells were left in $L6$ and none in $L7$ and $S1$, and no tendon organs or spindle primary sensory endings were found in the soleus muscle.

Staining methods

(1) *Methylene blue*

The method has been described previously (Boyd 1958*c*). Results obtained by the use of this method are included in the tables and histograms, but only gold-stained preparations are shown in the illustrations of isolated spindles since they provided better contrast for photographic purposes.

(2) *Gold chloride*

Several modifications of standard gold-staining techniques were employed. The method consists essentially of teasing the tissue, fixing with dilute formic acid, staining with gold chloride, reducing the gold, and then clearing the specimen in glycerine. Each stage of the method as outlined by Gairns (1930) was investigated in some detail to determine which stages required the most critical conditions. In particular, a method of reducing the gold by artificial light, similar to the development of a photographic print, was evolved. By this means it was possible to obtain uniform staining throughout the whole length of a muscle spindle. Full details of the method are given elsewhere (Boyd 1962*b*).

Results

The results are based on the examination of 78 muscle spindles which were serially sectioned transversely, and of 508 whole muscle spindles which were stained and then isolated by dissection from the rest of the muscle. The spindles were obtained from the hind-limb muscles of 36 cats. In 11 of these the afferent nerve fibres and nerve endings had degenerated after removal of certain of the dorsal spinal root ganglia, and in 5 cats the motor nerve fibres and nerve endings had degenerated after removal of a portion of the ventral spinal roots. The spindles in the soleus and tenuissimus muscles of the leg, and those in the small muscles of the foot, were studied in detail. In addition, a few spindles from the biceps femoris, gastrocnemius, extensor digitorum longus and tibialis anterior muscles were examined.

Muscle spindles consist of a varying number of specialized muscle fibres contained within a connective tissue sheath. About two-thirds of the myelinated afferent and efferent fibres in nerves to skeletal muscle innervate the spindles. In part I, the structure and arrangement of the intrafusal muscle fibres is described. In part II, details of the sensory and motor innervation of spindles are given. In part III, the distribution of spindles within certain muscles is described.

Part I. Structure and arrangement of intrafusal muscle fibres

All spindles in the muscles studied in this investigation contained two distinct types of intrafusal muscle fibre. The two types of muscle fibre may be distinguished by the arrangement of the nuclei which the fibres contain at the equator of the spindle, by the relative number of myofibrils per unit area of cross-section of each intrafusal muscle fibre, and by differences in the diameter and length of the muscle fibres.

(1) *Nuclear arrangement*

Intrafusal muscle fibres, like extrafusal skeletal muscle fibres, are multinucleated. A number of small, darkly staining nuclei are scattered along the length of each fibre, mostly at the periphery. As the intrafusal fibres enter the lymph space, additional centrally placed nuclei appear in each fibre, similar to those in the myotubes of developing skeletal muscle fibres, and these nuclei become more closely alined as the lymph space approaches its maximum diameter. At this point, some of the intrafusal fibres are packed full of nuclei, forming the 'nuclear bag'. This is shown in the diagrammatic reconstruction of spindles in figure 1. The intrafusal fibres marked with capital letters each contain a 'nuclear bag'. A transverse section through any such intrafusal fibre at this point contains three to five large nuclei completely filling the fibre. This is shown in the fibres marked '*n.b.*' in the spindles in figures 36, 40, 44, 49, plate 42. Serial transverse sections reveal the position and extent of each nuclear bag. Alternatively, isolated whole spindles, in which the sensory endings have degenerated following section of the dorsal spinal roots, often show the nuclear bags clearly (figure 73, plate 49; figure 98, plate 52). A fibre with a nuclear bag is rarely larger in diameter at the bag than elsewhere along its length, so that individual intrafusal fibres are not fusiform. The shape of an intrafusal fibre depends, to some extent, on whether fixation of the muscle is carried out when it is extended or relaxed.

Not all the intrafusal fibres, however, contain a nuclear bag. Some fibres, as they traverse the lymph space, contain nuclei arranged in a single central row, as shown diagrammatically in the numbered fibres in the spindles of figure 1. At no point along the length of such a fibre does a transverse section contain more than one nucleus, unless the section is so thick that it includes two nuclei out of the row; if these are slightly out of line, the fibre will appear to have two nuclei in one section. Fibres with a 'nuclear chain' can be seen in figure 36, 40, 44, 49, plate 42 (marked *n.c.*). A complete nuclear chain can be seen in one of the intrafusal fibres of the de-afferented spindle in figure 73, plate 49.

The two types of intrafusal fibre were present in all the spindles in all the muscles which were studied. Invariably the two types can be distinguished by the distinct difference in their nuclear arrangement described above. They are classified, therefore, as 'nuclear bag fibres' and 'nuclear chain fibres'. A classification in terms of size is less satisfactory since there are differences in length and diameter of the two types of fibre in muscles from different sites.

(2) *Myofibril density*

Nuclear bag fibres and nuclear chain fibres may also be distinguished by the difference in their staining properties in transverse sections of spindles. The difference is most marked when the fibres are stained with Masson's method, particularly in spindles in which the nuclear chain fibres are large in diameter. In this case, the nuclear bag fibres stain almost uniformly dark while the nuclear chain fibres have a stippled appearance, as shown in figures 54 to 57, plate 42, and figure 60*l*, *r*, plate 45. The staining difference is less obvious when sections of spindles are stained with haemalum and eosin, as shown in figures 37, 39, 45, plate 42, and figure 59*b*, plate 44. The difference is due to the fact that the *myofibril density is greater in the nuclear bag fibres* (*i.e. they are 'sarcoplasm poor'*) *than in the nuclear chain fibres* (*i.e. they are 'sarcoplasm rich'*).

The nuclear bag fibres are filled with numerous myofibrils of uniform size, uniformly distributed throughout the sarcoplasm. In cross-sections under the light microscope, the myofibrils show as closely packed dark dots. The individual myofibrils can occasionally be resolved in good sections under an oil-immersion lens, e.g. this was possible in the section in figure 60*l*, plate 45.

In the nuclear chain fibres the myofibrils produce the stippled appearance, clear regions of sarcoplasm separating individual myofibrils which show as dark areas. The dark areas vary greatly in size, but are much larger and much less numerous than the black dots in nuclear bag fibres.

That the staining differences described above for intrafusal fibres are not due to uneven staining is shown by the fact that the darker staining intrafusal fibres may be traced through serial sections quite distinct from the other intrafusal fibres.

(3) *Structure of individual spindles*

A description of the structure of several spindles, as observed in serial transverse sections, is given below. Five spindles are described: a normal spindle and a de-efferented tandem spindle from the muscles of the hind leg; a normal spindle, a de-efferented spindle, and a de-afferented spindle from the small muscles of the hind foot. Reconstructions of these spindles are drawn in figure 1. The diameter of the intrafusal fibres in transverse sections

at various points in each spindle is correctly represented, as is the length of each fibre. The position of the nuclei relative to the length of each fibre, and their diameter in relation to the diameter of the fibre, are approximately correct. But the actual number of nuclei in the spindles themselves is much greater than the number drawn in the figure. The different transverse and longitudinal scales made it impossible to put all the nuclei in the drawings. The position and length of the nuclear bags, where present, are depicted correctly in the figure. The extent of the lymph space and the total length of the sheath are approximately correct.

The sections which best showed the principle features of each spindle were drawn and are shown in figures 2 to 6. The lettered transverse lines in figure 1 show the position in the spindle of the sections which were drawn. The heavy transverse lines indicate the position of sections of which both drawings and photographs are reproduced. The photographs are shown in figures 58 to 62, plates 43 to 47, and are lettered to correspond with the labelling of sections in figure 1. The key to any photograph in a plate-figure is the drawing in the corresponding text-figure which has the same letter. Although only some transverse sections of each spindle are shown in the illustrations, the intrafusal fibres were traced through all the intervening serial sections.

I. *Tenuissimus muscle spindle, normal.* (*Figure* 1, *spindle I. Figure* 2 *and figure* 58, *plate* 43: *H. & E. staining.*) This spindle contains two nuclear bag fibres and four nuclear chain fibres, one of which divides into two as it traverses the lymph space. The nuclear bag fibres are about twice the length and twice the diameter of the nuclear chain fibres, and the spindle sheath is about the same length as the nuclear chain fibres. This spindle is typical of most spindles in the muscles of the leg, except that division of a nuclear chain fibre in the nuclear region is rare. It is just possible that fibre 1 *a* was a short fibre like fibre 3 of spindle IV.

The course of the individual muscle fibres in the spindle may be traced by following the lettered and numbered fibres in the drawings of transverse sections. At each end of the spindle the sections contain the two nuclear bag fibres only. The nuclear chain fibres appear between sections *c* and *e* at one end, and between sections *u* and *r* at the other. Sections *g* and *h* clearly contain only four nuclear chain fibres, while section *o* contains five such fibres, fibre 1 having divided into two. Sections *j* to *m* pass through the nuclear region, and the nuclear bags in fibres *A* and *B* can be seen in sections *k* and *l*.

II. *Soleus tandem muscle spindle, de-efferented* 62 *days; cat* 15. (*Figure* 1, *spindle II. Figure* 3 *and figure* 59, *plate* 44: *H. & E. staining.*) This spindle contains two nuclear regions (sections *e* and *r*). It has three nuclear bag fibres only one of which (*B*) is common to the two nuclear regions. There are seven nuclear chain fibres much shorter than the nuclear bag fibres, divided into two groups. Fibres 1 to 5 are associated with the principal part of the spindle, fibres 6 and 7 with the subsidiary part. Both ends of the nuclear bag fibres were contained in parts of the muscle in separate paraffin blocks from that containing the rest of the spindle, and the ends of the fibres could not be identified. The intrafusal fibres of this spindle do not divide to form new fibres or join each other at any point. Fibre *A*, however, divides to form a short side branch between sections *i* and *e*. If sections from a few positions only were taken, e.g. *c*, *g* and *s*, without examination of the serial sections in between, it might be concluded that extensive branching and reunion of fibres occurs in this spindle.

III. *Interosseous muscle spindle, normal (add. dig. long. V).* (*Figure* 1, *spindle III. Figure* 4 *and figure* 60, *plate* 45. *Masson staining.*) This spindle contains four densely stained nuclear bag fibres (black in figure 1), and four less densely stained nuclear chain fibres (stippled in figure 1). The difference in staining is particularly clear in sections *i*, *l* and *r*. All the intrafusal fibres are discrete and can be traced individually from end to end without branching or joining. The spindle is very asymmetrical, the nuclear region being much nearer one end than the other.

Sections *m* to *q* pass through the nuclear region but the four nuclear bags do not occur at the same point in the spindle. Section *n* passes through the bags of fibres *B* and *C*, while section *o* passes through the bags of fibres *A* and *D*.

The spindle sheath extends to one end of the spindle but not to the other. Two of the nuclear chain fibres, 1 and 2, are at least as long as the nuclear bag fibres. Elsewhere than in the nuclear region, there is no distinct difference in the diameter of the fibres of the two groups. The fibres at the 'long' end of the spindle are attached to the perimysium of an extrafusal fasciculus, in positions widely separate from each other. At the 'short' end of the spindle the fibres end close together in a bundle of connective tissue.

IV. *Interosseous muscle spindle, de-efferented* 83 *days (add. dig. long. V); cat* 14. (*Figure* 1, *spindle IV. Figure* 5 *and figure* 61, *plate* 46. *Masson staining.*) This spindle contains four nuclear bag fibres and five nuclear chain fibres, and is considerably shorter than spindle III. All the intrafusal fibres are discrete and can be traced from end to end without branching or joining. But, since one nuclear chain fibre (number 3) is present in one half of the spindle only, sections from the two ends contain a different number of fibres, and it might be thought that branching occurs when this is not, in fact, the case. Section *f* clearly contains five small nuclear chain fibres whereas section *q* contains only four such fibres. The principal result of ventral root transection is that the difference in diameter between the two types of intrafusal fibre is accentuated, since the nuclear chain fibres show a proportionately greater reduction in diameter than do the nuclear bag fibres (see later). The atrophied nuclear chain fibres stain darkly, and the staining differentiation between the two types of fibre is absent. This spindle, like spindle III, is asymmetrical, with the fibres at one end attached to an extrafusal bundle while at the other end they are embedded in connective tissue. In contrast to spindle III, however, the nuclear chain fibres are shorter than the nuclear bag fibres and are about the same length as the spindle sheath.

Sections *h* to *q* pass through the nuclear region. The nuclear bags of fibres *B* and *C* are present in section *k*, those of *A* and *B* in section *l*, and those of *A* and *D* in section *m*.

V. *Interosseous muscle spindle, de-afferented* 225 *days (add. dig. long. V); cat* 6. (*Figure* 1, *spindle V. Figure* 6 *and figure* 62, *plate* 47. *Masson staining.*) This spindle contains four nuclear bag fibres, which in most sections are densely stained, and nine nuclear chain fibres of granular appearance with Masson staining. It is probable that all the fibres were considerably longer than is shown in the diagram, perhaps as long as those in spindle III. At one end of the spindle it was impossible to trace the individual intrafusal fibres beyond section *a* since the sections of the muscle became oblique. The whole spindle, however, could be seen to extend some distance beyond the position of section *a*. The intrafusal fibres at this end are divided into two groups by a thin septum of connective tissue; towards the other end another septum appears. Fibres 1, 2, 3, 4 and *A* project farther than the others,

but all end in the same connective tissue bundle. All thirteen intrafusal fibres were traced individually without branching or joining through the part of this spindle in which the sections were transverse.

The principal change in the structure of the intrafusal fibres after dorsal root section is a gradual disappearance of the nuclear bags and nuclear chains following degeneration of the sensory nerve endings. Sections *g* to *k* pass through the nuclear region of this spindle. The nuclear chains have completely disappeared, while the number and size of the nuclei in the nuclear bag fibres is reduced. A single central nucleus is visible in each nuclear bag fibre in sections *g* and *h* which pass through the point of maximum diameter of the spindle lymph space.

(4) *Diameter of intrafusal and extrafusal muscle fibres*

Individual intrafusal muscle fibres may vary in diameter as they traverse the spindle. The measurements of intrafusal fibre diameter which are quoted below were made, therefore, at a standard point in both serially sectioned and isolated whole spindles, namely, close to one or other end of the lymph space. At this point the space is very small, but the fibres are separate from the sheath and from each other, and the central nuclei are absent. In addition, there are differences in the diameter and length of intrafusal fibres in spindles from different sites. Therefore, the size of the intrafusal fibres in spindles in the leg muscles and spindles in the interosseous muscles of the foot are described separately below.

(*a*) *Diameter of muscle fibres in normal spindles.* The intrafusal fibres in spindles in the muscles of the leg fall into two distinct diameter groups, large and small. The diameter of the large fibres is about twice that of the small fibres. When the large fibres are traced through serial transverse sections to the spindle equator they always have a nuclear bag at this point, whereas the small fibres always contain a nuclear chain. *In leg muscle spindles, therefore, the terms 'nuclear bag fibre' and 'large fibre' are synonymous, as are the terms 'nuclear chain fibre' and 'small fibre'.* Thus, the two spindles in figures 37, 39, plate 42, contain 2 nuclear bag fibres plus 5 nuclear chain fibres, and 3 nuclear bag fibres plus 4 nuclear chain fibres, respectively. It is not necessary to trace the fibres through serial sections to confirm this.

Fibre-size histograms for the diameter of the intrafusal fibres in transverse sections of 8 normal spindles from a soleus muscle, and 25 normal spindles from two tenuissimus muscles are shown in figure 7*a*, *c*. In both soleus and tenuissimus muscles the diameter distribution of the intrafusal fibres is clearly bimodal. The two groups are completely separate in the soleus histogram, and overlap in the tenuissimus histogram. Measurements of a random sample of extrafusal fibres lying close to the spindles are included in each histogram.

The distinct difference in diameter of the nuclear bag and nuclear chain fibres is very obvious in whole spindles isolated from leg muscles (e.g. figures 78, 80, 85, plate 50; figure 89, plate 51).

In the interosseous muscles from the hind foot the intrafusal fibres in normal spindles do not fall into two distinct diameter groups (figure 8*a*). Transverse sections through the end of the lymph space of normal spindles from the adductor digiti minimi longus muscle, the most superficial of the interosseous group of muscles in the cat, are shown in figures 45

to 47, plate 42. Some spindles contain large and small fibres (figures 46, 47), while in others all the intrafusal fibres are of about the same diameter (figure 45). However, sections through the point of maximum diameter of the lymph space of interosseous muscle spindles (figures 44, 49, plate 42) are similar to those of spindles from the leg muscles (figures 36, 40, plate 42).

Muscle spindles in interosseous muscles, therefore, contain the same two types of intrafusal fibre, nuclear bag fibres and nuclear chain fibres, as are found in other spindles. The diameter groupings of the two types overlap extensively, however, and it is often necessary to trace the fibres through serial sections to the equator to determine to which group they belong. This was done for the 14 normal spindles whose intrafusal fibre diameters are shown in the histogram in figure 8*a*.

In table 2 the diameter of intrafusal fibres in transverse sections of spindles is compared with the diameter measured in isolated whole spindles fixed in formic acid and stained with gold chloride. Formic acid fixation produces swelling of connective tissue, but the intrafusal muscle fibre diameter in spindles fixed in this way appeared to be about the same as the intrafusal fibre diameter in isolated, living spindles. A shrinkage of 20% or even more may occur as a result of formalin fixation and embedding in paraffin wax.

In normal isolated whole interosseous muscle spindles it is rarely possible to trace the individual muscle fibres, which are numerous, to the nuclear region. Hence, the mean diameter of all the muscle fibres of both types together in these spindles is given in table 2. The mean diameters of the nuclear bag and nuclear chain fibres separately may be deduced by calculating the shrinkage due to fixation by comparing the overall means from the two methods, and then correcting the means of the two groups from transverse sections for shrinkage.

The mean diameters of the nuclear bag fibres and nuclear chain fibres are about 30 *and* 14 μ, *respectively, in normal soleus spindles,* 21 *and* 11 μ *in normal tenuissimus spindles, and about* 22 *and* 18 μ *in normal interosseous muscle spindles. The extrafusal fibres are two to three times as large as the nuclear bag intrafusal fibres in all muscles.*

(*b*) *The effect of cutting the ventral spinal roots.* Both types of intrafusal muscle fibre atrophy more slowly than the extrafusal fibres after the ventral roots are cut; the nuclear chain intrafusal fibres, however, atrophy more rapidly than the nuclear bag intrafusal fibres. Measurements of intrafusal and extrafusal fibre diameter in a soleus muscle from one cat 2 months after ventral root transection, and in an interosseous muscle from another cat 3 months after ventral root transection, are represented in the histograms of figures 7*b* and 8*b*, respectively. These histograms are directly comparable with the histograms in figures 7*a* and 8*a*, since the values in the latter were obtained from the corresponding normal muscle of the opposite hind limb in each case. The mean diameter of a random sample of extrafusal fibres is 60% of normal in the de-efferented soleus muscle, and 45% of normal in the de-efferented interosseous muscle. A complete cross-section of the atrophied interosseous muscle is shown in figure 48, plate 42, and the corresponding normal muscle is shown in figure 43, plate 42. The shrinkage of individual extrafusal fibres away from their endomysium, so that there is a clear space round each fibre, can be seen in figures 41, 42, 50, plate 42.

The mean diameter of the nuclear chain intrafusal fibres is reduced to about two-thirds of normal in both the soleus and interosseous muscles, as a result of de-efferentation

(figures 7*b*, 8*b*). The reduction in the mean diameter of the nuclear bag fibres is less than this in the soleus muscle after 2 months, while the nuclear bag fibres in the interosseous muscle show no statistically significant change in diameter at all 3 months after de-efferentation.

The result of the greater rate of atrophy of the nuclear chain fibres is that there is a marked difference in the diameter of the two types of intrafusal fibre in de-efferented spindles, not only in the soleus muscle where it was already evident in normal spindles, but also in the interosseous muscle where a distinct difference was absent in normal spindles. This can be seen in the spindles in figures 50, 51, plate 42, (interosseous), and also in figures 41, 42, plate 42 (soleus).

Confirmation of this difference in the effect of cutting the ventral roots on the two types of intrafusal fibre was provided by measurements of diameter in isolated whole spindles from a number of cats (table 2). The nuclear bag fibres and nuclear chain fibres in de-efferented isolated soleus spindles fell into two groups widely separated from each other, the largest nuclear chain fibre being 12 μ, and the smallest nuclear bag fibre 18 μ, in diameter. Also, in de-efferented isolated interosseous spindles the intrafusal fibres fell into two distinct groups with little or no overlap, so that differentiation of nuclear chain fibres from nuclear bag fibres was easy, whereas in normal spindles it was often impossible unless the fibres were traced to the nuclear region.

In the soleus spindles the percentage reduction in intrafusal fibre diameter as a result of de-efferentation is less in isolated spindles than in transverse sections, while in the interosseous spindles it is greater in isolated spindles. In all spindles, however, with both methods, the reduction in the diameter of nuclear chain fibres is much greater than the reduction in diameter of nuclear bag fibres.

Thus, in all the muscles studied, 2 to 3 months after transection of the appropriate ventral spinal roots the mean diameter of the extrafusal fibres was reduced to about 50 % of the value in normal muscle, the diameter of the nuclear chain intrafusal fibres was about 65 % of normal, and the diameter of the nuclear bag fibres was about 90 % of normal.

(*c*) *The effect of cutting the dorsal spinal roots.* After the dorsal roots are cut the primary sensory ending degenerates; the intrafusal muscle fibres gradually lose their central nuclei and increase slightly in diameter. Complete disappearance of central nuclei in all intrafusal fibres takes about a year, but the loss of some and atrophy of those that remain can be seen within a few months (figure 74, plate 49; figure 62*g*, plate 47; figures 52, 53, plate 42).

The diameters of the intrafusal fibres in transverse sections of 13 spindles from an interosseous muscle, 7·5 months after dorsal root section are represented in the histogram of figure 8*c*, which includes a random sample of extrafusal fibres. The diameter groups of nuclear bag fibres and nuclear chain fibres overlap extensively, and there is no significant difference between the mean diameters of either group and the corresponding group in a normal interosseous muscle from a different cat (figure 8*a*).

A comparison of the diameters of intrafusal fibres in normal and de-afferented isolated whole spindles (table 2) from soleus, tenuissimus and interosseous muscles reveals, however, a slight increase in intrafusal fibre diameter in soleus and tenuissimus spindles, and a slight decrease in fibre diameter in interosseous muscle spindles, in de-afferented material.

It is probable that most of these differences, though significant, represent a difference between cats rather than one attributable to section of the dorsal spinal roots. The increase of about 20% in the diameter of the nuclear chain fibres in tenuissimus spindles, however, confirms the general visual impression gained from examination of a large number of spindles in different muscles, that *in spindles in which the nuclear chain fibres are small in diameter compared with the nuclear bag fibres, the former increase in diameter relative to the latter when the central nuclei disappear after transection of the dorsal spinal roots.*

(5) *Length of intrafusal fibres*

(*a*) *Spindles in muscles of the leg.* In these spindles the nuclear chain muscle fibres are about half the length of the nuclear bag fibres, and the arrangement is approximately symmetrical, with the nuclear region about midway along both types of fibre. The total length of the spindle is the same or slightly greater than the length of the longest nuclear bag fibre since different fibres may protrude farthest at the two ends. The nuclear chain fibres are, therefore, about half the total length of the spindle. The relative lengths of the intrafusal fibres in the reconstruction of a normal tenuissimus spindle in figure 1, spindle I, are typical of most leg muscle spindles.

FIGURE 1. Reconstruction of spindles from serial transverse sections, 6 or 10μ thick. The transverse scale is five times the longitudinal scale. The transverse scale applies to individual intrafusal fibres only; the fibres have been spaced apart for clarity. The thin lettered transverse lines indicate the positions of sections reproduced in text-figures; the thick lines indicate sections reproduced in both text-figures and plates. The ends of fibres which could not be traced are drawn with broken lines. The continuous lines down the side of each spindle represent the spindle sheath (sh). Lettered fibres, nuclear bag fibres. Numbered fibres, nuclear chain fibres. For description of individual spindles, see text.

I. Normal tenuissimus spindle (figure 2 and figure 58, plate 43).
II. De-efferented soleus spindle (figure 3 and figure 59, plate 44).
III. Normal interosseous spindle (figure 4 and figure 60, plate 45).
IV. De-efferented interosseous spindle (figure 5 and figure 61, plate 46).
V. De-afferented interosseous spindle (figure 6 and figure 62, plate 47).

DESCRIPTION OF PLATE 42

FIGURES 34 TO 57. *Transverse sections of spindles.* The scale in figure 38 applies to all figures unless otherwise indicated.

Tenuissimus muscle, normal. Figures 34 *to* 38. *H. & E. staining.*

FIGURES 34, 35. T.S. of two complete muscles. In each case a spindle, cut through the lymph space, lies in the centre close to the intramuscular nerve trunk and blood vessels.

FIGURE 36. T.S. of nuclear region of spindle with nuclear bags in three fibres and nuclear chains in four fibres. Coagulated lymph surrounds the bundle of intrafusal muscle fibres.

FIGURES 37, 38. T.S. of two spindles through a point near the end of the lymph space to show the distinct difference in diameter between nuclear bag (large) and nuclear chain (small) intrafusal muscle fibres. (*Continued on second page of art insert*).

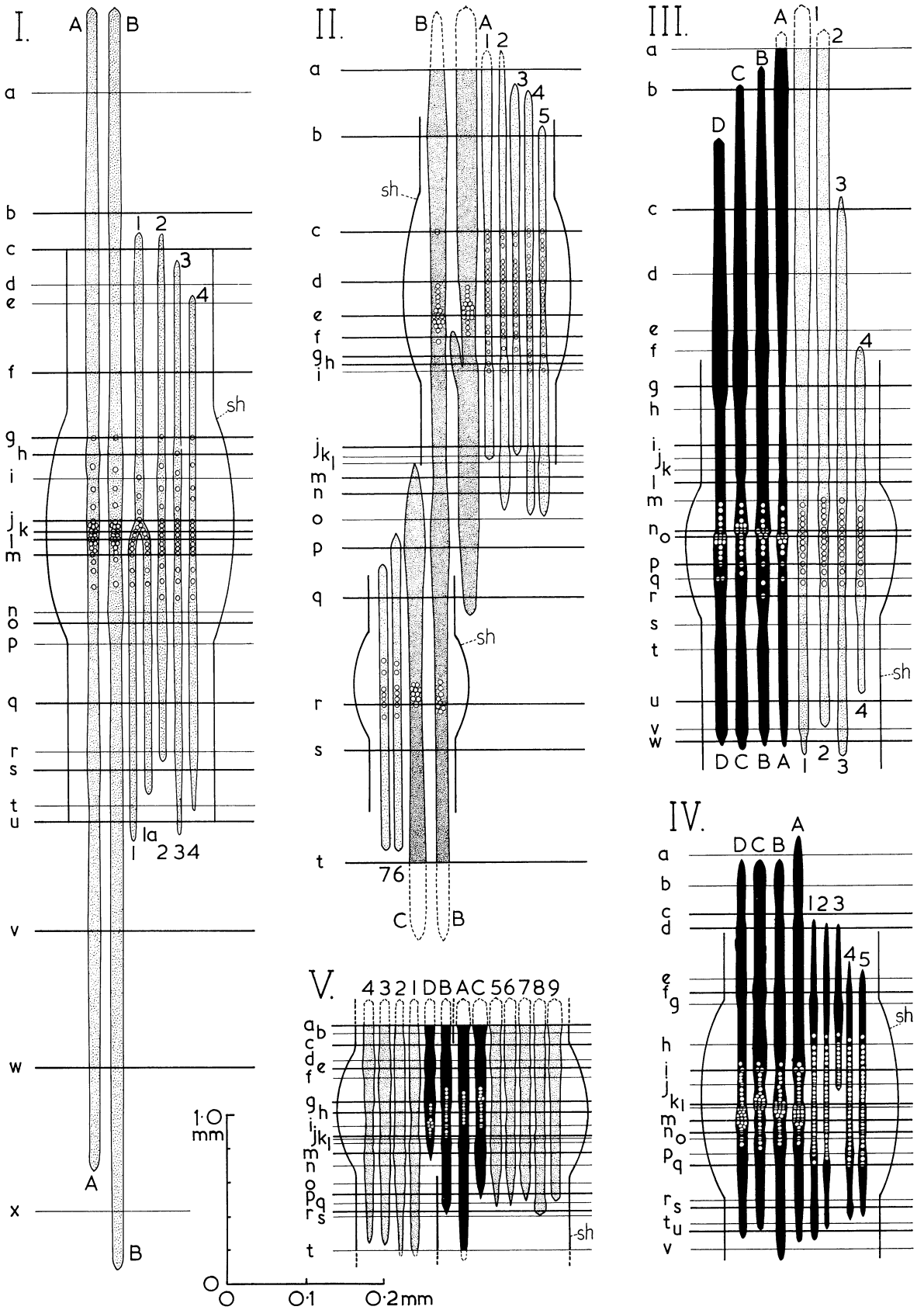


FIGURE 1. For legend see facing page.

(*Facing p. 96*)

Description of Plate 42 (*continued from* p. 96)

Soleus muscle. Figure 39, *normal. Figures* 40 *to* 42; *cat* 15, *de-efferented* 62 *days. H. & E. staining.*

Figure 39. T.S. of spindle at end of lymph space, with three large nuclear bag fibres and four small nuclear chain fibres. Note the large diameter of both extrafusal and intrafusal fibres compared with those of the tenuissimus muscle (figure 37).

Figure 40. T.S. of nuclear region of spindle with nuclear bags in two fibres and nuclear chains in four fibres.

Figures 41, 42. T.S. at the end of the lymph space of spindles with two large nuclear bag fibres plus five small nuclear chain fibres, and two large nuclear bag fibres plus three small nuclear chain fibres, respectively. The difference in size of the two types of fibre is accentuated because the nuclear chain fibres atrophy more rapidly than the nuclear bag fibres after de-efferentation. Note also the shrinkage of each extrafusal fibre from its endomysium.

Interosseous muscle (add. dig. long. V), normal; cat 14. *Figures* 43 *to* 47. *H. & E. staining.*

Figure 43. T.S. of complete muscle. One spindle (*S*) is present in this section.

Figure 44. T.S. of nuclear region of spindle with nuclear bags in two fibres and nuclear chains in four fibres. The appearance is similar to that seen in spindles from leg muscles.

Figure 45. T.S. through end of lymph space of same spindle as figure 44. All the intrafusal fibres are about the same size. The two darker fibres contained the nuclear bags, and the four less dense fibres contained the nuclear chains, at the spindle equator.

Figures 46, 47. T.S. of two normal spindles to show that in the small muscles of the foot the difference in size of the two types of intrafusal fibre is less noticeable than in spindles from the leg muscles.

Interosseous muscle (add. dig. long. V); cat 14, *de-efferented* 83 *days. Figures* 48 *to* 51. *Masson staining.*

Figure 48. T.S. of complete muscle. Note the small cross-sectional area of the atrophied muscle compared with the corresponding normal muscle from the opposite foot of the same cat (figure 43).

Figure 49. T.S. of nuclear region of spindle with nuclear bags in two intrafusal fibres and nuclear chains in five fibres. The appearance is similar to that in normal spindles.

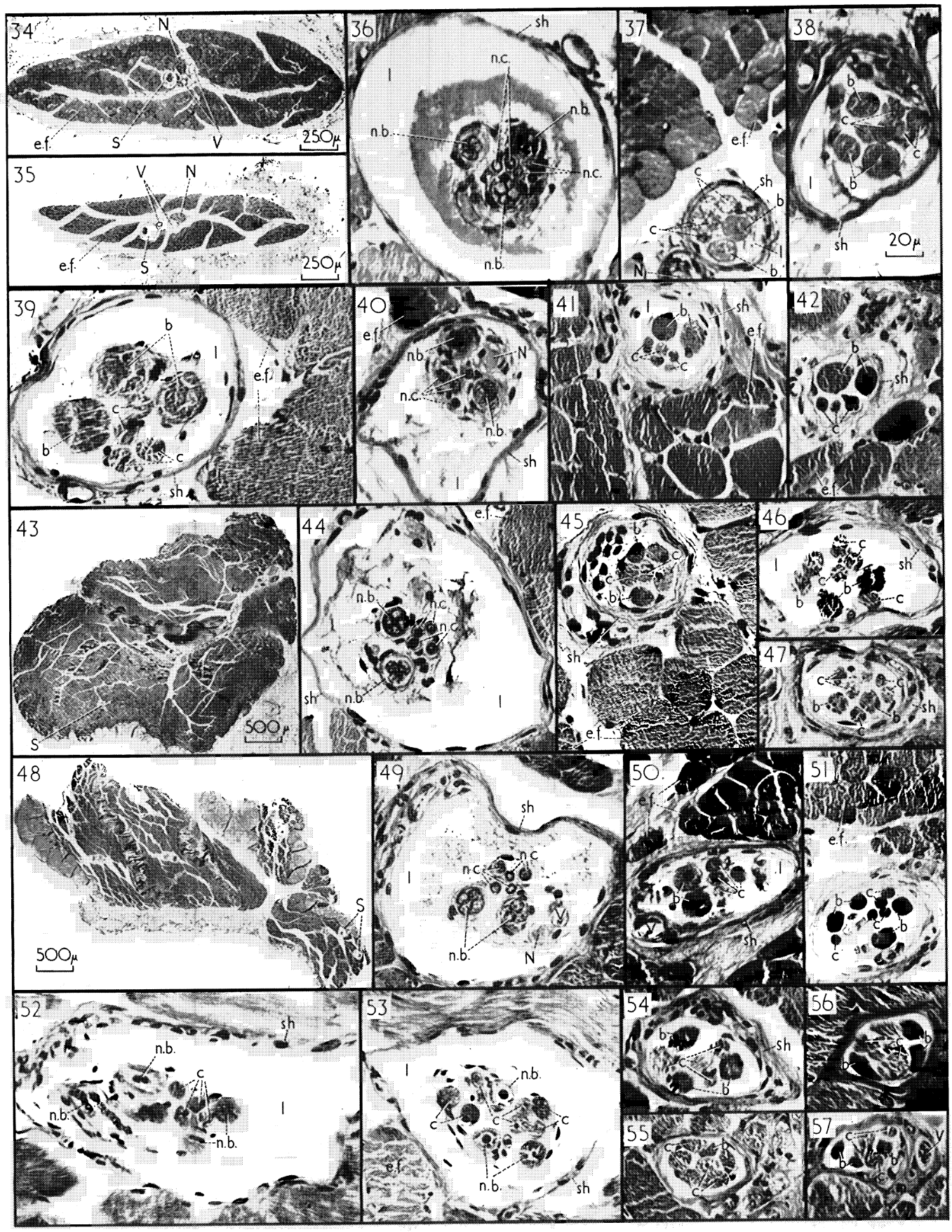
Figures 50, 51. T.S. through the end of the lymph space of spindles with two nuclear bag fibres plus four nuclear chain fibres, and four nuclear bag fibres plus five nuclear chain fibres, respectively. Because the nuclear chain fibres atrophy more rapidly than the nuclear bag fibres when denervated, there is a striking difference in the diameter of the fibres of the two types (cf. normal spindles in figures 45 to 47).

Interosseous muscle (add. dig. long. V); cat 6, *de-afferented* 225 *days. Figures* 52 *to* 57. *Masson staining.*

Figures 52, 53. T.S. through the point of maximum diameter of the lymph space of two spindles. Spindle in figure 52 cut obliquely. Most nuclei have disappeared from the nuclear chain fibres, and those in the nuclear bag fibres are atrophied and reduced in number.

Figures 54 to 57. T.S. of four spindles at the end of the lymph space. Note the distinct difference in the staining of the two types of intrafusal fibre with Masson's method, but the absence of any noticeable difference in size. Spindles in figures 54, 56 and 57 contain three darkly staining nuclear bag fibres, and four less densely stained nuclear chain fibres. Spindle in figure 55 has two nuclear bag fibres and five nuclear chain fibres.

S	spindle	*c*	nuclear chain muscle fibre
N	nerve fibre or bundle of fibres	*n.b.*	nuclei of nuclear bag
V	blood vessel	*n.c.*	nuclei of nuclear chain
e.f.	extrafusal muscle fibres	*l*	lymph space
b	nuclear bag muscle fibre	*sh*	spindle sheath



FIGURES 34 TO 57

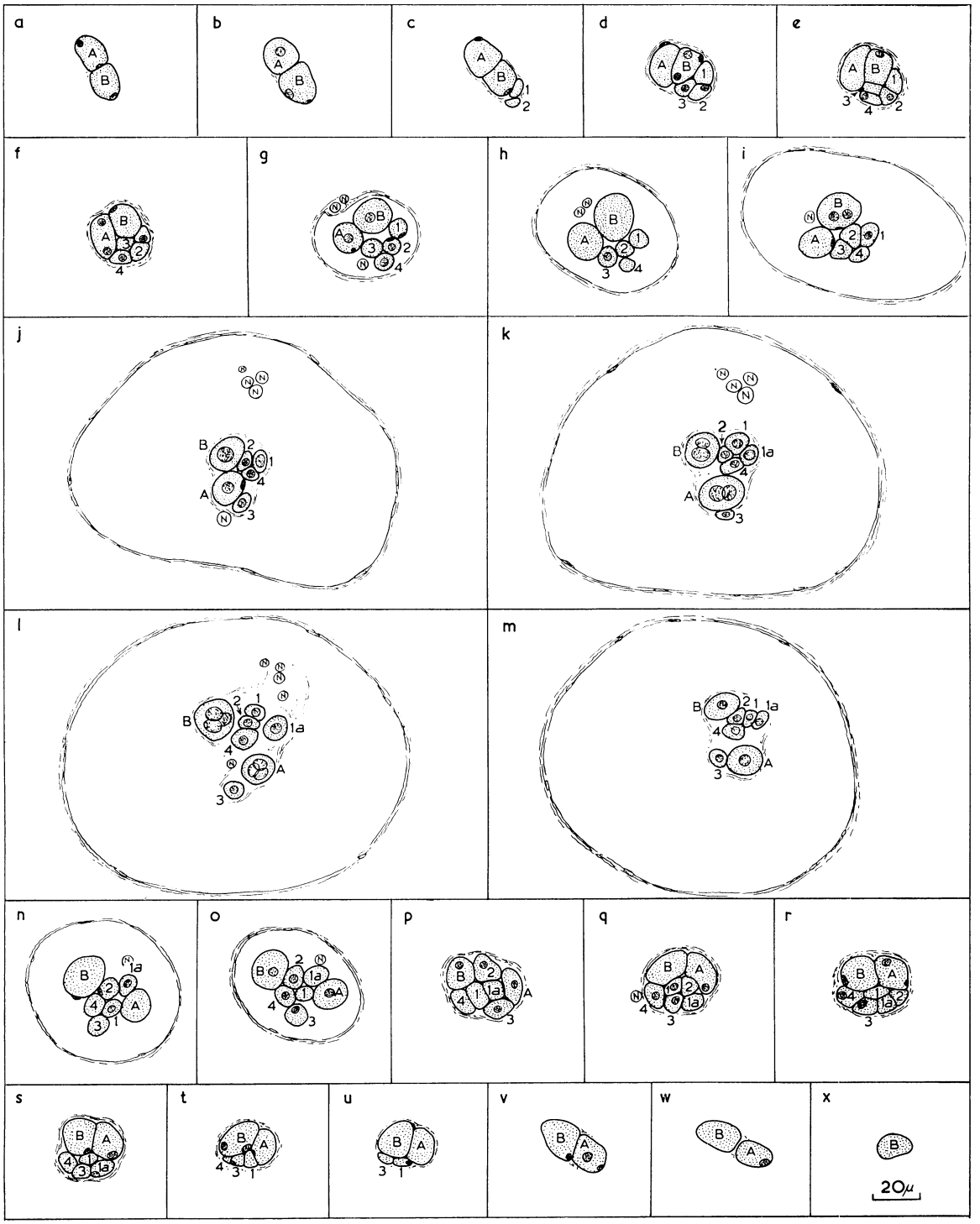


FIGURE 2 and FIGURE 58, PLATE 43 opposite. Normal tenuissimus spindle. H. & E. staining. Projection tracings and photomicrographs of transverse sections from spindle I of figure 1. The positions of the sections in the spindle are indicated by the lettered transverse lines in figure 1. Only some of the sections drawn in figure 2 are reproduced in figure 58. For detailed description see text.

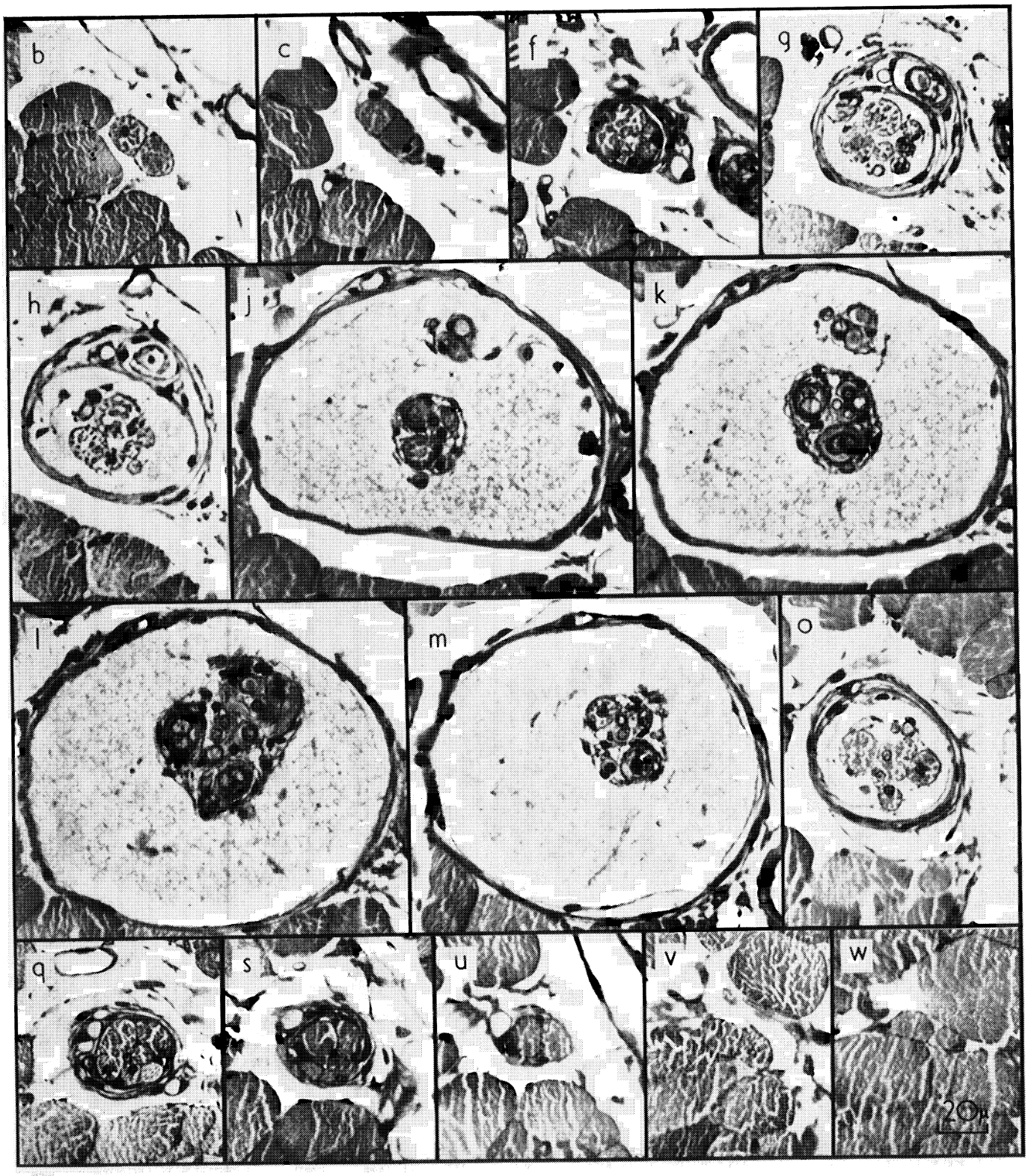


FIGURE 58. Key opposite.

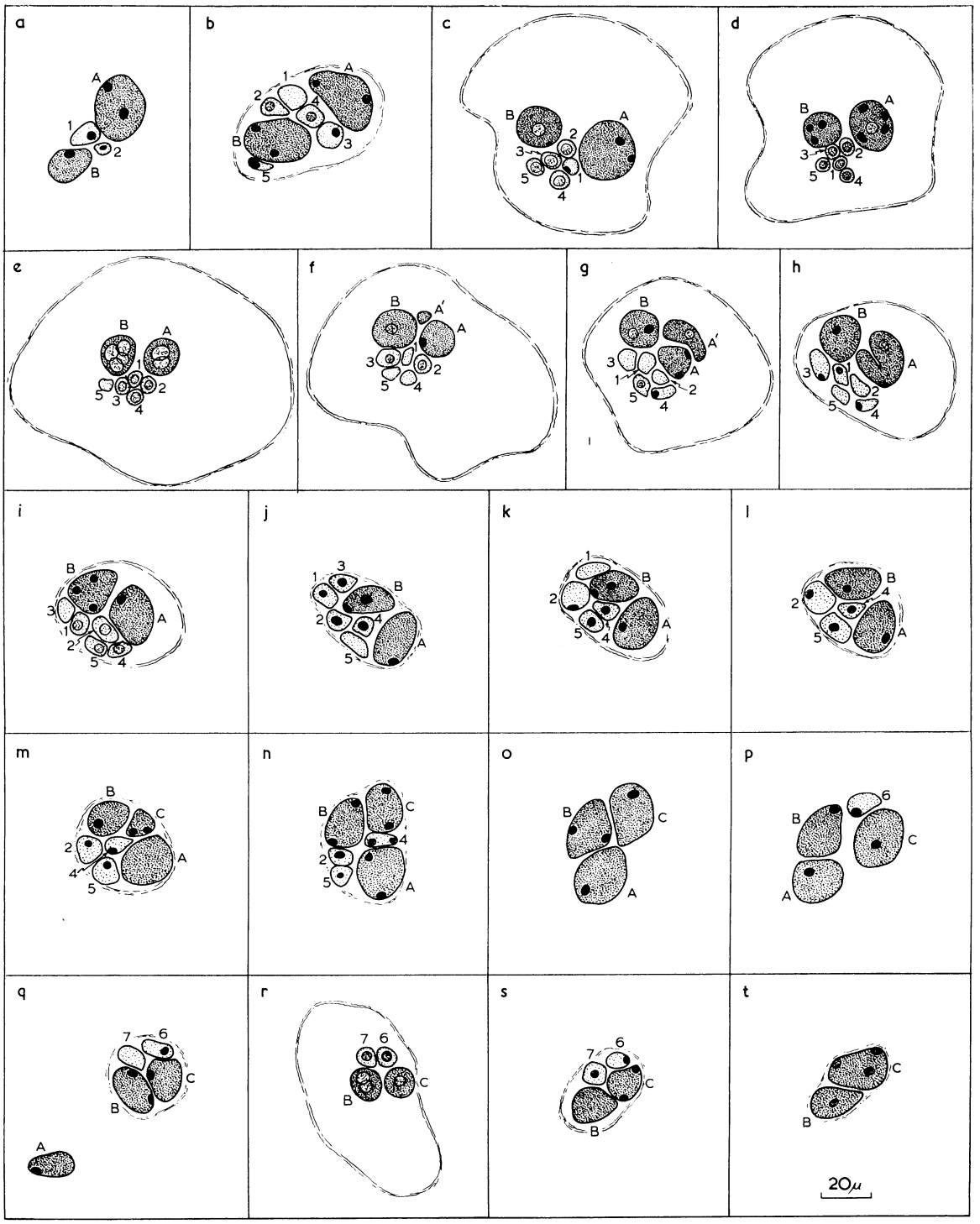


FIGURE 3 and FIGURE 59, PLATE 44 opposite. Soleus tandem muscle spindle, de-efferented 62 days; cat 15. H. & E. staining. Projection tracings and photomicrographs of transverse sections from spindle II of figure 1. For detailed description see text.

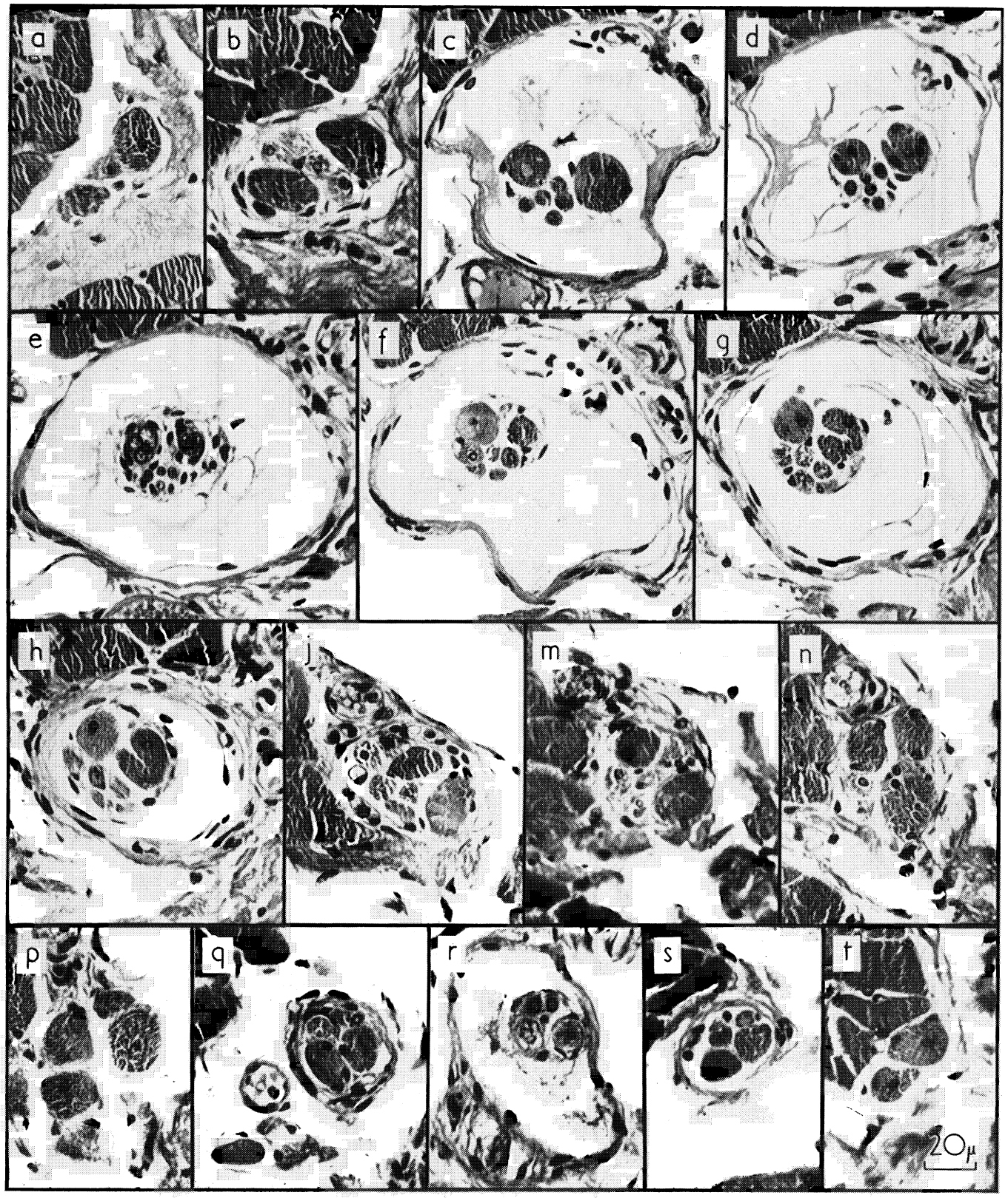


FIGURE 59. Key opposite.

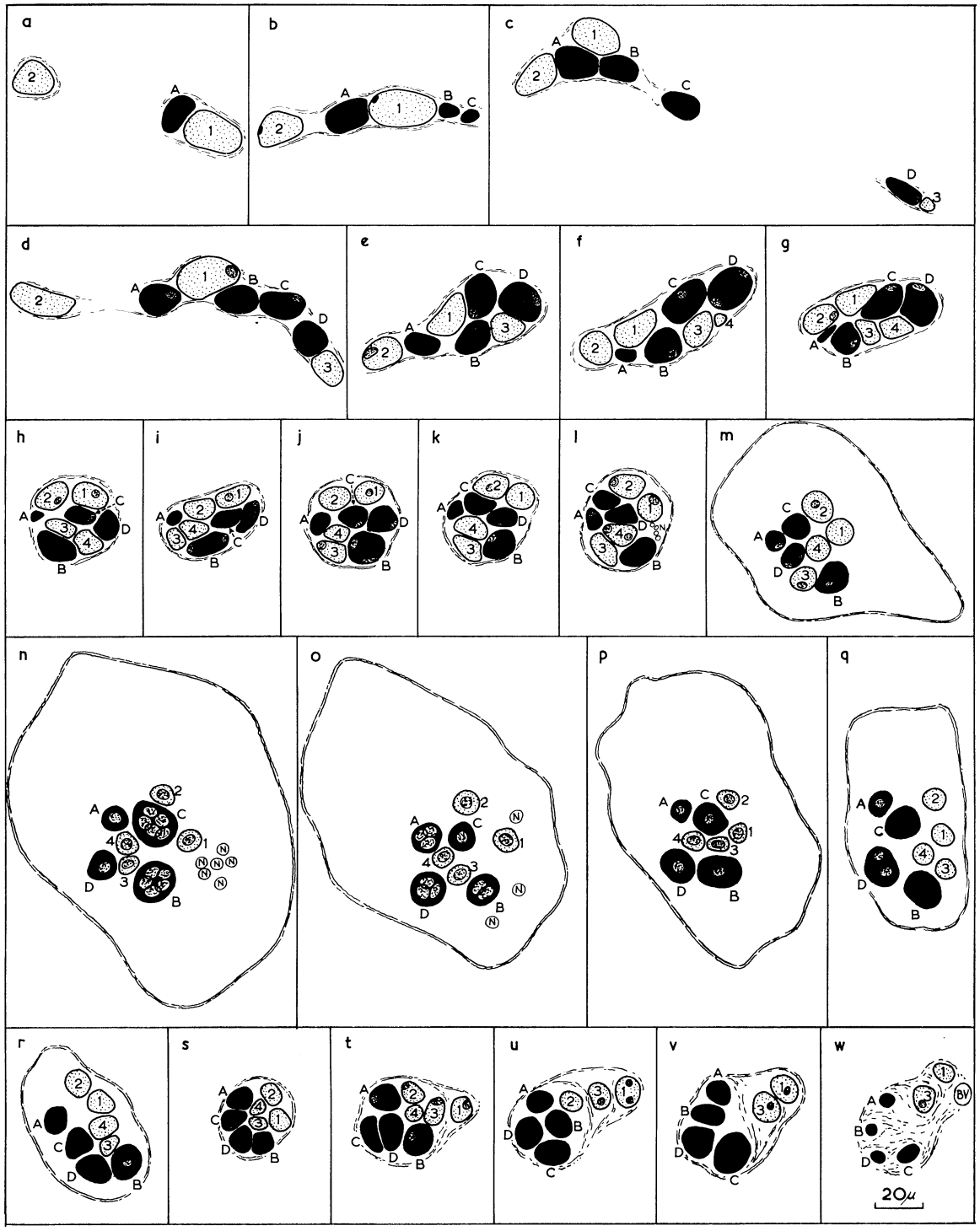


FIGURE 4 and FIGURE 60, PLATE 45 opposite. Normal interosseous muscle spindle (add. dig. long. V). Masson staining. Projection tracings and photomicrographs from spindle III of figure 1. For detailed description see text.

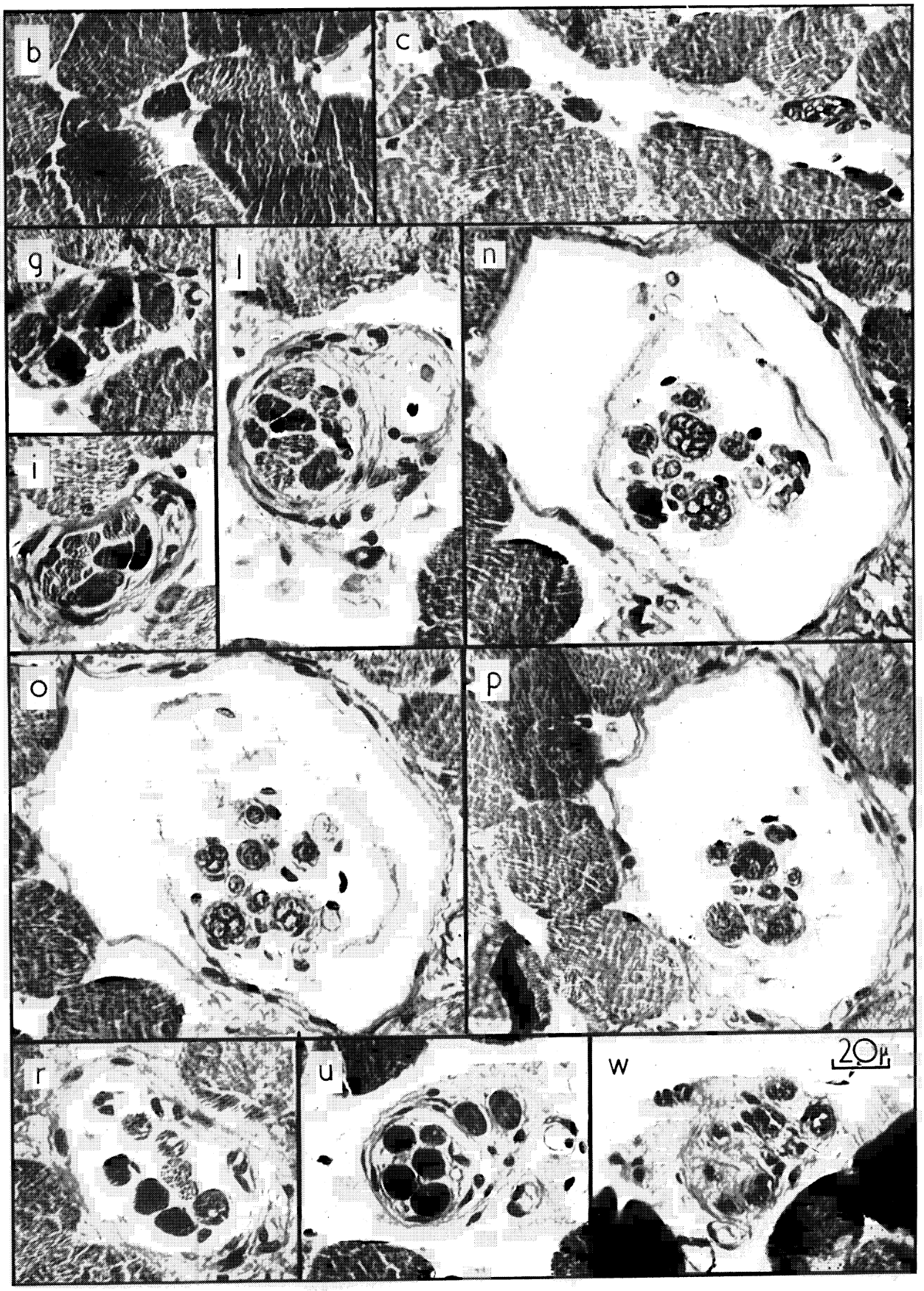


FIGURE 60. Key opposite.

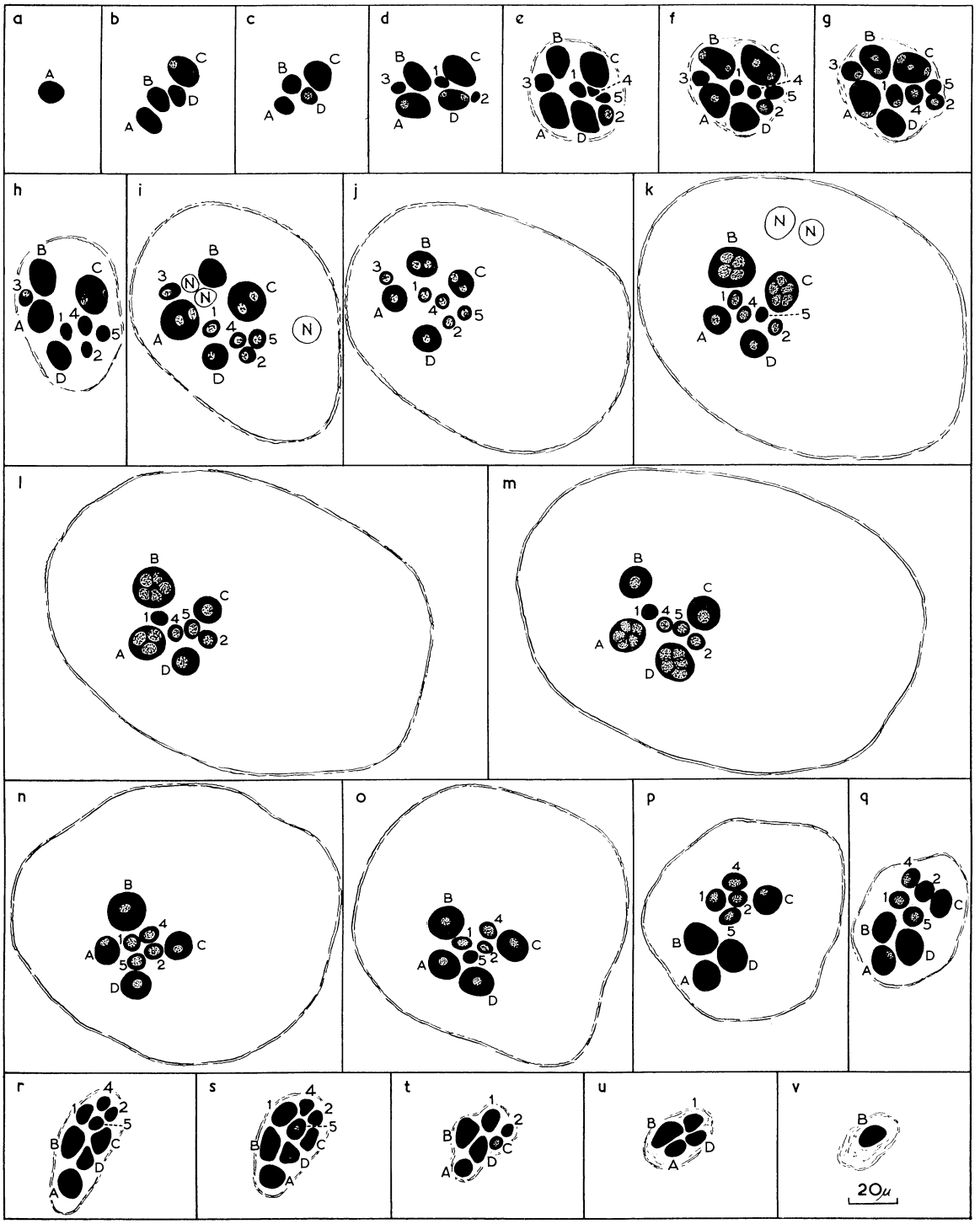


FIGURE 5 and FIGURE 61, PLATE 46 opposite. Interosseous muscle spindle, de-efferented 83 days (add. dig. long. V); cat 14. Masson staining. Projection tracings and photomicrographs from spindle IV of figure 1. For detailed description see text.

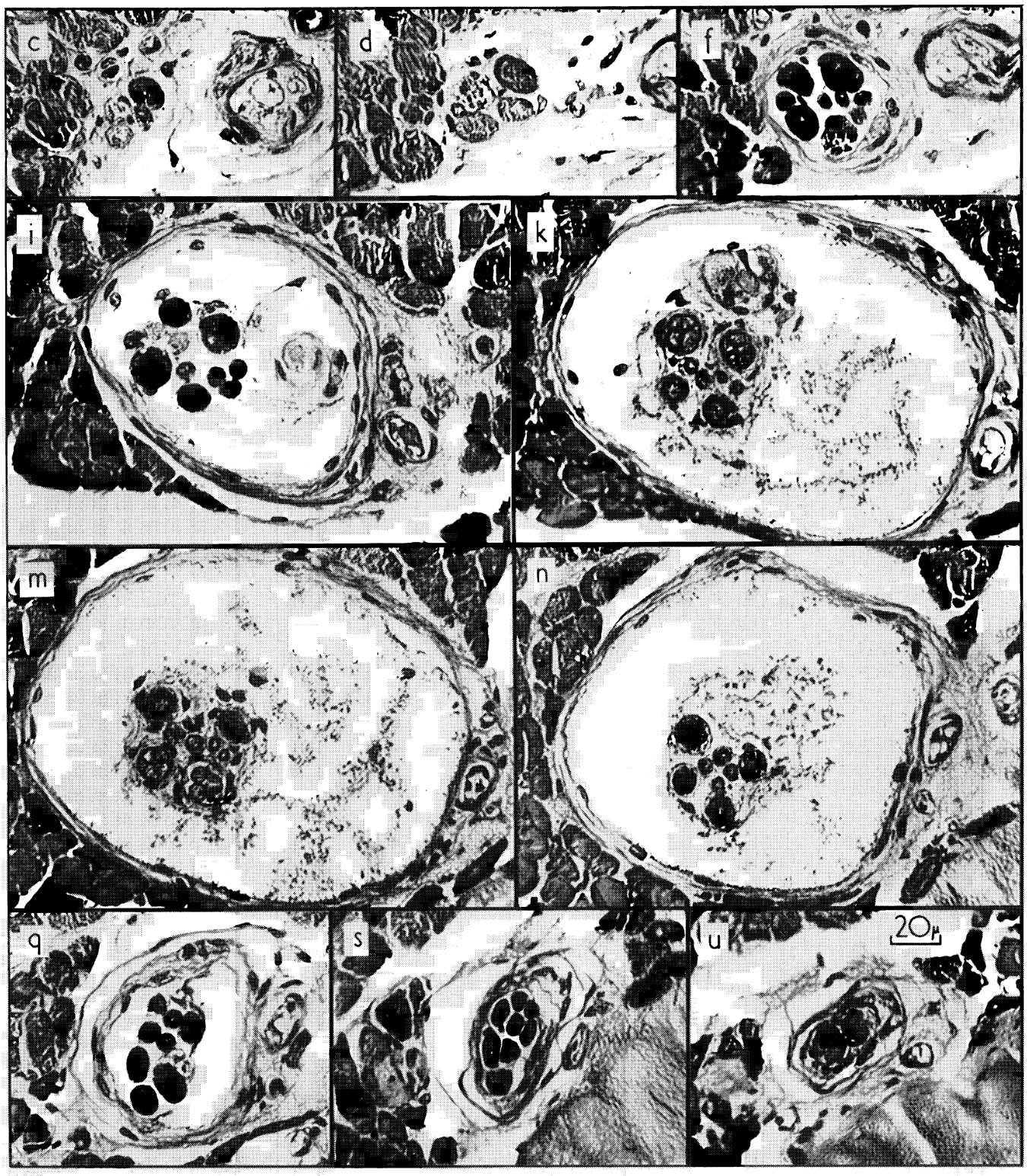


FIGURE 61. Key opposite.

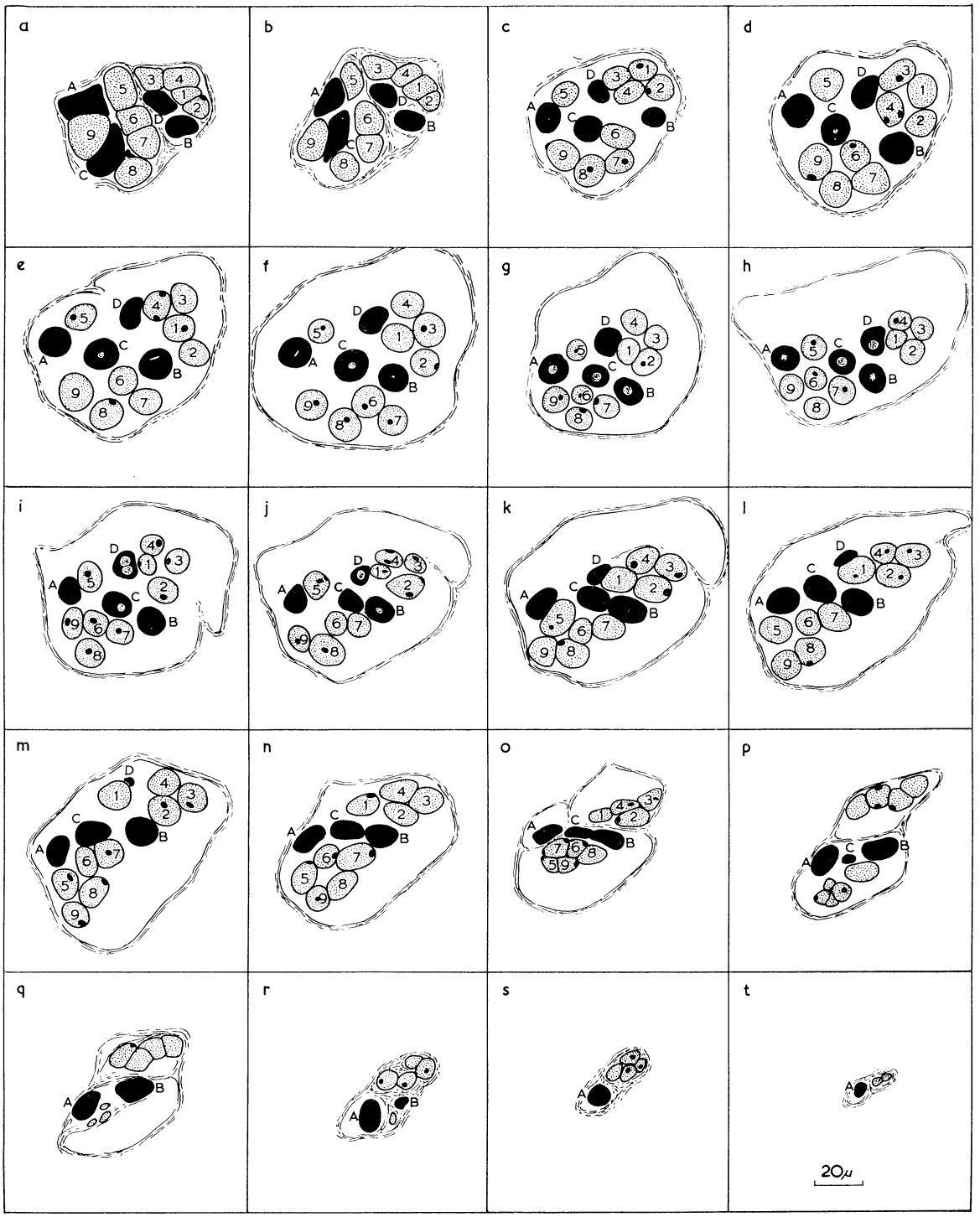


FIGURE 6 and FIGURE 62, PLATE 47 opposite. Interosseous muscle spindle, de-afferented 225 days (add. dig. long. V); cat 6. Masson staining. Projection tracings and photomicrographs from spindle V of figure 1. For detailed description see text.

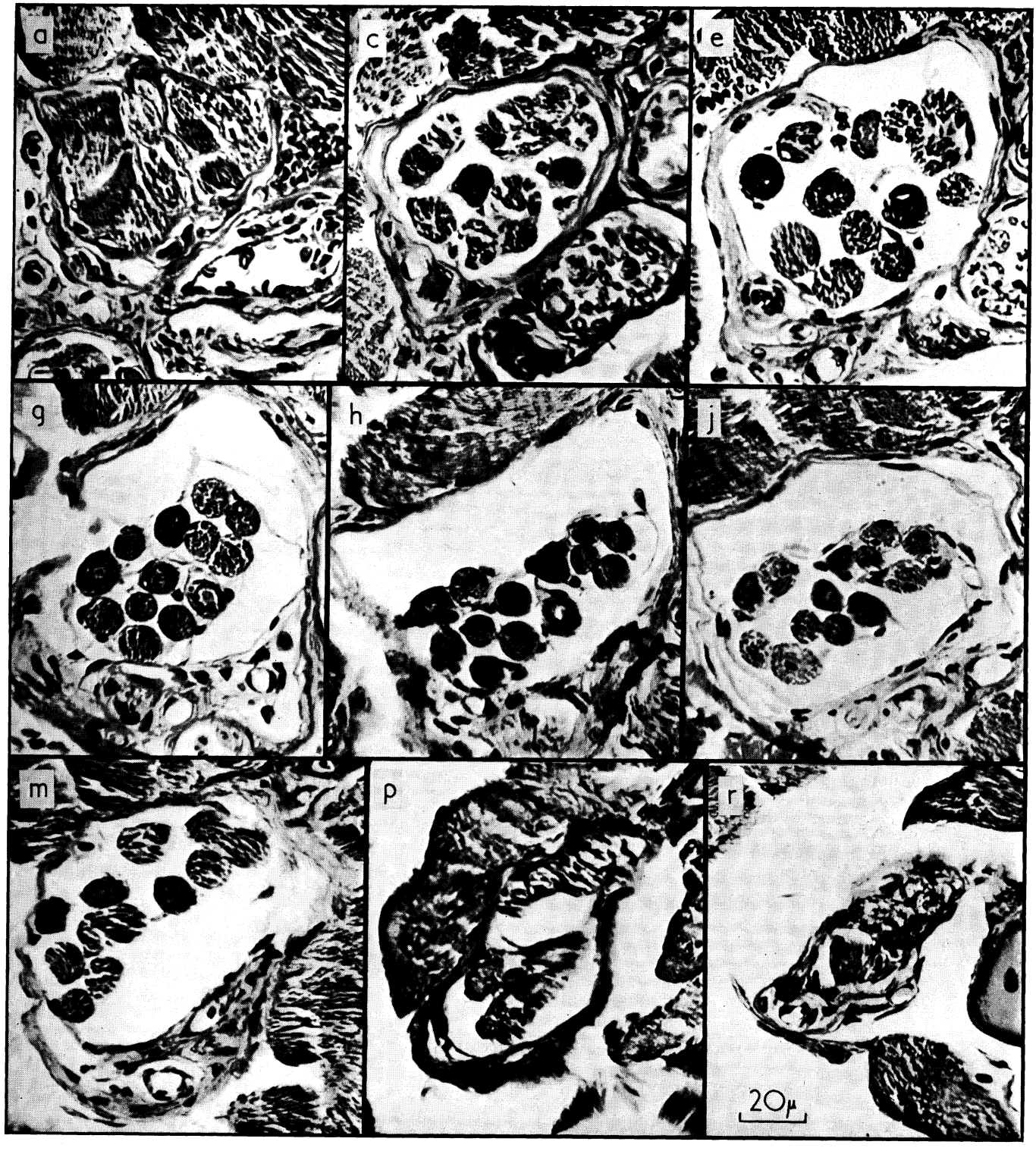


FIGURE 62. Key opposite.

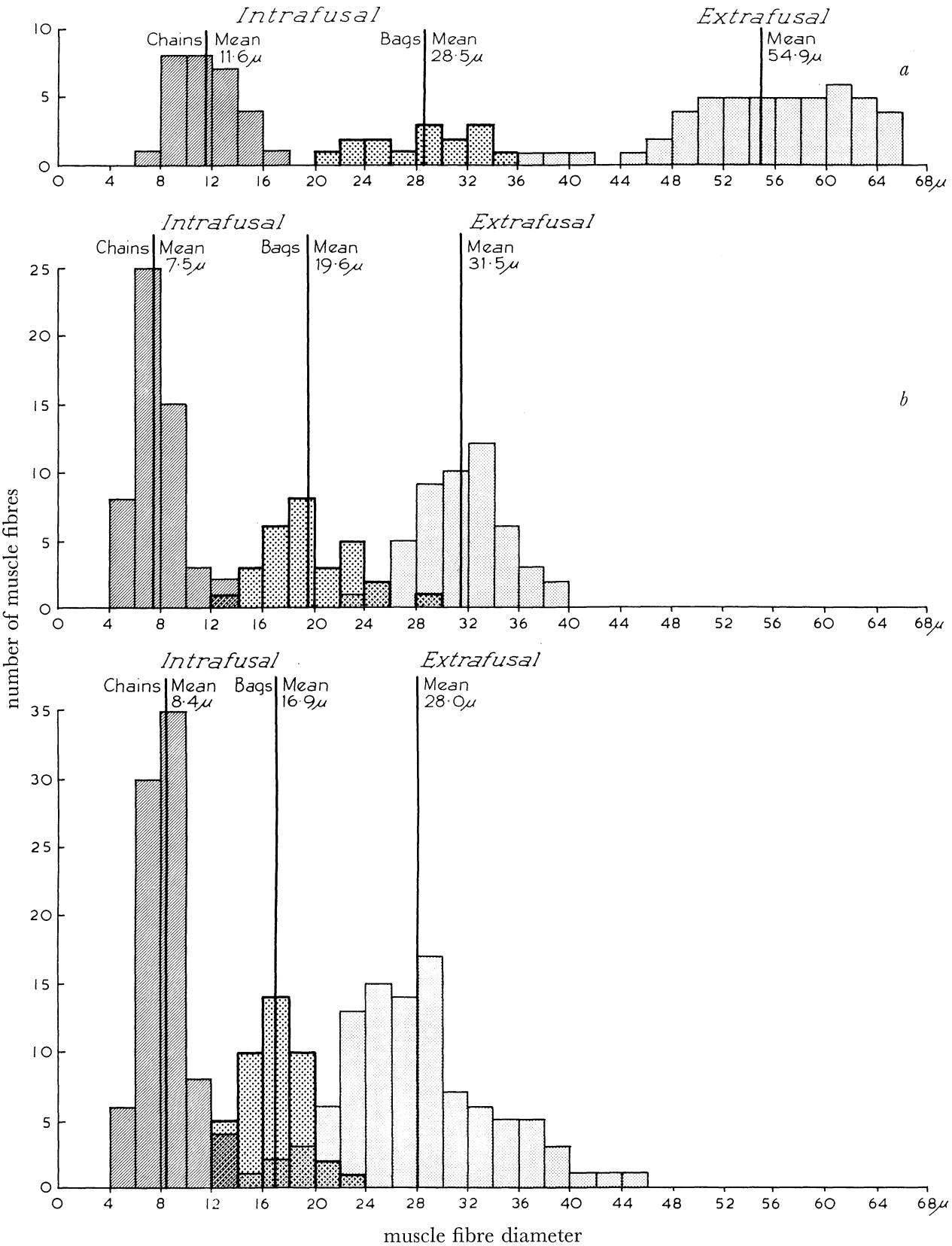


FIGURE 7. Fibre size histograms of the diameter of nuclear chain intrafusal fibres (hatched), nuclear bag intrafusal fibres (coarse stipple), and random samples of extrafusal muscle fibres (fine stipple) in the soleus and tenuissimus muscles. See also table 2.

a. Soleus muscle, normal; fixed when relaxed. Cat 15.

b. Soleus muscle, de-efferented 62 days previously, fixed when relaxed. Cat 15.

c. Tenuissimus muscle, normal; fixed *in situ*.

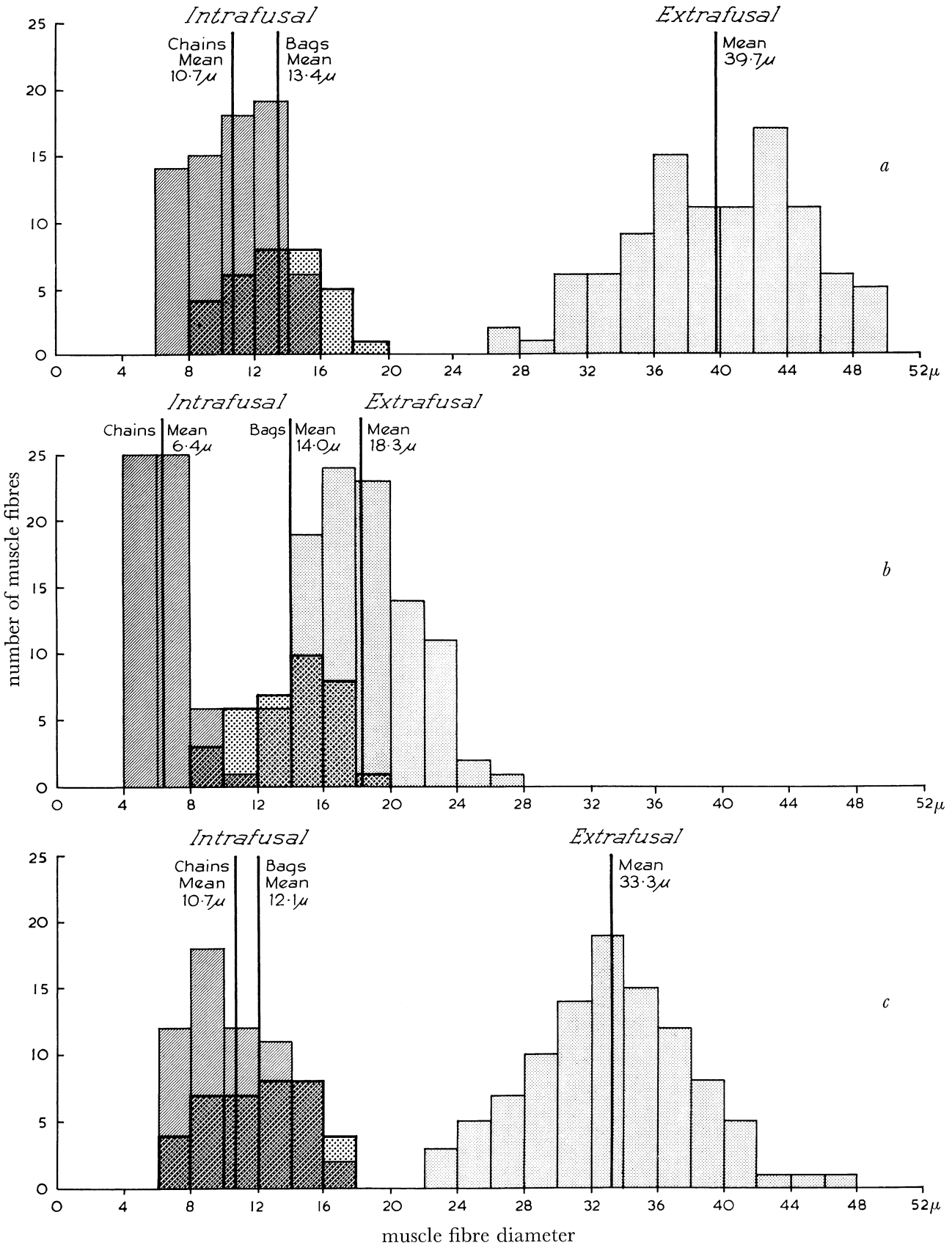


FIGURE 8. Fibre size histograms of the diameter of intrafusal and random samples of extrafusal muscle fibres in an interosseous muscle from the hind foot (add. dig. long. V). See also table 2.

a. Normal; fixed when relaxed. Cat 14. The groups of nuclear bag intrafusal fibres (coarse stipple) and nuclear chain intrafusal fibres (hatched) overlap extensively. The two types were distinguished by tracing them individually through serial transverse sections to the nuclear region.

b. De-efferented 83 days previously; fixed when relaxed. Cat 14.

c. De-afferented 225 days previously; fixed when relaxed. Cat 6.

TABLE 2. COMPARISON OF THE DIAMETER OF NUCLEAR BAG AND NUCLEAR CHAIN MUSCLE FIBRES IN NORMAL, DE-EFFERENTED AND DE-AFFERENTED SPINDLES FROM THE SOLEUS, TENUISSIMUS AND INTEROSSEOUS MUSCLES OF THE HIND LIMB OF THE CAT

Values are given for the diameter measured both in transverse sections of muscles fixed and embedded in paraffin wax, and in whole spindles isolated by microdissection after staining with gold chloride. Measurements were made close to one end of the spindle lymph space. d.r., dorsal roots; v.r., ventral roots.

muscle	fixation method	type of preparation	staining method	operation	degeneration time (months)	no. of spindles	diameter of intrafusal muscle fibres (mean ± S.D. (μ), no. of fibres in parentheses)	
							nuclear bag fibres	nuclear chain fibres
soleus	formalin (relaxed)	serial transverse sections	haemalum and eosin	normal	—	8	28·47 ± 4·32 (15)	11·56 ± 2·50 (29)
				v.r. cut	2	13	19·62 ± 3·08 (29)	7·72 ± 1·89 (53)
	formic acid (relaxed)	isolated whole spindles	gold chloride	normal	—	79	30·24 ± 6·32 (148)	13·60 ± 2·28 (230)
				v.r. cut	3	16	26·31 ± 3·92 (32)	9·78 ± 1·07 (49)
				d.r. cut	1·5 to 2	33	32·60 ± 6·76 (61)	14·34 ± 2·86 (100)
tenuissimus	Susa (*in situ*)	serial T.S.	haemalum and eosin	normal	—	25	16·86 ± 2·35 (42)	8·37 ± 1·85 (83)
	formic acid (natural length)	isolated whole spindles	gold chloride	normal	—	115	21·48 ± 4·84 (249)	10·62 ± 2·46 (291)
				d.r. cut	1·5 to 7·5	42	24·37 ± 5·38 (89)	13·13 ± 2·12 (108)
interosseous	formalin (relaxed)	serial T.S.	Masson	normal	—	14	13·44 ± 2·75 (32)	10·67 ± 2·60 (72)
				v.r. cut	3	13	13·97 ± 2·68 (35)	6·40 ± 1·46 (57)
				d.r. cut	7·5	13	12·10 ± 3·08 (38)	10·71 ± 2·85 (63)
	formic acid (relaxed)	isolated whole spindles	gold chloride	normal	—	29	19·95 ± 6·24 (154)	
				v.r. cut	3 to 8	46	18·88 ± 2·93 (120)	9·81 ± 1·46 (116)
				d.r. cut	1·5 to 7·5	23	17·75 ± 4·68 (126)	

The intrafusal fibres within each type in any spindle differ in length. In most spindles, however, there is not more than 0·5 mm difference between the longest and the shortest fibre of each type. The average length of the nuclear bag fibres and of the nuclear chain fibres was measured to the nearest 0·5 mm in each spindle. The mean ±S.D. of these values in the total number of spindles measured is given in table 3, where the mean values in isolated whole spindles are compared with those derived from serial transverse sections of spindles. The values from the two methods for tenuissimus spindles agree closely. Those for the soleus spindles differ since longitudinal shrinkage occurred in the spindles for sectioning which were not fixed *in situ*.

The values for fibre length in the isolated whole spindles may be taken as close to the values in living spindles. *The spindles in the tenuissimus and soleus muscles and in other muscles of the leg are very similar, the nuclear bag fibres being about 7·5 mm, and the nuclear chain fibres about 4 mm, in length.*

(*b*) *Spindles in interosseous muscles of the hind foot.* The nuclear bag fibres in these spindles are shorter than those in the leg muscles; the range of length of nuclear chain fibres is about the same in all spindles. In interosseous spindles the nuclear chain fibres may be slightly shorter than the nuclear bag fibres (figure 1, spindle IV; figures 11, 13), longer than the nuclear bag fibres (figure 1, spindle III), or about the same length (figure 14). Thus, values for the length of the fibres in each of the two types are difficult to obtain. *Interosseous muscle spindles are about 5 mm in length.* The mean total length of isolated whole spindles is compared with the length derived from serial transverse sections in table 3. Formalin fixation produced shortening of the spindles in the interosseous muscles to 60% of the value for isolated spindles.

TABLE 3. COMPARISON OF THE LENGTH OF NUCLEAR BAG AND NUCLEAR CHAIN MUSCLE FIBRES IN SPINDLES FROM THE TENUISSIMUS, SOLEUS AND INTEROSSEOUS MUSCLES OF THE HIND LIMB OF THE CAT

Values are given for the length estimated from serial transverse sections of spindles, and measured in isolated whole spindles. Individual intrafusal fibres were not measured; the average length of the group of nuclear bag fibres and of the group of nuclear chain fibres in each spindle was estimated to the nearest 0·5 mm. In interosseous muscle spindles the two groups are not clearly separate; the mean of the total lengths of the spindles is given. The ends of some of the sectioned normal soleus spindles could not be traced since the sections became oblique—only an approximate value for the total length is given.

muscle	fixation method	type of preparation	staining method	length of intrafusal muscle fibres (mean ± S.D. (mm) no. of spindles in parentheses)	
				nuclear bag fibres	nuclear chain fibres
tenuissimus	formic acid (natural length)	isolated whole spindles	gold chloride	7·75 ± 1·66 (134) (range 4·5 to 13)	3·93 ± 0·61 (62) (range 2 to 6)
	Susa (*in situ*)	serial transverse sections	haemalum and eosin	6·83 ± 1·96 (27) (range 4 to 11·5)	3·56 ± 1·08 (26) (range 2 to 6)
soleus	formic acid (relaxed)	isolated whole spindles	gold chloride	7·12 ± 2·18 (51) (range 4 to 13)	4·09 ± 0·72 (71) (range 2·5 to 5·5)
	formalin (relaxed)	serial transverse sections	haemalum and eosin	About 5	2·34 ± 0·51 (16) (range 1·5 to 3)
interosseous	formic acid (relaxed)	isolated whole spindles	gold chloride	4·86 ± 1·32 (66) (range 2 to 8)	
	formalin (relaxed)	serial transverse sections	Masson	2·87 ± 0·98 (23) (range 1·5 to 5)	

In all the spindles which were examined in this investigation, therefore, the intrafusal muscle fibres were of two distinct types, nuclear bag fibres, and nuclear chain fibres. The differences between them are less obvious in spindles in the small muscles of the foot since the nuclear bag fibres are shorter, and the nuclear chain fibres may be of larger diameter, than in spindles in the muscles of the leg. Both types of intrafusal fibre have pronounced cross-striations.

(6) *Branching of intrafusal fibres*

Branching was seen in only two nuclear bag intrafusal fibres in this study. In both cases the division resulted in the formation of a short side branch, or 'thumb' on the intrafusal fibre, in which central nuclei were absent. In spindle II of figure 1, fibre *A* branched in this fashion (figure 3*i* to *f* and figure 59*h* to *f*, plate 44). *Branching of nuclear bag fibres is so rare as to be negligible.*

Nuclear chain intrafusal fibres sometimes divide into two, but such division usually occurs in one fibre only in any one spindle (fibre 1 of spindle I in figure 1). In some spindles the nuclear chain fibres come into close apposition for part of their length, and the whole bundle so formed may be surrounded by a thin layer of connective tissue. Short, very asymmetrical nuclear chain fibres in which the central nuclei lie at one end, are found occasionally (fibre 3 of spindle IV in figure 1). *In many spindles all the nuclear chain fibres can be traced from end to end as discrete entities.*

(7) *Number and arrangement of intrafusal fibres*

All spindles contain some fibres of each of the nuclear bag and nuclear chain types, but the number of fibres of each type varies from spindle to spindle. The composition of 78 spindles which were serially sectioned transversely is given in table 4.

In spindles from the leg muscles, the arrangement encountered most frequently is two nuclear bag fibres plus either four or five nuclear chain fibres. Most of the soleus and tenuissimus spindles shown in the illustrations have this composition. Few spindles in the leg muscles contain more than a total of eight fibres.

The total number of muscle fibres in interosseous spindles often exceeds eight and there may be as many as thirteen fibres in one spindle (figure 62*g*, plate 47). The usual number of nuclear chain fibres is four or five, but spindles with three or four nuclear bag fibres occur much more frequently than in leg muscle spindles.

TABLE 4. NUMBER OF INTRAFUSAL MUSCLE FIBRES IN 78 SPINDLES, DERIVED FROM SERIAL TRANSVERSE SECTIONS

The combinations of nuclear bag and nuclear chain fibres which were encountered are given at the top of the table; the number of spindles of each type is given in the corresponding column.

	number of spindles containing:																
muscle	1 n.b. fibre + 4 n.c. fibres	2 nuclear bag fibres + nuclear chain fibres						3 nuclear bag fibres + nuclear chain fibres					4 nuclear bag fibres + nuclear chain fibres				
(no. of muscles in parentheses)		2	3	4	5	6	7	3	4	5	6	8	3	4	5	8	9
tenuissimus (2)	2	1	1	6	6	—	—	1	2	1	—	—	—	—	—	—	—
soleus (2)	1	—	3	6	5	1	—	1	1	—	1	—	1	—	—	—	—
interosseous (3)	1	—	1	3	9	4	1	4	7	—	—	1	—	2	3	1	1
total in all muscles	4	1	5	15	20	5	1	6	10	1	1	1	1	2	3	1	1

In a total of 237 *isolated whole spindles and sectioned spindles from all the muscles examined the mean number of nuclear bag fibres was* 2·2 (*two fibres most common*), *and the mean number of nuclear chain fibres was* 4·1 (*four fibres most common*), *per spindle.*

(8) *Origin and insertion of intrafusal fibres*

Most spindles in the leg muscles are approximately symmetrical about the nuclear region, both ends being attached to extrafusal fasciculi. The spindle has its origin in one fasciculus, becomes separated from it and closely related to an intramuscular nerve trunk and to blood vessels in the region of the spindle lymph space. Its other end is inserted into a different extrafusal fasciculus, which is closely related, however, to the fasciculus of origin. Two, or occasionally more, spindles are sometimes arranged in series, in which case the two groups of nuclear bag fibres overlap and are bound together.

At the extremities, beyond the ends of the nuclear chain fibres, the nuclear bag fibres are without a connective tissue sheath (figure 58*b*, *w*, plate 43). The fibres lie close together on the edge or near the apex of an extrafusal muscle fasciculus (figure 59*t*, plate 44). They are not tightly bound to the extrafusal fasciculus until almost at their ends where they taper suddenly over a relatively short distance (figure 1). They end in tendinous strands of connective tissue, 0·5 to 1 mm long, attached to the perimysium of the extrafusal fasciculus.

Most interosseous muscle spindles are asymmetrical, the nuclear region being nearer to one end of the spindle, which is often attached to the connective tissue sheath of the whole muscle or to tendon (figure 1, spindles III and IV; figure 32.) At this end of the spindle the sheath extends right to the end and is continuous with a bundle of connective tissue (figure 15 and figure 97, plate 52). There is sometimes a tendon organ on tendon fibres in series with the spindle, as was the case with the spindle in figure 11. The intrafusal fibres of both types end in the bundle of connective tissue at about the same level (figure 4*t* to *w*; figure 5*s* to *v*).

At the other end of the spindle, if the nuclear chain fibres are shorter than the nuclear bag fibres (figure 1, spindle IV), they are attached to the nuclear bag fibres (figure 5*c* to *e*) as in spindles in leg muscles. *If the nuclear chain fibres are as long, or longer, than the nuclear bag fibres, they are attached in the same manner as the latter, deep in the muscle and often well separated from each other* (figure 4*a* to *d*); the fibres are attached to the surface of the same extrafusal fasciculus, however.

Although symmetrical spindles occur typically in the leg muscles, and asymmetrical spindles occur typically in the small muscles of the foot, most muscles contain examples of both forms. The difference in form of spindles is probably related to the length and to the mode of origin and insertion of the muscles rather than to their position in the limb.

Part II. Innervation of muscle spindles

The total number of nerve fibres entering any one spindle varies from about eight in some simple spindles to about twenty-five in some complex spindles (figure 28, and figure 116, plate 54), while tandem spindles may receive nearly forty fibres (figure 17, and figure 99, plate 52). The complexity of the innervation of many normal spindles makes it difficult to decide which nerve endings are sensory and which are motor. Separate descriptions of the afferent and efferent innervation of spindles, from cats in which the ventral and

dorsal spinal roots, respectively, were cut some time previously, are given below. The results in each case are correlated with the innervation of normal spindles. The information was derived from a study of over 500 isolated spindles.

Sensory innervation

(9) *Diameter and number of afferent nerve fibres*

The diameters of the afferent nerve fibres of 222 spindles teased out of muscles from different sites were measured under an oil-immersion lens. Gold chloride stains the axon purplish black, and the colour diffuses into the surrounding myelin sheath which stains faintly. In photographs of gold-stained spindles, however, the myelin sheath is not usually visible. The axon diameters of the largest and smallest afferent nerve fibres from spindles are about half and two-thirds of the total diameter respectively. *Values for the diameter of afferent nerve fibres from spindles given in this paper all refer to the total diameter.* A direct comparison may thus be made with the diameter of the fibres in the nerves to the muscle, stained with osmium tetroxide which is reduced by the myelin of the myelin sheath and therefore reveals the total diameter of the fibre. Close to the spindles some of the afferent fibres, especially the largest ones, divide into a number of branches all of which supply the same nerve ending. *The measurements of diameter quoted were made about* 1 *mm from the spindle,* before any such branching had taken place.

Fibre-size histograms were constructed for the afferent nerve fibres of 95 de-efferented spindles, i.e. spindles in which all the motor nerve fibres had degenerated following transection of the ventral spinal roots. On the basis of the study of the nerve fibres to, and nerve endings in, these de-efferented spindles, fibre-size histograms were also constructed for the afferent nerve fibres to 127 normal spindles. These in no way differed from the histograms for the de-efferented spindles, and the combined results of the two sets of measurements are presented in figure 9 *a*, *b*, *c*. In the soleus muscle, tenuissimus muscle, and the interosseous muscles *the afferent nerve fibres fall into two distinct groups. The group of larger fibres with a mean diameter of* 11 *to* 12 μ *correspond with the group I a afferent fibres in the nerves to skeletal muscle. They*

FIGURES 9 and 10. Fibre size histograms of the diameter of nerve fibres to isolated spindles stained with gold chloride. Measurements of diameter were made about 1 mm from the spindles.

FIGURE 9. Afferent nerve fibres. Values for total diameter are given. Fibres from primary sensory endings (group I*a* fibres), stippled shading; fibres from secondary sensory endings (group II fibres), uniform dark shading.

a. Soleus muscle. 39 de-efferented + 14 normal spindles. Mean diameters; group I*a*, 12·1μ; group II, 6·0μ.

b. Tenuissimus muscle. 11 de-efferented + 91 normal spindles. Mean diameters: group I*a*, 12·4μ; group II, 6·0μ.

c. Interosseous muscles. 45 de-efferented + 22 normal spindles. Mean diameters: group I*a*, 10·8μ; group II, 5·1μ.

FIGURE 10. Motor nerve fibres. Values for axon diameter are given. Axons less than 2μ in diameter belong to the γ_2 motor group, and the peak at $\frac{1}{2}$–1μ is formed by unmyelinated terminal branches of γ_2 axons. Axons greater than 3μ belong to the γ_1 motor group. Axons between 2μ and 3μ are mostly γ_1 axons, but a few γ_2 axons occur in this range, also. All measurements from de-afferented spindles.

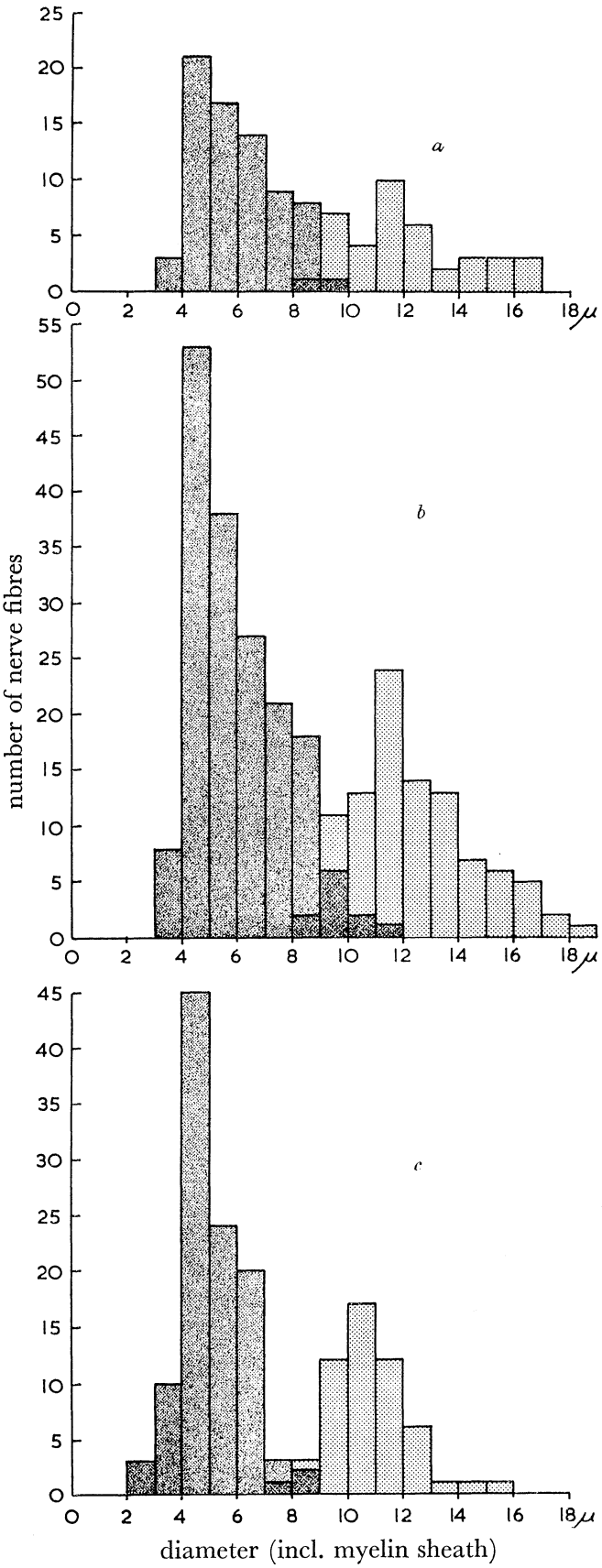


FIGURE 9

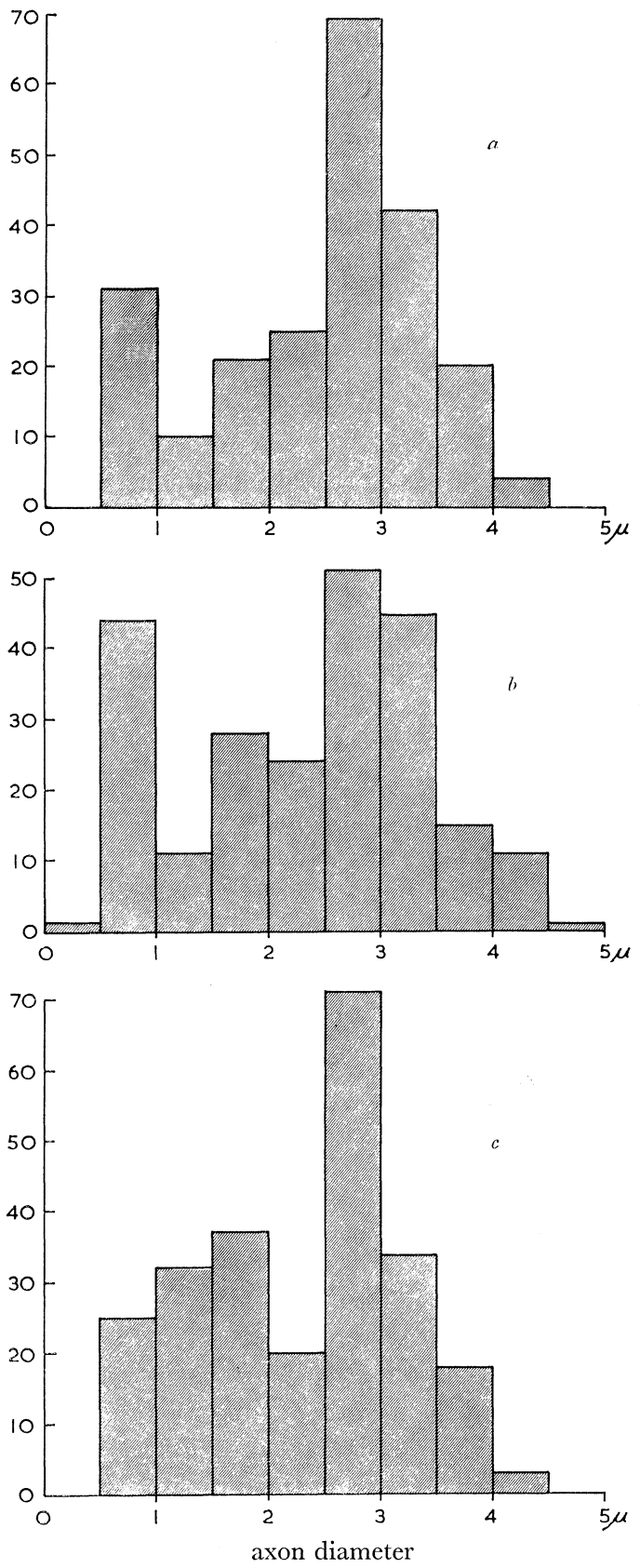


FIGURE 10

For legends see facing page.

supply the primary sensory nerve ending which overlies the centre of the nuclear region and are represented by the part of the histograms with light shading. *The group of smaller fibres with a mean diameter of* 5 *to* 6 μ *correspond with the group II fibres in muscle nerves. They innervate the secondary sensory nerve endings* elsewhere in the spindle and are represented by the darkly shaded areas in the histograms. Where the two groups overlap the two types of shading are superimposed. *Each spindle receives one group Ia fibre and from zero to five group II fibres.* The larger group II fibres usually supply secondary sensory endings in the S_1 position (see later). The mean diameters of corresponding groups are almost the same in the soleus and tenuissimus muscles, and rather less in the interosseous muscles.

(10) *The primary sensory nerve ending*

(*a*) *Site and form of the primary ending.* The primary sensory nerve ending lies approximately at the centre of the lymph space and its terminations cover most of the nuclear region of the intrafusal muscle fibres. A tandem spindle, which has two nuclear regions, has two primary sensory endings. Occasionally, two spindles lie side by side and their intrafusal fibres may be contained in the same connective tissue sheath for part of their length (previously termed a 'compound spindle' by Sherrington (1894)); the two primary sensory nerve endings in such spindles may lie end to end or may overlap to a varying degree, but the terminations of each nerve ending lie only on the intrafusal fibres of the appropriate spindle. Apart from these anatomical peculiarities *each spindle always has one, and only one, primary sensory nerve ending. Each primary ending is the termination of one of the group Ia fibres in the muscle nerve* ('stem' or 'parent' fibres); very occasionally one axon may branch to supply primary endings in two simple spindles. Sometimes, close to the spindle, the primary ending appears to be supplied by two fibres, but if these are traced back into the muscle they are found to be branches of a single nerve fibre (figure 12). The primary endings are present in spindles after transection of the ventral spinal roots (figures 63 to 67, plate 48; figure 75, plate 49) and degenerate after section of the dorsal spinal roots (figures 70 to 74, plate 49).

The primary sensory ending consists of a number of spirals. Each spiral surrounds one intrafusal fibre, and every intrafusal fibre of both the nuclear bag and nuclear chain fibre groups has one such spiral. Since in the nuclear region in all spindles the nuclear bag fibres are always about twice as large in diameter as the nuclear chain fibres, there are always two distinct sizes of spiral termination. In spindles from the leg muscles, in which there are usually two nuclear bag fibres, these two muscle fibres often move to the sides of an isolated spindle when it is mounted under a cover glass. Thus, two large spirals are visible at the edges of the spindle, while the small spirals round the nuclear chain fibres are grouped in the centre (figures 64, 67, plate 48, and figure 12; figure 75, plate 49). In these three spindles the nuclei of the nuclear bags and nuclear chains can be seen underlying the large and small spirals, respectively. Figures 11 to 14 are projection tracings of four de-efferented isolated spindles: photographs of the sensory endings only of these spindles are shown in figures 63 to 66, plate 48. The arrangement of the large and small spirals is less distinct in interosseous muscle spindles because of the larger number of intrafusal fibres, but the basic pattern of one large spiral per nuclear bag fibre and one small spiral per nuclear chain fibre is the same as in other spindles (figures 63, 65, 66, plate 48, and figures 11, 13, 14).

Each individual spiral is supplied about halfway along its length by a branch of the group I*a* axon. The spiral sometimes terminates in a small spray on the surface of the intrafusal muscle fibre which it surrounds (figure 67, plate 48). Such small sprays are not always present, however (figure 75, plate 49).

The primary sensory ending is between 250 and 400 μ long, and the average length is about 300 μ. The term 'annulo-spiral' ending was used in the past to describe what is here called the 'primary sensory ending'. The former term is descriptive of the rings and spirals which are present but, as will be shown later, other sensory endings in the spindle frequently have a spiral form. The term previously applied to these other endings was 'flower-spray ending', which is not appropriate for many of them. The descriptive terms have, therefore, been replaced by the terms 'primary sensory ending' (supplied by a primary, or group I*a*, nerve fibre) and 'secondary sensory ending' (supplied by a secondary, or group II, nerve fibre). This terminology was first proposed by Ruffini (1898) and later advocated by Barker (1948).

(*b*) *Degeneration of the primary ending.* Following transection of the appropriate dorsal spinal root containing the group I*a* axon which supplies it, the primary sensory ending degenerates. The process of degeneration is illustrated in figures 70 to 74, plate 49. A normal primary ending is shown in figure 70, plate 49. About 3 days after dorsal root transection the spirals disintegrate, as shown in figure 71, plate 49, and also in figure 68, plate 48. In the latter, degeneration is commencing close to the nerve endings in the group I*a* axon which enters the spindle from the right. The remains of a primary ending 4 days after dorsal root transection are shown in figure 72, plate 49. The material of the nerve endings is seen as isolated black 'blobs' and the underlying nuclei of two nuclear bags are now visible. The primary axon shows extensive degeneration close to the nerve ending. After 6 days the primary ending has completely disappeared (figure 73, plate 49) and both the nuclear bags and nuclear chains can be seen. The degeneration process proceeds centrally up the afferent fibres, and 6 days after the dorsal roots are cut it is clearly seen in the intramuscular nerve branches. This is shown in figure 95, plate 51, in which degenerating group I*a* and group II fibres are present beside two intact motor axons. Degeneration is evident in the nerves to the muscles about 2 weeks after root transection but the degeneration process and removal of the myelin is not complete until about 5 to 6 weeks have elapsed.

After several months the nuclei of the intrafusal fibres begin to disappear, as has been described earlier; the *P* region of a spindle 7·5 months after dorsal root section is shown in figure 74, plate 49. There is no trace of the primary ending or its axon, but the lymph space, and some of the nuclei in the nuclear bag fibres, are still present.

(11) *Secondary sensory nerve endings*

(*a*) *Number of secondary endings. The number of secondary sensory endings in a spindle varies from zero to five.* In most isolated spindles each of the secondary endings appears to arise from a different group II fibre. It is not usually possible, however, to trace the fibres far enough back in the intramuscular nerve trunks to determine whether fibres branch to supply several secondary endings in the same spindle. In one particular spindle a single fibre was observed to divide as it approached the spindle, the branches supplying two

secondary endings one on each side of the primary ending. On several occasions a group II fibre was seen to divide and to supply secondary sensory endings in different spindles.

(*b*) *Classification and arrangement of secondary endings. All spindles which receive innervation from both group Ia and group II afferent fibres are termed 'complex spindles', in contrast to 'simple spindles' which have group Ia innervation only.* The terms 'intermediate spindle' and 'myotube ending' used by some writers (Ruffini 1898; Barker 1948; Cooper 1960) have been omitted from the descriptions which follow. Since the nuclear chain fibres have an arrangement of nuclei like the myotubes of developing muscle fibres through the whole of the nuclear region, the term 'myotube ending', applied to some secondary sensory endings, is not sufficiently specific. Many secondary endings are situated on regions of intrafusal muscle fibres where there are no central nuclei at all.

A new nomenclature, which may be used to indicate the position in the spindle of either sensory or motor endings, is adopted in this paper. It also provides a simple way of classifying all spindles in terms of the number and position of the secondary sensory endings which they contain. Each secondary sensory ending occupies a length of spindle which varies from 300 to 500 μ, the average length being about 400 μ. Each spindle may be considered to be divided into a *P* region (primary region) about 300 μ in extent, and a series of *S* regions each about 400 μ in length, on either side of the *P* region. The *S* region

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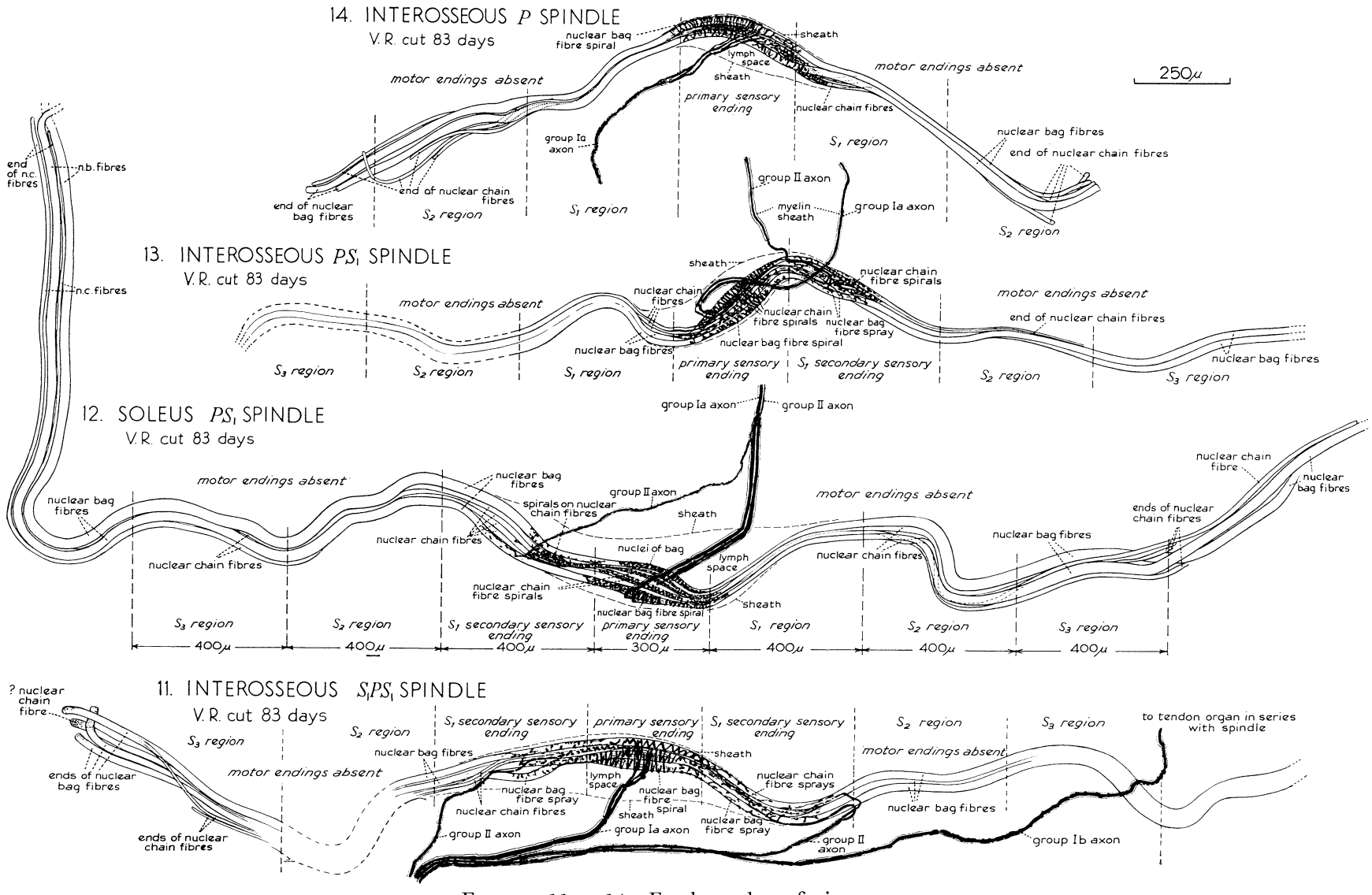
FIGURES 11 to 14. *Tracings of de-efferented spindles (gold chloride staining).* Projection tracings of four isolated whole spindles from cat 14 (table 1), in which complete de-efferentation of one hind limb was carried out 83 days before the muscles were stained with gold chloride. In each case part of the spindle was located in the microscope field under a low-power objective lens. The image was projected through a prism, and the outline of the spindle and its nerve endings was traced. A number of fields of view were drawn so that a tracing of the complete spindle was obtained. The detailed structure, seen in all planes of focus with an oil-immersion lens, was then added to the drawing. The lines transverse to the spindle indicate the boundaries between *P* and *S* regions. In each spindle the *P* region is 300 μ long and each *S* region is 400 μ long. For details of this nomenclature, see above. The nuclear bag fibres are drawn on top of the nuclear chain fibres at all points where they cross or are superimposed. In regions in which individual intrafusal fibres could not be distinguished the edge of the spindle is indicated by a broken line. Photomicrographs of the sensory regions of these spindles are shown in figures 63 to 66, plate 48.

FIGURE 11. *De-efferented interosseous spindle, type* S_1PS_1. This spindle has three nuclear bag fibres and at least three nuclear chain fibres; one end was inserted in muscle and the other in tendon in series with a tendon organ. There is a secondary sensory ending in the S_1 region on each side of the primary sensory ending (figure 63, plate 48).

FIGURE 12. *De-efferented soleus spindle, type* PS_1. This spindle has four nuclear chain fibres, and two nuclear bag fibres both ends of which were inserted in muscle and are not shown. There is a secondary sensory ending in the S_1 region on one side of the primary ending (figure 64, plate 48).

FIGURE 13. *De-efferented interosseous spindle, type* PS_1. This spindle has two nuclear bag fibres the ends of which are not shown, and four nuclear chain fibres which end in the S_2 region at one end; the fibres were not distinguishable at the other end. There is a secondary sensory ending in the S_1 region on one side of the primary ending (figure 65, plate 48).

FIGURE 14. *De-efferented interosseous spindle, type P.* This spindle has two nuclear bag fibres and four nuclear chain fibres; all the fibres are about the same length. The spindle has a primary sensory ending but no secondary sensory endings (figure 66, plate 48).



FIGURES 11 to 14. For legend see facing page.

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PLATE 48

FIGURES 63 to 69. *Sensory nerve endings (gold chloride staining).*

FIGURE 63. *Complete sensory innervation of an interosseous spindle, type* S_1PS_1. *Cat* 14, *de-efferented* 83 *days.* (See also figure 11.) The sensory ending has spiral terminations round each of the nuclear bag and nuclear chain muscle fibres. The secondary sensory terminations lie on both types of muscle fibre, but are denser on the nuclear chain fibres which lie down the centre of the spindle. Note that no small or very fine nerve fibres accompany the nerve fibres supplying the sensory endings.

FIGURE 64. *Complete sensory innervation of a soleus spindle, type* PS_1. *Cat* 14, *de-efferented* 83 *days.* (See also figure 12.) The primary sensory ending has a large spiral round each of the two nuclear bag fibres at the top and bottom edges of the spindle, and a small spiral round each of the four nuclear chain fibres in the centre. The nuclei of the nuclear bags and chains are visible beneath the spirals. The nerve fibres to the spirals are all branches of the same group I*a* fibre. The secondary sensory terminations are of irregular spiral form, and lie almost entirely on the nuclear chain fibres, with small accessory sprays on the two nuclear bag fibres. Note the absence of very small nerve fibres to the spindle.

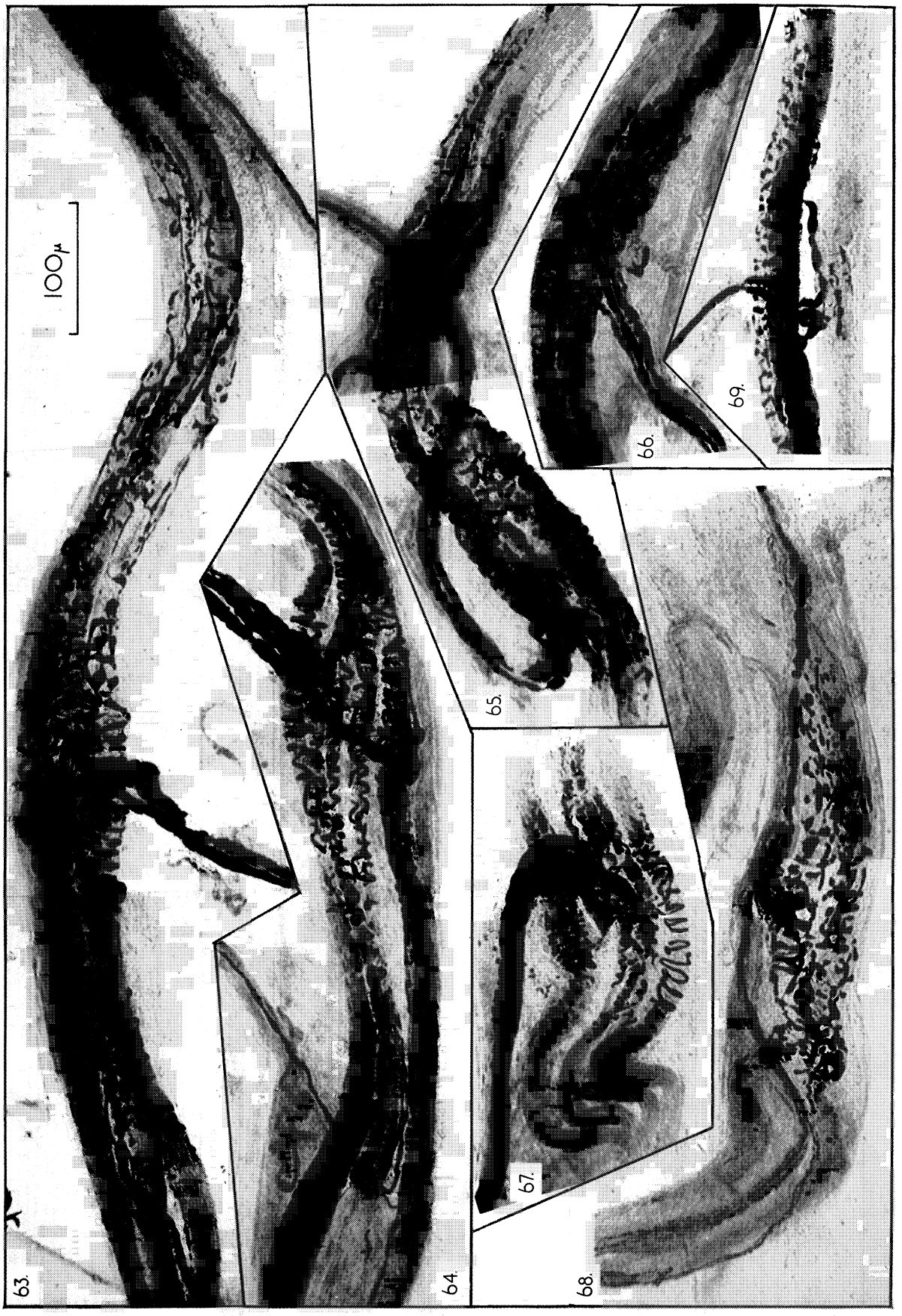
FIGURE 65. *Complete sensory innervation of an interosseous spindle, type* PS_1. *Cat* 14, *de-efferented* 83 *days.* (See also figure 13.) The primary sensory ending has large spirals round the two nuclear bag fibres and small spirals round the four nuclear chain fibres in the centre. The secondary sensory terminations lie predominantly on the nuclear chain fibres which cross to the top edge of the spindle in the S_1 region. Note the absence of very small nerve fibres to the spindle.

FIGURE 66. *Complete sensory innervation of an interosseous spindle, type P. Cat* 14, *de-efferented* 83 *days.* (See also figure 14.) The primary sensory ending has large spirals round the two nuclear bag fibres at the top and bottom edges of the spindle, and small spirals round each of the four nuclear chain fibres which lie in the centre and cross to the bottom edge at the right hand end of the photograph. The nuclei are visible beneath the spirals. Note the absence of very small nerve fibres to the spindle.

FIGURE 67. *Primary sensory ending in a soleus spindle, type* PS_2. *Cat* 14, *de-efferented* 83 *days.* This spindle had a secondary sensory ending in one S_2 region, but none in either S_1 region. It may be a PS_1S_2 spindle in which the S_1 secondary ending degenerated completely following damage to its nerve fibre when the ventral roots were cut. The primary ending has a large spiral round each of the two nuclear bag fibres at the top and bottom edges of the spindle; each spiral ends in a small terminal spray. It also has small spirals round each of the four small nuclear chain fibres in the centre. Note the absence of very small nerve fibres to the spindle.

FIGURE 68. *Primary sensory ending in an interosseous spindle, type P. Cat* 3, *de-afferented* 3 *days.* The primary sensory ending is degenerating; the spirals are breaking up, and the group I*a* nerve fibre shows segmentation of its axonic material. Two distinct sizes of nerve fibre remain intact. A bundle of small fibres (γ_1 motor fibres) passes down the centre of the spindle to the left of the primary ending. A bundle of very fine fibres travels to the same end along the lower edge of the spindle while several other fine fibres traverse the primary ending and pass to the other end (γ_2 motor fibres).

FIGURE 69. *Secondary sensory ending in the* S_1 *region of a tenuissimus spindle, type* PS_1S_2. *Cat* 12, *de-efferented* 247 *days.* The secondary sensory terminations form incomplete spirals round nuclear chain fibres which lie in a bundle on top of a nuclear bag fibre. A second nuclear bag fibre, almost free of sensory terminations, lies along the lower edge of the spindle. Note the distinct cross striations of the intrafusal muscle fibres, and the absence of any very small nerve fibres accompanying the group II fibre.



FIGURES 63 TO 69

PLATE 49

FIGURES 70 TO 77. *Degeneration of the primary sensory nerve ending (gold chloride staining).*

FIGURE 70. *Tenuissimus spindle, type* $PS_1S_2S_3$*; normal.* Primary sensory ending with three large spirals and several small spirals; group I*a* axon enters top left. Part of an S_1 secondary ending is visible on the right; its group II axon enters bottom left and traverses the primary ending.

FIGURE 71. *Interosseous spindle, type P; cat* 3, *de-afferented* 3 *days.* The spirals of the primary sensory ending are breaking up, and the underlying nuclei are just visible. The group I*a* axon still appears normal; three intact fine γ_2 motor axons enter the spindle with the afferent axon, and a small γ_2 motor ending lies close to the spirals. (See also figure 19.)

FIGURE 72. *Soleus spindle, type* PS_1*; cat* 7, *de-afferented* 4 *days.* The spirals of the primary sensory ending have almost disappeared, and two nuclear bags are visible. The group I*a* axon is degenerating but a γ_2 motor axon entering with it is intact.

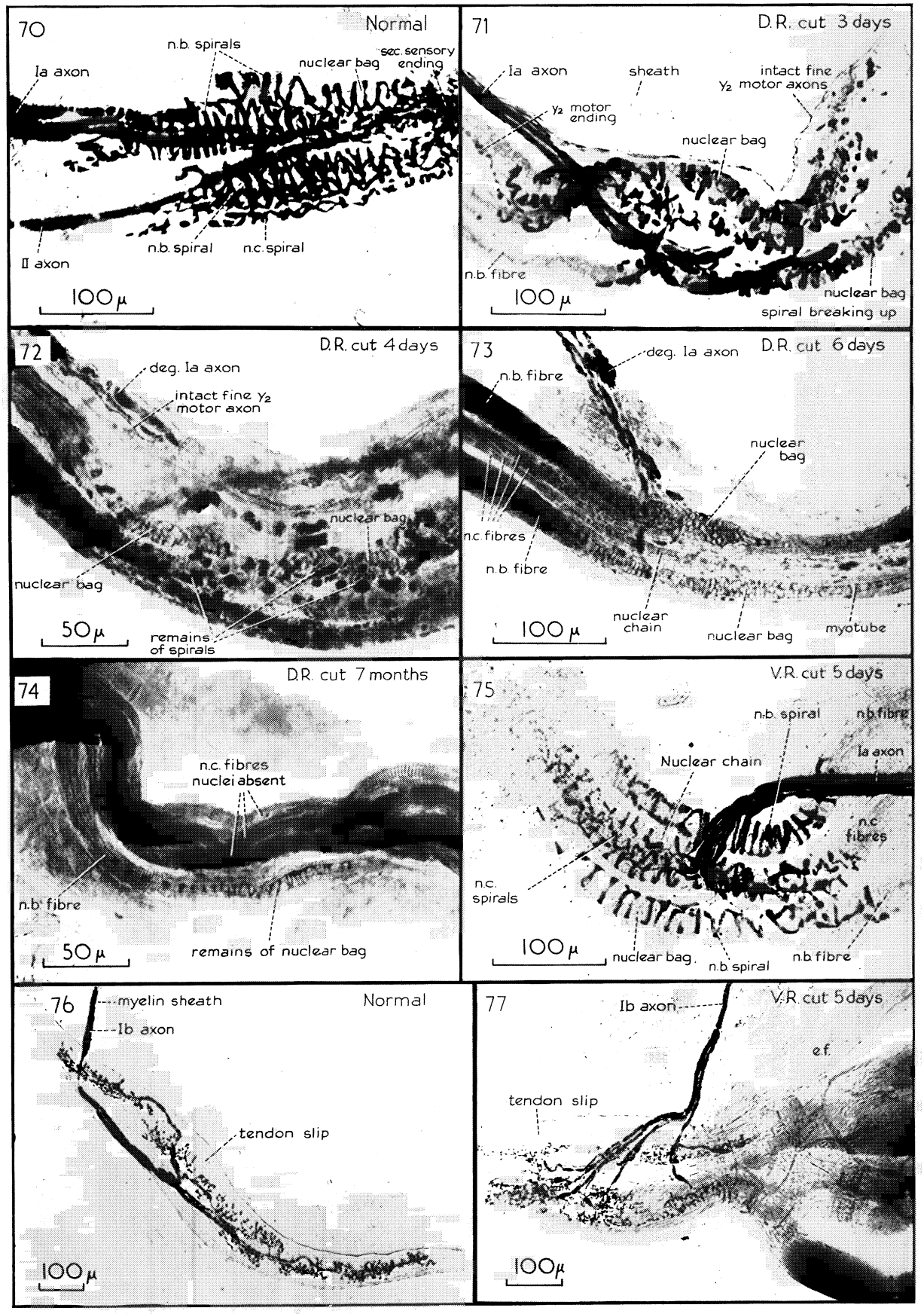
FIGURE 73. *Soleus spindle, type* PS_1*; cat* 5, *de-afferented* 6 *days.* The primary sensory ending has completely degenerated, and its group I*a* axon shows extensive degeneration. Two nuclear bags and one nuclear chain are clearly visible. The other nuclear chains do not lie in this plane of focus, but several nuclear chain fibres are visible between the two nuclear bag fibres on the left.

FIGURE 74. *Tenuissimus spindle; cat* 6, *de-afferented* 225 *days.* The sensory endings and their nerve fibres have disappeared. The atrophied nuclei of one nuclear bag are visible in one intrafusal fibre. The other fibres contain no central nuclei, and are clearly striated through what was previously the nuclear region.

FIGURE 75. *Soleus spindle, type* PS_1*; cat* 12, *de-efferented* 5 *days.* Primary sensory ending intact after transection of the ventral roots. The ending has two large spirals round nuclear bag fibres at top and bottom edges of the spindle, and small spirals encircling each of the nuclear chain fibres in the bundle in the centre.

FIGURE 76. *Interosseous tendon organ; normal.* Multiple sprays of a Golgi tendon organ lying on the surface of an isolated slip of tendon, seen in cross section in the top left corner.

FIGURE 77. *Soleus tendon organ; cat* 12, *de-efferented* 5 *days.* Intact tendon organ at the junction of a bundle of extrafusal fibres with a slip of tendon.



FIGURES 70 TO 77

Plate 50

FIGURES 78 TO 86. *Secondary sensory nerve endings (gold chloride staining).* Width of spindle indicated by broken lines and arrow heads. n.b., nuclear bag fibre; n.c., nuclear chain fibre.

FIGURE 78. *Soleus spindle, type* PS_1S_2*; cat* 14, *de-efferented* 83 *days.* The S_1 and S_2 regions are shown. The nuclear chain fibres in the bundle in the centre are completely covered in secondary sensory terminations of spiral form while two nuclear bag fibres, one above and one below, are almost free of nerve endings.

FIGURE 79. *Soleus spindle, type* $S_1PS_1S_2$*; normal.* The S_2 and S_3 regions of the spindle drawn in figure 29 are shown. The nuclear chain fibres in the bundle at the lower edge in the S_2 region are covered with secondary sensory terminations consisting of incomplete spirals. This ending extends into the S_3 region where it is poorly stained. Small accessory sprays lie on nuclear bag fibres in the S_2 region.

FIGURE 80. *Soleus spindle, type* PS_1*; cat* 14, *de-efferented* 83 *days.* The S_1 region is shown. The nuclear chain fibres in the centre are completely covered with secondary sensory terminations of spiral form while two nuclear bag fibres above and below are almost free of nerve endings.

FIGURE 81. *Tenuissimus spindle, type* $PS_1S_2S_3$*; normal.* The S_2 and S_3 regions, of the same spindle as figure 70, plate 49, are shown. The bundle of nuclear chain fibres lies along the lower edge of the spindle and the fibres are covered in secondary sensory terminations of spray and incomplete spiral form. One nuclear chain fibre is separate from the bundle and can be identified by its covering of nerve endings. Three nuclear bag fibres, free of nerve endings, are scarcely visible.

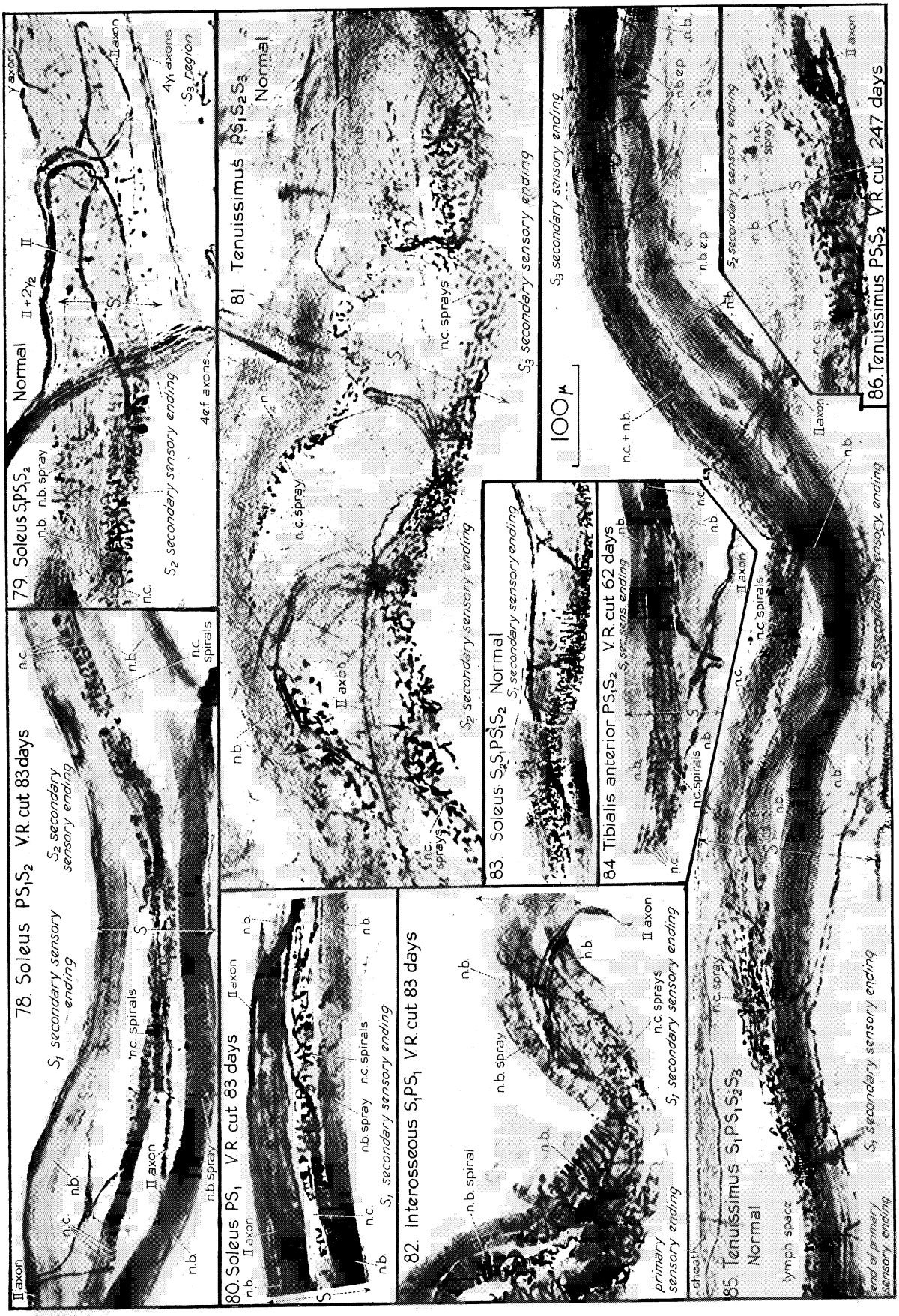
FIGURE 82. *Interosseous spindle, type* S_1PS_1*; cat* 14, *de-efferented* 83 *days.* The P and S_1 regions are shown. Large spirals forming part of the primary sensory ending lie to the left, and a secondary sensory ending lies to the right. The secondary sensory terminations are of spray form and lie on all intrafusal fibres.

FIGURE 83. *Soleus spindle, type* $S_2S_1PS_1S_2$*; normal.* The S_1 region of the spindle drawn in figure 28 is shown. The bundle of nuclear chain fibres lies in the centre and crosses to the lower edge on the right; each of these fibres is covered in secondary sensory terminations of spiral form, while two nuclear bag fibres are almost free of nerve endings.

FIGURE 84. *Tibialis anterior spindle, type* PS_1S_2*; cat* 15, *de-efferented* 62 *days.* The S_1 region is shown. Each of the nuclear chain fibres in the bundle in the centre is covered in secondary sensory terminations of spiral form, while two nuclear bag fibres above and below are almost free of nerve endings.

FIGURE 85. *Tenuissimus spindle, type* $S_1PS_1S_2S_3$*; normal.* The S_1, S_2 and S_3 regions to the right of the P region are shown, and there is a secondary sensory ending in each position; the end of the primary sensory ending is visible on the left. Two large clearly striated nuclear bag fibres have no sensory nerve endings on them. The secondary sensory terminations, of spiral and spray form, lie on the bundle of nuclear chain fibres which is separate from the nuclear bag fibres in the S_2 region, and elsewhere lies on top of one of these fibres.

FIGURE 86. *Tenuissimus spindle, type* PS_1S_2*; cat* 12, *de-efferented* 247 *days.* The S_2 region is shown. Secondary sensory terminations of spray form cover the nuclear chain fibres, while the nuclear bag fibres are free of nerve endings. One nuclear bag fibre lies beneath the bundle of nuclear chain fibres; the other crosses the field above the secondary sensory ending and is scarcely visible.



FIGURES 78 TO 86

nearest to the P region is termed the 'S_1 region', the next one the 'S_2 region' and so on until the 'S_4 region' is reached. This method of zoning is illustrated in figure 12, in which broken transverse lines separate each region from the next. The zoning is only approximate since isolated spindles are not quite straight.

The total length of spindle lying between the distal ends of the S_4 regions at the two ends of a spindle is thus 3·5 mm, which is slightly less than the mean total length of the nuclear chain muscle fibres (table 3). The nuclear bag fibres in leg muscle spindles extend well beyond the S_4 region, but since most of the sensory and motor innervation lies within the regions described, the nomenclature has not been extended beyond the S_4 region. Many spindles, especially those from the small muscles of the foot, are shorter than 3·5 mm and have no S_4 regions and sometimes no S_3 regions (figure 14).

An S_1 secondary sensory ending is one which lies in the S_1 region, and so on. For example, the spindle in figure 28 is an $S_2S_1\,PS_1S_2$ spindle since it has four secondary sensory endings, two on each side of the primary ending in the S_1 and S_2 regions.

The arrangement of the secondary sensory endings in 311 isolated spindles is shown in table 5. All the possible arrangements occur up to a maximum of three secondary endings one one side of the primary ending plus two on the other side. PS_1 spindles occur most frequently, making up 41 % of the total. P spindles and S_1PS_1 spindles occur with equal frequency, each contributing 16 % of the total. The PS_1S_2 and $S_1PS_1S_2$ arrangements are also quite commonly found, but spindles with more than three secondary sensory endings are few in number. A difference between spindles from different sites is that the PS_1S_2 arrangement is as common as the S_1PS_1 arrangement in leg muscle spindles, while $PS_1\,S_2$ spindles are less common in the small muscles of the foot.

TABLE 5. CLASSIFICATION OF 311 ISOLATED SPINDLES STAINED WITH GOLD CHLORIDE ACCORDING TO THE ARRANGEMENT OF THE PRIMARY AND SECONDARY SENSORY NERVE ENDINGS WHICH THEY CONTAINED

P, primary sensory ending; S, secondary sensory ending; e.g. an $S_1PS_1S_2$ spindle has a primary sensory ending with one secondary sensory ending on one side of it and two secondary sensory endings on the other side.

muscle	total of all types	number of spindles with sensory nerve endings arranged as under								
		P	PS_1	S_1PS_1	PS_1S_2	$S_1PS_1S_2$	$S_2S_1PS_1S_2$	$PS_1S_2S_3$	$S_1PS_1S_2S_3$	$S_2S_1PS_1S_2S_3$
tenuissimus	134	21	47	21	20	15	2	4	1	3
soleus	93	10	48	9	10	10	1	2	2	1
interosseous	84	16	33	19	6	5	1	1	2	1
total in all muscles	311	47	128	49	36	30	4	7	5	5
percentage of each type	100	16	41	16	12	10	1	2	1	1

The ratio of secondary sensory endings to primary sensory endings in 134 tenuissimus spindles was 1·56 to 1; in 93 soleus spindles it was 1·49 to 1; in 84 interosseous spindles, 1·40 to 1; for the 311 spindles together the ratio was 1·50 to 1.

A ratio of 1·5 *secondary endings to* 1 *primary ending may be taken as representative of all the muscles examined, i.e.* 1·5 *secondary sensory endings per spindle.*

(*c*) *Site of secondary sensory terminations. In spindles in the leg muscles the terminations of the secondary sensory endings lie predominantly on the nuclear chain intrafusal fibres.* This is especially true of soleus spindles, where the bundle of nuclear chain fibres may often be traced through the spindle by following the course of the secondary endings. In figure 28, and figure 116, plate 54, for example, four secondary endings outline the course of the nuclear chain fibres. Although most of each nerve ending lies on the nuclear chain fibres it is usual for small sprays associated with it to lie on the nuclear bag fibres. The de-efferented soleus spindle in figure 12, and figure 64, plate 48, has one S_1 secondary ending on the bundle of nuclear chain fibres in the centre of the spindle while the two large nuclear bag fibres on either side are almost entirely free of secondary terminations. A similar arrangement is present in the parts of de-efferented spindles in figures 78, 80, plate 50 (soleus), and in figure 84, plate 50 (tibialis anterior). Figure 69, plate 48 and figure 86, plate 50, show S_1 and S_2 secondary sensory endings, respectively, lying almost exclusively on the nuclear chain fibres in two de-efferented PS_1S_2 tenuissimus spindles. A nuclear bag fibre crosses the field in each photograph and is scarcely visible because there are no nerve terminals on it to outline its edges. The predominance of secondary sensory material on the nuclear chain fibres may also be seen in normal spindles (figures 79, 81, 83, 85, plate 50).

In spindles from the small muscles of the foot the picture is not so clear, since in short spindles with many intrafusal fibres of greatly varying diameter it is more difficult to be certain on which type of intrafusal fibre the nerve terminals are situated. While it is true in this case, also, that most of the secondary sensory innervation is concentrated on the nuclear chain fibres, the proportion of sensory material on the nuclear bag fibres is usually larger than in leg muscle spindles (figures 11, 13, and figures 63, 65, plate 48; figure 82, plate 50).

(*d*) *Form of secondary endings.* The classical description of the form of a secondary sensory ending is that of a 'flower-spray'. Barker (1948) states that some such endings in the rabbit have a spiral form. *In most of the spindles from the cat studied in this investigation, one at least of the secondary sensory endings was definitely of spiral form.* They differ from the primary ending, however, not only in the type of nerve fibre supplying them, but also because they never include any large spirals round the nuclear bag fibres; all the spirals are small and each surrounds a nuclear chain fibre. Any associated nerve terminals on the nuclear bag fibres are always in the form of small sprays. Secondary sensory endings of spiral form are very common in the S_1 region (figure 64, plate 48; figures 78, 80, 83, plate 50). Apart from small accessory sprays on nuclear bag fibres, complete secondary sensory endings of spray form are rare in leg muscle spindles, i.e. endings in which the afferent axons branch in the form of a tree with small sprays at the end of each branch, as is usual in tendon organs (figures 76, 77, plate 49). The nearest approach to this in the spindles illustrated in this paper is the S_2 secondary ending in figure 79, plate 50, and the S_1 endings in figure 117, plate 54, and figure 85, plate 50. In interosseous spindles, which often have more than two large intrafusal fibres, secondary sensory endings of spray form are more common (figure 63, plate 48; figure 82, plate 50).

The secondary sensory endings of many spindles have the form of those shown in figures 81, 86, plate 50, and figure 69, plate 48. The general appearance is that of a spray, but closer examination of the terminations which stain almost black shows that along the course of an individual nuclear chain fibre these black terminal points are arranged in a

regular pattern ('*n.c.* spray' in figure 86, plate 50). The black dots are probably parts of a small spiral in which very thin connecting links between the dots are unstained. Sometimes, however, the black dots lie along the edges of the intrafusal muscle fibres only. Since this appearance does not depend on the orientation of the intrafusal fibre, it is probable that a complete spiral is present but is not deeply stained, so that the turns of the spiral are not noticeable where they cross the fibre; where they curve round the edge of the fibre, however, the turns of the spiral are viewed along their length and are seen as black terminal points apparently separate from one another. Thus, secondary sensory endings on nuclear chain muscle fibres are probably more often of spiral form than appears at first sight, differences in density of staining accounting for some of the differences in form of the endings observed in gold stained preparations.

Motor innervation

(12) *Fusimotor fibres*

The motor nerve fibres to spindles are referred to, in general, as fusimotor fibres as proposed by Hunt & Paintal (1958).

(*a*) *Types of fusimotor fibre. In muscle spindles in which all afferent nerve fibres and nerve endings have completely degenerated after transection of the appropriate dorsal spinal roots, two distinct types of nerve fibre remain which may be distinguished by their diameter close to or within the spindle, and by the site and form of their nerve endings.*

The two types of nerve fibre can be seen clearly in the spindle in figure 18, which was isolated from a soleus muscle 45 days after transection of the dorsal roots which was completely satisfactory (table 1, cat 8). Part of this spindle is shown enlarged in figure 87, plate 51. Several very fine nerve fibres, with an axon diameter of 1 μ or less, enter the spindle along with some small nerve fibres with an axon diameter of about 4 μ. The apparent discontinuities in the 4 μ fibres are an artifact due to stretching of the fibres during teasing, and the appearance differs in a number of ways from the segmentation of axonic material which occurs during degeneration. Any fibres cut or damaged at the time of operation would have degenerated and completely disappeared, as have the afferent fibres and nerve endings in this spindle, in much less than 45 days.

Separate groups of intact small and very fine nerve fibres can be seen also in the simple spindle in figure 68, plate 48, which was isolated 3 days after satisfactory cutting of the appropriate dorsal spinal roots (table 1, cat 3), and in which the primary sensory ending is degenerating. Small nerve fibres in the spindles show extensive degeneration or are absent 3 days after the appropriate spinal root is cut, so that neither the small fibres nor the very fine fibres in this spindle can have entered or emerged from the spinal cord via the dorsal roots. Another spindle in which very fine nerve fibres are intact 3 days after dorsal root transection is shown in figure 71, plate 49. Two sizes of nerve fibre which were present in addition to those supplying the sensory endings are visible in the normal spindles in figures 102, 112, plate 53, also. Both the small and the very fine nerve fibres have always been found in all de-afferented and normal spindles from the soleus and interosseous muscles which were well stained.

Both small and very fine fibres enter normal spindles with the primary and secondary afferent fibres. In the de-efferented spindles illustrated in figures 11 to 14, and figures 63

to 67, 69, plate 48, no fibres with an axon diameter of less than 4 μ are present. In general, no nerve fibres to spindles with an axon diameter less than 2 μ are present more than a few days after the lumbar ventral roots are cut, and any other small nerve fibres (axon diameter 2 to 5 μ) which remain can be traced to secondary sensory nerve endings. The very fine nerve fibres often appear to be absent when the staining with gold chloride is not optimum; such fibres were absent, however, in all well-stained spindles from cats 14, 15 and 16 (table 1) in which complete ventral root transection had been carried out 48 to 83 days previously. In particular, there were no very fine nerve fibres in twelve of these spindles in which the staining throughout the spindle was so good that they would certainly have been seen had they been present.

Thus, both types of nerve fibre which remain in the spindles of the hind limb after the appropriate dorsal roots are cut, disappear after the ventral roots are cut. Hence they all definitely leave the spinal cord through ventral roots L5 to S2 and are 'motor' fibres in the usual sense of the word. In this paper the group of small fibres are termed γ_1 fibres and the group of very fine fibres are termed γ_2 fibres. The reasons for adopting this nomenclature are given in the Discussion.

(*b*) *Branching and diameter of γ_1 and γ_2 fusimotor fibres. The values of diameter given in this description of the motor innervation of spindles are those of axon diameter*, but it may be assumed that the total diameter was only slightly greater (cf. description of afferent nerve fibres above where values for the total diameter were given). The term 'axon' rather than 'fibre' is used below when reference is made to the diameter of fusimotor fibres, to indicate that the values are those of axon diameter.

Axons of the γ_1 type are 3 to 5 μ in diameter in the intramuscular nerve branches. Some division of γ_1 axons certainly takes place as they approach the spindles, and sometimes the divisions supply different spindles. An example is shown in figure 16; a γ_1 axon approaches the spindle along with a degenerating group II afferent fibre and divides at a node, one branch supplying the spindle shown and the other joining a small nerve branch to another spindle. *Branching of γ_1 axons within the last few millimetres of their course to the spindles and within the spindles is not extensive. Most γ_1 axons near to the spindles are 2·5 μ to 4 μ in diameter and typically they continue their course within the spindle to their nerve endings with little further reduction in size.* Sometimes a single γ_1 axon between 4 and 5 μ in diameter enters one end of the spindle and divides into several branches of 2 to 3 μ which continue to the nerve endings. This has been found infrequently in this investigation.

Axons of the γ_2 type are about 2 μ, or sometimes 3 μ, in diameter in the intramuscular nerve branches. At this point it is difficult, and often impossible, to distinguish them from γ_1 axons. *The γ_2 axons branch much more extensively than the γ_1 axons near to and within the spindles. Close to the spindles the γ_2 axons are usually 1·5 to 2 μ in diameter. Most of them, however, undergo a sudden reduction to 1 μ or less before they reach the spindles.* If they enter the spindles more than about a millimetre from their nerve endings, they may still be about 2 μ at the point of entry (figure 23). They then traverse the spindle, becoming very fine at intervals over a short distance, after which they continue to their endings as typical γ_2 axons of less than 1 μ in diameter (figures 16, 18).

Thus, in the intramuscular nerve branches two groups of fusimotor axons of different diameter are not obvious. A few fine γ_2 axons are usually visible in the small nerve branches to individual spindles and the proportion of fine γ_2 axons to other γ_2 and γ_1 axons increases as the spindle is approached, partly due

to the transition of γ_2 axons from 2 μ to less than 1 μ, and partly to branching of fine γ_2 axons. In the spindles themselves the difference in diameter of the two types of axon is often very striking, the diameter of the γ_2 axons being less than one third of that of the γ_1 axons.

Sometimes it was not possible to trace the motor axons individually into the spindles, and axons 2 to 3 μ in diameter could not be classified as γ_1 or γ_2 axons, especially if the staining was poor. Such axons are labelled γ axons in the diagrams.

The diameters of fusimotor axons were measured to the nearest 0·5 μ, under an oil-immersion lens, in the small nerve branches about 1 mm from the spindles. The largest motor axon encountered was 5 μ in diameter. The diameters of the axons to 25 soleus, 41 tenuissimus and 32 interosseous, de-afferented spindles are represented in the histograms in figure 10*a*, *b*, *c*. It is probable that a number of γ_2 axons were not measured because they were unstained or obscured, so that the proportion of γ_2 axons in the histograms is less than the proportion of γ_2 axons, out of the total number of motor axons, actually present in the spindles.

The histograms of soleus and tenuissimus axons are similar; there are two peaks, one at 0·5 to 1 μ and the other at 2·5 to 3 μ. The smaller group between 0·5 and 1·5 μ is definitely formed by γ_2 axons. The larger group ranging from 1·5 to 4·5 μ consists of γ_1 axons, and γ_2 axons which were measured at a point where they were still relatively large. The interosseous histogram has two peaks, the larger one at 2·5 to 3 μ as before but the smaller one is at 1·5 to 2 μ; the tenuissimus histogram has a small peak at the latter position, also. In the nerve branches to the interosseous spindles the γ_2 axons became very thin closer to the spindles than in the other muscles, and less γ_2 axons broke and had to be measured close to the spindles, so that proportionally less of them were measured at the part of their course where they were very thin. In the interosseous spindles themselves, however, the difference in size of the γ_1 and γ_2 axons was very marked as in the spindles from the leg muscles.

It can be said with reasonable certainty that the axons less than 1·5 μ, and most of those less than 2·5 μ in diameter in the histograms are γ_2 axons. Those greater than 3 μ are γ_1 axons, and the large group between 2·5 and 3 μ consists of γ_1 axons with a few of the largest γ_2 axons in addition. The sudden, rather than gradual, transition of γ_2 axons from about 2 μ to less than 1 μ as they approach the spindles accounts for the relatively small number of 1 to 1·5 μ axons in histograms *a* and *b* of figure 10.

In muscles from different cats the axons within the γ_1 and γ_2 groups differ in size, e.g. in some muscles the γ_2 axons were between 1 and 2 μ, and the γ_1 axons were 3 to 4 μ in diameter, while in others most of the γ_2 axons were less than 1 μ and the γ_1 axons were 2 to 3 μ in diameter. Measurements from 7 cats are contained in the histograms, and the separation of the axons into two groups of differing diameter is not nearly so obvious here as it was in the actual isolated spindles themselves.

(13) *Form and site of motor nerve endings*

When spindles, which are illustrated both in drawings and in photographs, are referred to in the descriptions which follow, references to the drawings only are given in the text, in most cases. The drawings or legends contain cross-references to the corresponding photographs.

(*a*) γ_1 *nerve endings*. The γ_1 motor fibres terminate in motor end-plates on the nuclear bag intrafusal muscle fibres; examples of γ_1 end-plates in de-afferented spindles are shown in figures 88, 92, 93, 94, plate 51. A typical feature of γ_1 fibres is that the terminal axon branches do not diminish appreciably in diameter and are still larger than 2μ at the end-plate. This can be seen in all the examples quoted above. One γ_1 fibre may supply more than one end-plate, but the plates are discrete; they are never linked by axons which arise at a different part of the end-plate from the point of entry of its γ_1 axon and pass to another plate, as is common with γ_2 nerve endings. Sometimes, however, a γ_1 axon branches close to its main end-plate to supply a second, smaller, plate usually on the same muscle fibre (figure 107, plate 53).

If the γ_1 fibres end in the spindle near or beyond the ends of the nuclear chain muscle fibres then their end-plates obviously lie on the nuclear bag fibres (figures 92, 94, plate 51). If they lie in the S_2, S_3 or S_4 regions of a spindle it may be difficult to tell on which type of intrafusal fibre they are situated (figure 112, plate 53); but in any spindle, or part of a spindle, in which the individual intrafusal muscle fibres are separate from each other, any γ_1 end-plates which are present lie on the nuclear bag fibres (labelled *n.b.* in the figures).

Each γ_1 end-plate is usually 50 to 75μ in length and when viewed from above it covers most of the width of the muscle fibre on which it lies, i.e. it may be 30 to 40μ in width (figure 92, plate 51). An individual γ_1 end-plate is relatively coarse in structure compared with the γ_2 nerve endings, and is wrapped round the surface of the muscle fibre so that when viewed side on it occupies about half the width of the nuclear bag fibre, i.e. the end-plate is between 10 and 20μ in depth (figures 93, 94, plate 51; figures 111, 112, plate 53). In spindles in which the nuclear bag and nuclear chain fibres cannot be seen individually, γ_1 end-plates are often found which are much too wide to lie on a small nuclear chain fibre and must, therefore, lie on a large fibre (figure 88, plate 51; figure 20). Some γ_1 end-plates are much longer than 75μ (figure 22) and a variety of different forms have been seen, but most of them have the form and dimensions given above.

Thus, the γ_1 *nerve fibres terminate in discrete motor end-plates which are always situated on nuclear bag muscle fibres; these* γ_1 *end-plates are not unlike the end-plates on extrafusal muscle fibres.*

(*b*) γ_2 *nerve endings*. In spindles from the soleus and interosseous muscles, and most of those from the tenuissimus muscle, the γ_2 axons become less than 1μ in diameter some distance before they reach their endings. These fine terminal branches link up with each other and link a number of small nerve endings together so that each γ_2 ending may receive several fine axons which join it at different points. This network of axons and nerve endings is designated the 'γ_2 network' and examples are shown in de-afferented spindles in figures 15, 21, 23, 24, and in normal spindles in figures 103, 104, 106, 108, plate 53.

The γ_2 nerve endings vary greatly in form in different spindles. The term 'γ_2 ending' rather than 'γ_2 end-plate' is used to avoid confusion with the typical end-plates of γ_1 nerve fibres, though in some spindles the γ_2 endings have the form of small end-plates generally much smaller and finer in structure than γ_1 end-plates (figure 89, plate 51; figures 102, 108, plate 53). In many spindles the γ_2 endings are narrow, elongated, delicate structures linked by very fine axon branches and frequently arranged in a row end to end along the border of a muscle fibre. Viewed side on they consist of a series of densely stained particles which are often scarcely visible even in well-stained preparations (figure 91, plate 51); they

are apparently absent in less well-stained regions where the γ_2 axons seem to terminate without any specialized nerve endings (*P* region, figure 23). The form and arrangement of γ_2 endings in figures 22, 23, 24 are typical of soleus spindles in general, in which γ_2 endings are numerous.

Not all γ_2 endings are very small and of fine structure, however. In some tenuissimus spindles they may be 50 μ or more long and up to 20 μ wide (figure 103, plate 53). The fact that they are connected in an axon network which may include typical small γ_2 endings, and that they lie on nuclear chain muscle fibres, make it almost certain that they are part of the γ_2 innervation (figure 20).

In many spindles the γ_2 endings definitely lie on the nuclear chain muscle fibres and not on the nuclear bag fibres (figures 19, 21, 23). In other spindles the γ_2 network is associated with the bundle of nuclear chain fibres but the actual site of the endings cannot be seen (figures 18, 28). In many spindles at least one of the nuclear bag fibres does not receive any γ_2 innervation, while the other nuclear bag fibre or fibres are obscured by the bundle of nuclear chain fibres, and it is probable that these other nuclear bag fibres are also without γ_2 innervation (figures 15, 23, 24).

In most spindles, therefore, the γ_2 nerve fibres terminate in a 'γ_2 motor network' of fine axons and small, elongated nerve endings situated exclusively on the nuclear chain muscle fibres.

FIGURE 15 and FIGURE 97, PLATE 52. *Type S_1PS_1 spindle; interosseous muscle de-afferented 6 days; cat 5.* In cat 5 not all the afferent fibres from the interosseous muscle were cut (table 1). There is an intact secondary sensory ending in the S_1 region of this spindle to the right of the *P* region. The primary sensory ending has completely degenerated though the degnerating group I*a* axon is still visible. There are two nuclear bags in the *P* region. A degenerating group II axon is present in the other S_1 region, showing that this spindle had a sensory ending on each side of the primary ending; the rest of the spindle at this end is missing.

At the other end the intrafusal fibres end in a tendon slip. Four γ_1 axons and two γ_2 axons approach this end with the intact group II axon. Two very fine γ_2 axons enter with the degenerating group I*a* axon and pass through the *P* region and the intact sensory ending. The total of four γ_1 axons and four γ_2 axons supply five relatively large γ_1 end-plates on nuclear bag fibres in the S_3 region, and about ten small γ_2 endings on nuclear chain fibres in the S_2 region, respectively. The two groups of nerve endings overlap slightly where the S_2 and S_3 regions meet. The nuclear bag fibre on the outer edge of the spindle in figure 15 has no motor innervation in the S_1 and S_2 regions; the area within the rectangle is shown enlarged in figure 88, plate 51.

FIGURE 16 and FIGURE 98, PLATE 52. *Type PS_1S_2 spindle; soleus muscle de-afferented 6 days; cat 5.* All the sensory nerve endings in this spindle have disappeared; degenerating group I*a* and group II axons enter the *P* region, where there are two nuclear bag fibres on the outside edges of the spindle and five nuclear chain fibres between them; the group II axon ends in the S_1 region. Another degenerating group II axon enters the same end of the spindle between the S_1 and S_2 regions, i.e. there were two secondary sensory endings on the same side of the primary ending before the dorsal spinal roots were cut.

The lower part of the spindle is incomplete; at this end a γ_1 axon and a γ_2 axon enter together and supply nerve endings on nuclear bag and nuclear chain fibres, respectively. The other end of the spindle receives a total of three γ_1 axons which supply six γ_1 end-plates, four definitely and two probably on nuclear bag fibres, in the S_3 and S_4 regions and beyond, and three γ_2 axons which branch to innervate about eight small γ_2 endings, most of them in the S_2 region, on nuclear chain fibres.

In a few spindles, however, a nuclear bag muscle fibre may have a γ_2 ending in addition to the usual γ_1 innervation. This is rare in soleus and interosseous muscle spindles (figure 111, plate 53) but is more common in tenuissimus spindles, in which γ_2 nerve fibres sometimes supply nerve endings on both types of intrafusal muscle fibre (figures 26, 27). The γ_2 axons in tenuissimus spindles may also be relatively large (2 to 3 μ), but in this case the γ_1 axons are usually still larger, perhaps more than 4 μ at the end-plate (figure 112, plate 53).

(14) *Number of motor fibres and nerve endings per spindle*

The number of motor fibres entering any of the de-afferented spindles examined was never less than 7; even simple spindles receive at least this number. The maximum number of motor fibres entering one spindle was 23. The fibres were counted at the same point at

PLATE 51

FIGURES 87 to 96. *Motor nerve endings in de-afferented spindles (gold chloride staining).*

FIGURE 87. *Soleus spindle; cat* 8, *de-afferented* 45 *days.* The S_1 region of the spindle drawn in figure 18 is shown. Very fine γ_2 motor axons, and small γ_1 motor axons, enter the spindle together. The γ_2 axons supply the bundle of nuclear chain fibres in the centre.

FIGURE 88. *Interosseous spindle, type* S_1PS_1*; cat* 5, *incompletely de-afferented* 6 *days.* The S_2 and S_3 regions of the spindle drawn in figure 15 are shown. Three poorly stained γ_1 motor axons pass along the top of the spindle to large end-plates in the S_3 region. One relatively large γ_1 axon passes down the centre of the spindle and ends in a large end-plate between the S_2 and S_3 regions. Several very fine γ_2 motor axons supply a network of small γ_2 endings in the S_2 region.

FIGURE 89. *Tenuissimus spindle, type* PS_1*; cat* 10, *incompletely de-afferented* 35 *days.* Parts of the S_1 and S_2 regions of the spindle drawn in figure 21 are shown. An intact S_1 secondary sensory ending lies on the right. Two large nuclear bag fibres, free of motor endings in this region, lie at the top, and four small nuclear chain fibres below are innervated by a network of fine γ_2 motor axons and γ_2 endings. A γ_1 motor axon crosses the lower left corner of the field.

FIGURE 90. *Soleus spindle, type* PS_1*; cat* 5, *de-afferented* 6 *days.* The S_1 and part of the S_2 regions of the spindle drawn in figure 24 are shown. A network of γ_2 motor axons and small γ_2 endings innervates the nuclear chain fibres. A nuclear bag fibre, free of nerve endings in this region, crosses the field at the top.

FIGURE 91. *Soleus spindle, type* PS_1*; cat* 5, *de-afferented* 6 *days.* Part of the S_1 region of the spindle drawn in figure 23 is shown. Very small γ_2 endings lie on the edges of the nuclear chain fibres. A nuclear bag fibre, free of nerve endings, crosses the field at the top.

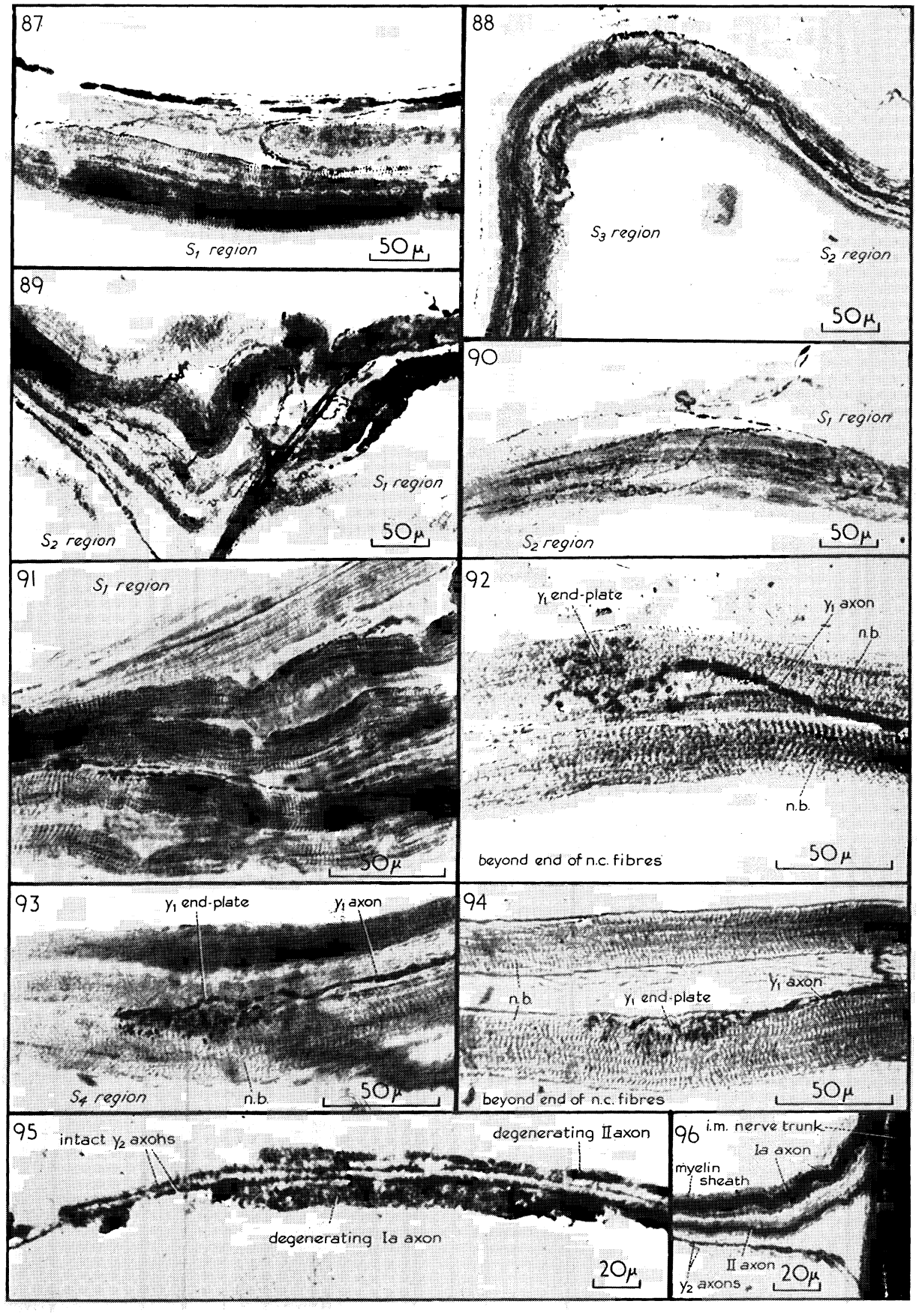
FIGURE 92. *Soleus spindle; cat* 8, *de-afferented* 45 *days.* A large γ_1 motor end-plate on a nuclear bag fibre in the region of the spindle beyond the end of the nuclear chain fibres.

FIGURE 93. *Tenuissimus spindle; cat* 4, *de-afferented* 3 *days.* A large γ_1 motor end-plate on a nuclear bag fibre in the S_4 region.

FIGURE 94. *Soleus spindle, type* PS_1*; cat* 5, *de-afferented* 6 *days.* A large γ_1 motor end-plate on a nuclear bag fibre beyond the end of the nuclear chain fibres.

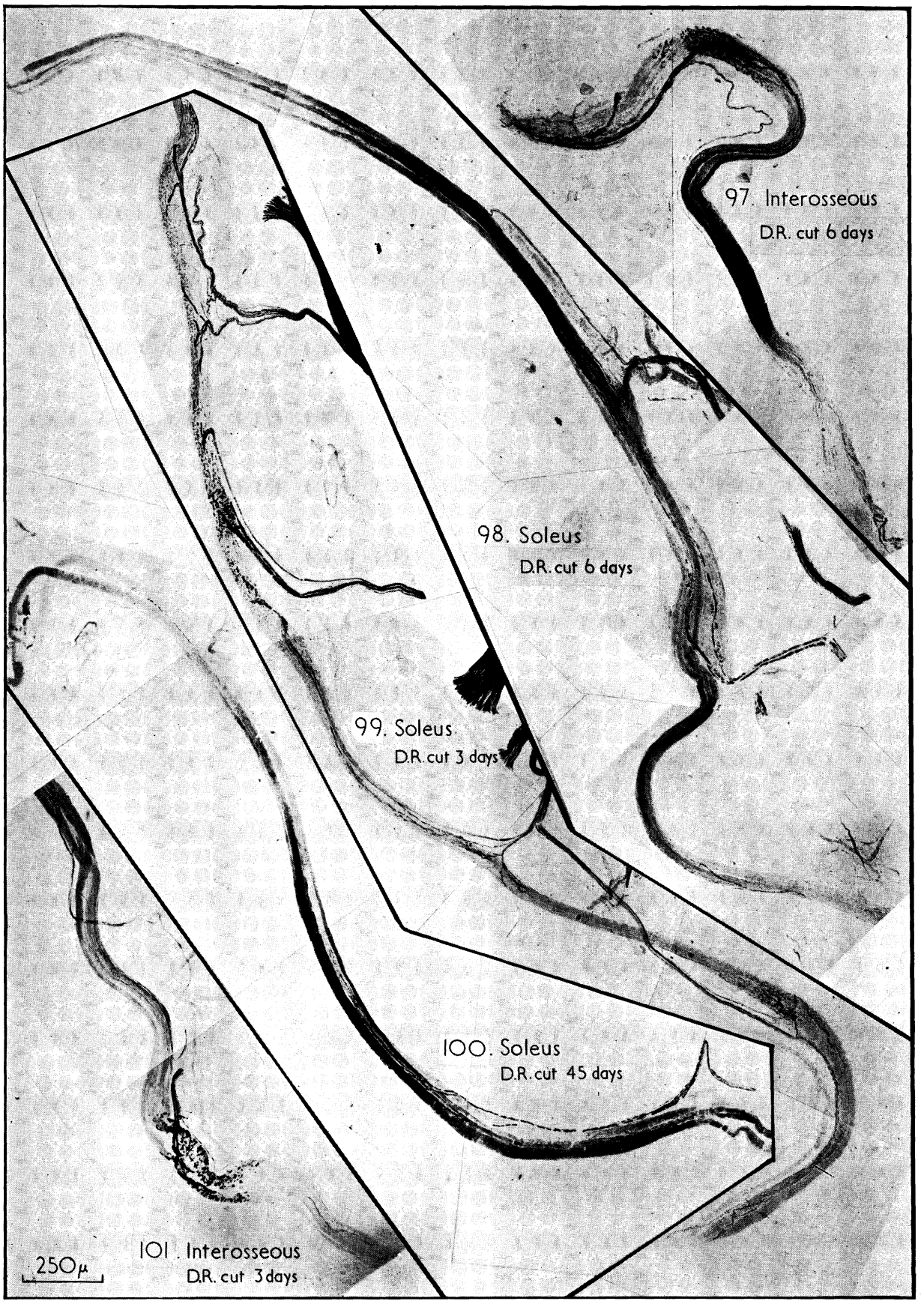
FIGURE 95. *Soleus muscle; cat* 5, *de-afferented* 6 *days.* Degenerating group I*a* and group II afferent axons close to their point of entry into a spindle. Two fine γ_2 motor axons beside the afferent axons are intact.

FIGURE 96. *Soleus muscle; cat* 4, *de-afferented* 3 *days.* Group of nerve fibres leaving an intramuscular nerve trunk to supply the spindle drawn in figure 17. Degeneration of afferent axons has not reached this point; a large group I*a* afferent axon, a medium-sized group II afferent axon, and two γ_2 motor axons, one of which is very small, are present.



FIGURES 87 TO 96

(*Facing p.* 112)



FIGURES 97 TO 101

FIGURE 17 and FIGURE 99, PLATE 52. *Tandem spindle, type $S_1PS_1S_2S_3$ plus type P; soleus muscle de-afferented 3 days; cat 4.* This spindle has a degenerating primary sensory ending with three degenerating secondary sensory endings on one side of it and one on the other. Some of the intrafusal muscle fibres are continuous with those of a second, simple spindle with a degenerating primary sensory ending only, the whole forming a tandem spindle. The degenerating secondary sensory nerve endings lie on the nuclear chain fibres only, outlining the course of the bundle of these muscle fibres through the spindle.

In addition to the five afferent axons, this spindle receives 21 γ motor axons, 9 axons to one end where their endings could not be seen, 10 axons to the other end, and two fine γ_2 axons which enter with the group I*a* axon and terminate amid the secondary sensory endings. The area within the rectangle is shown enlarged in figure 96, plate 51. A number of γ axons could not be traced individually into the spindle and are not classified into the γ_1 or γ_2 groups.

FIGURE 18 and FIGURE 100, PLATE 52. *Soleus muscle spindle de-afferented 45 days; cat 8.* The sensory axons and nerve endings in this spindle have completely degenerated, so that the type of the spindle is unknown. There are two nuclear bags and four nuclear chains in the *P* region; one end of the spindle is missing while the other end is almost complete. The nuclear bag fibres can be traced throughout their whole course at this end. In the S_1 and S_2 regions the nuclear chain fibres lie in a bundle in the centre of the spindle.

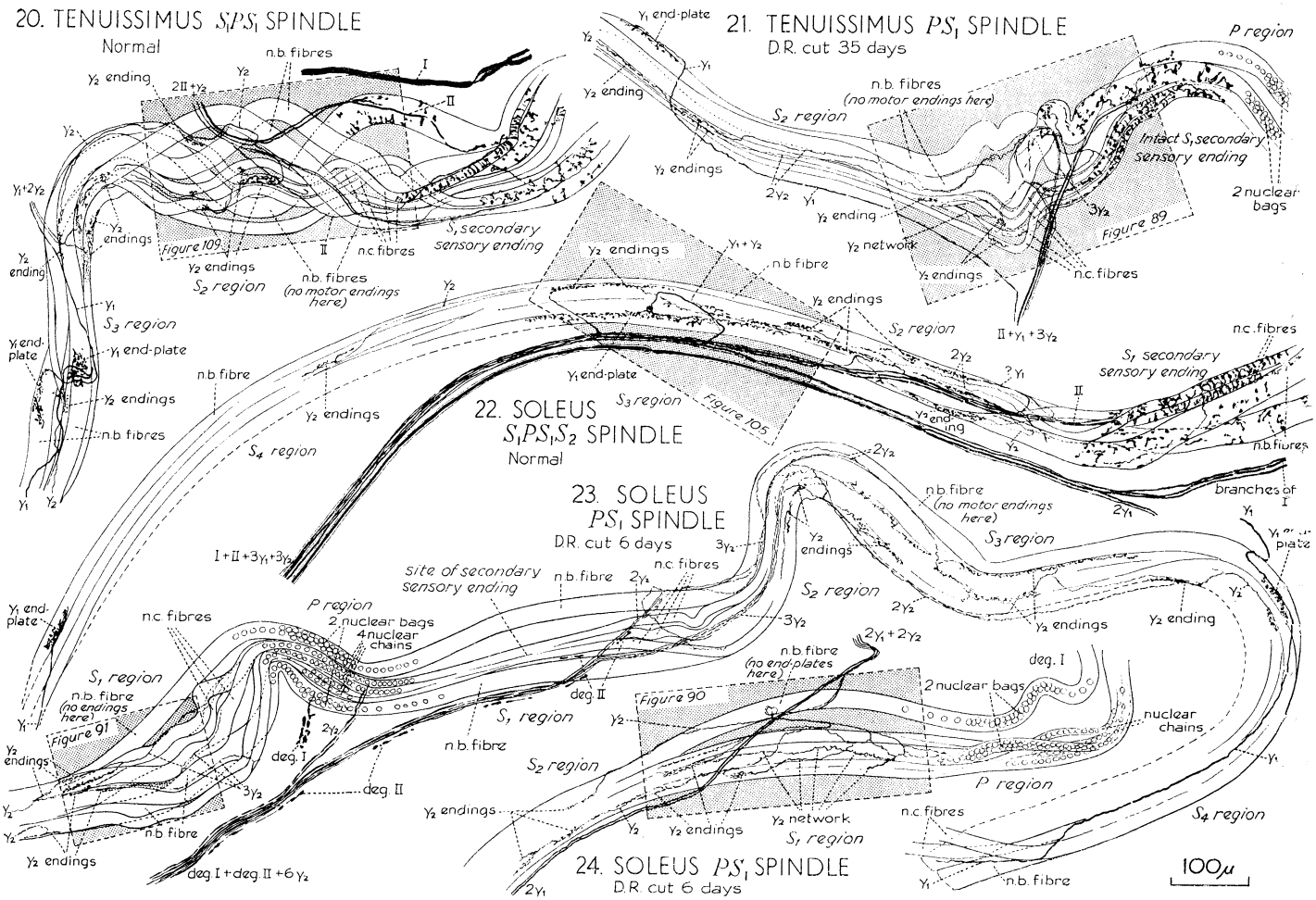
In the nerve bundle approaching the spindle there are five axons 2 to 3μ in diameter, and two γ_2 axons which are much smaller. Close to the spindle, two of the larger axons branch to give rise to typical γ_2 axons, while a third becomes very thin at intervals and finally ends in fine branches innervating γ_2 endings. The remaining two larger axons are γ_1 axons, and they continue in the spindle unchanged in diameter; one of them supplies a γ_1 end-plate on one nuclear bag fibre, while the other goes to two γ_1 end-plates, one on each of the nuclear bag fibres, in the S_3 region. Each nuclear bag fibre has an additional end-plate; one lies in the S_4 region and its axon is missing; the other end-plate lies much farther along the spindle and its γ_1 axon leaves a bundle of extrafusal axons to enter the spindle near to the end-plate. The nuclear chain fibres have a network of fine axons and very small endings scattered along their length. They are concentrated mainly in four areas, two in the S_1 region and two in the S_2 region, and this γ_2 network is joined at intervals by the fine terminal branches of the five γ_2 axons.

This spindle, taken from cat 8, in which dorsal root section was complete (see table 1), shows clearly the two types of motor axon, and the distinct difference in diameter between them close to, and within, the spindle. The area with in the rectangle is shown enlarged in figure 87, plate 51.

FIGURE 19 and FIGURE 101, PLATE 52. *Type P spindle; interosseous muscle de-afferented 3 days; cat 4.* This spindle has a degenerating primary sensory ending and no secondary sensory endings. In the *P* region two nuclear bag fibres lie on either side of the bundle of nuclear chain fibres; this bundle crosses to the edge of the spindle in the S_1 region. The motor innervation in the S_1 and S_2 regions is almost entirely confined to this edge, while one of the nuclear bag fibres lies on the opposite edge and receives no motor innervation until the S_3 region. The area within the rectangle is shown enlarged in figure 71, plate 49.

Three γ_2 axons enter with the group I*a* axon, and divide to form six branches. Two of these pass along the top of the primary ending to one end of the spindle, which is incomplete, and a third traverses the primary ending to the same end of the spindle. At the other end the remaining three γ_2 axon branches and three more γ_2 axons, which enter further along, innervate about twelve small γ_2 endings on nuclear chain fibres in the S_1 and S_2 regions; one of these γ_2 endings lies very close to the primary sensory ending. Three γ_1 axons innervate four γ_1 end-plates on nuclear bag fibres, one γ_1 end-plate lying in the S_2 region and three γ_1 end-plates lying in the S_3 region.

Thus, this simple spindle which has no secondary sensory endings nevertheless contains both types of intrafusal muscle fibre, each with its characteristic motor innervation.



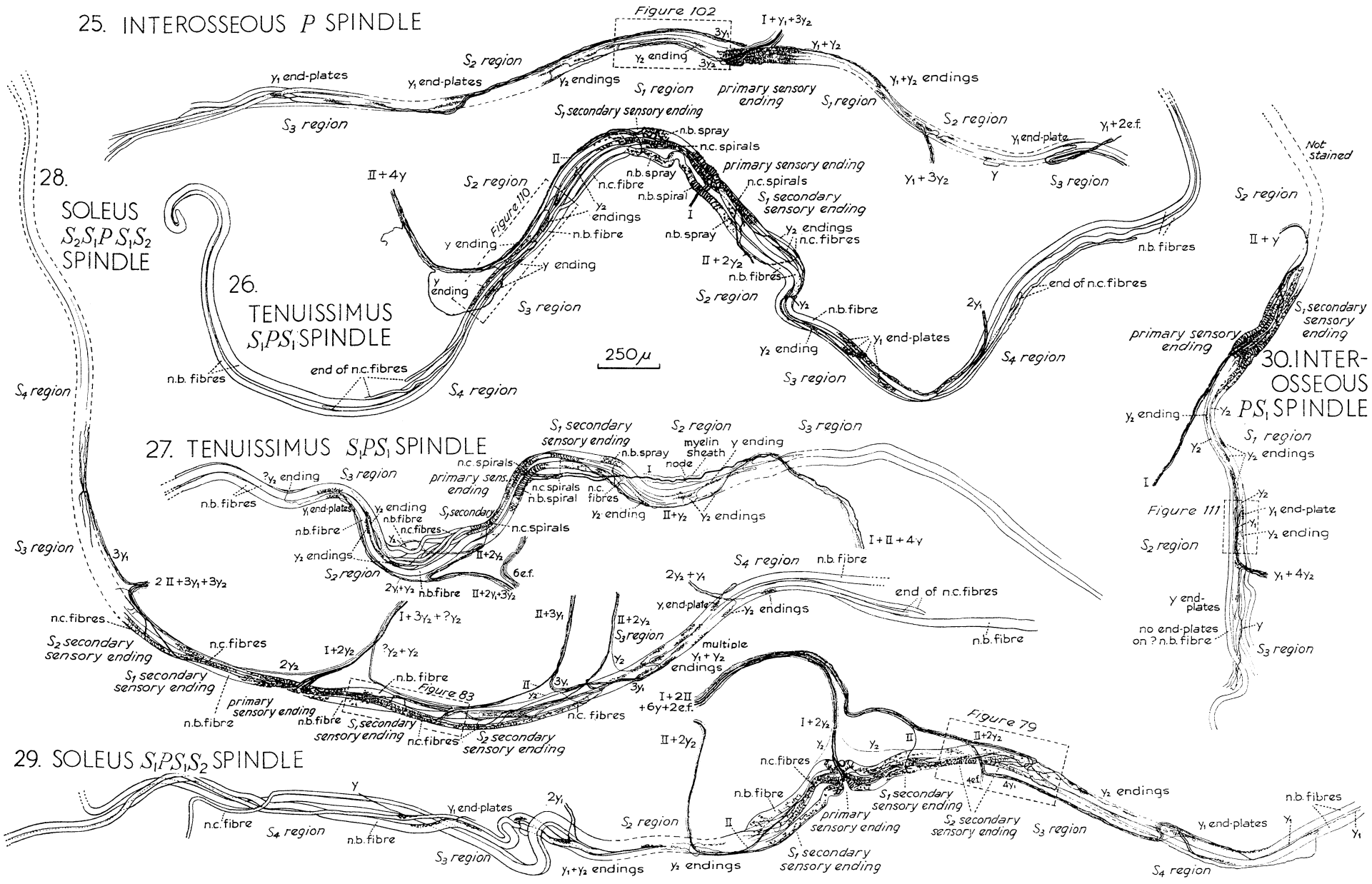
FIGURES 20 TO 24. *Parts of de-afferented and normal spindles (gold chloride staining).*

FIGURE 20. *Type S_1PS_1 spindle; tenuissimus muscle, normal.* The S_1 to S_3 region from one end is shown. The shaded area is the key to figure 109, plate 53. The spindle has three large nuclear bag fibres and four small nuclear chain fibres. The terminations of a secondary sensory ending in the S_1 region lie principally on the nuclear chain fibres; two branches of group II axons traverse the S_2 region to reach it.

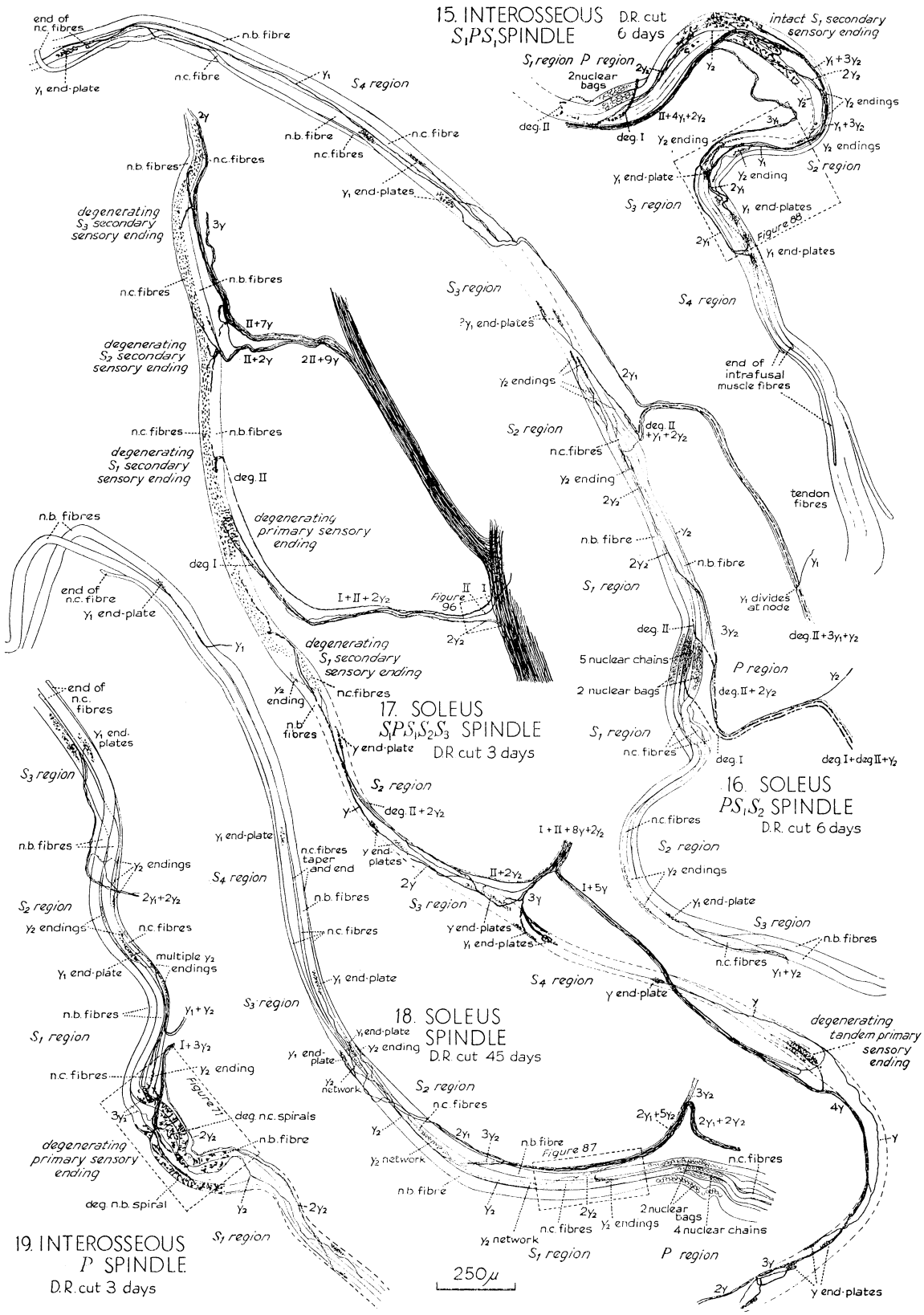
Two γ_1 axons each supply a large γ_1 end-plate on different nuclear bag fibres in the distal part of the S_3 region. The nuclear bag fibres have no other motor innervation at this end of the spindle. Three γ_2 axons end in a network of about twelve γ_2 endings on the nuclear chain fibres in the S_2 and part of the S_3 regions. A fourth fine γ_2 axon approaches from the S_4 region and supplies two small γ_2 endings in the centre of the spindle, probably on nuclear chain fibres. The other end of the spindle had a similar γ_2 network on the nuclear chain fibres.

FIGURE 21. *Type PS_1 spindle; tenuissimus muscle, de-afferented 35 days; cat* 10. In this cat some ganglion cells in dorsal roots *L* 5 and *S* 1 were not removed, hence some afferent fibres did not degenerate. The primary sensory ending in this spindle has disappeared so that the nuclear bags are visible, but a secondary sensory ending remains intact in the S_1 region. There are two large nuclear bag fibres and four small nuclear chain fibres. The shaded area is the key to figure 89, plate 51.

One γ_1 axon passes through the S_2 region and supplies a large γ_1 end-plate on a nuclear bag fibre in the S_3 region. One of the nuclear bag fibres had a γ_1 end-plate in the S_4 region (not shown). Neither nuclear bag fibre has any motor innervation in the S_1 or S_2 regions. Three γ_2 axons branch to form a network of fine axons with at least seven small endings in two groups on the nuclear chain fibres in the proximal and distal parts of the S_2 region.



FIGURES 25 TO 30. Normal spindles (gold chloride staining). Key to figures 113 to 118, plate 54. Legends facing plate 54.



FIGURES 15 TO 19. *De-afferented spindles (gold chloride staining).* Key to figures 97 to 101, plate 52.

For legends see p. 111 and opposite.

FIGURE 22. *Type $S_1PS_1S_2$ spindle; soleus muscle, normal.* The complete motor innervation of one end of this spindle is shown. The shaded area is the key to figure 105, plate 53. Part of a secondary sensory ending in the S_1 region is present on the right; most of its terminations lie on a bundle of three or four nuclear chain fibres. There are two nuclear bag fibres. The spindle had a primary ending, and two secondary sensory endings in the S_1 and S_2 positions on the other side of the primary ending. The group I*a* axon and two γ_1 axons in the nerve branch to the spindle go to the part which is not shown. The group II axon supplies the S_1 sensory ending shown.

One γ_1 axon and three γ_2 axons end in extensive motor innervation in the S_2 and S_3 regions. The γ_1 axon ends in a very large γ_1 end-plate extending over a long distance on one intrafusal fibre in the S_3 region. Beyond the S_4 region a separate γ_1 axon supplies a discrete γ_1 end-plate definitely lying on one of the two nuclear bag fibres. The three γ_2 axons innervate a complex γ_2 network of at least 12 nerve endings on nuclear chain fibres in the S_2 and S_3 regions. The extensive motor innervation in this area might easily be confused with a secondary sensory ending of spray form.

FIGURE 23. *Type PS_1 spindle; soleus muscle, de-afferented 6 days; cat 5.* This spindle has two nuclear bag fibres and four nuclear chain fibres. The primary sensory ending and a secondary sensory ending in the S_1 region to the right of the primary ending have completely disappeared, but traces of the group I*a* and group II axons remain.

One γ_1 axon enters the spindle between the S_3 and S_4 regions; a branch innervates a discrete γ_1 end-plate on a nuclear bag fibre and a second branch continues through the S_4 region probably to another end-plate at the end of the spindle, part of which is missing. Six γ_2 axons approach with the afferent axons. Two of these γ_2 axons apparently end in the nuclear region. Fine branches (unstained) from these axons probably join the γ_2 network in the S_1 region to the left of the nuclear region. Four of the γ_2 axons enter the S_2 region with the degenerating group II axon. One of them is very small throughout its course; the other three become very thin at intervals and all four enter the spindle as typical fine γ_2 axons. They branch extensively to supply a complex γ_2 network of at least thirteen γ_2 endings in the S_2 and S_3 regions, presumably associated with the nuclear chain fibres since the nuclear bag fibre at the top edge of the spindle has no motor innervation at all in the S_1, S_2 and S_3 regions. The S_1 region where the secondary ending was situated is completely free of motor nerve endings. In the other S_1 region, there is a network of fine γ_2 axons and at least seven very small γ_2 endings on the edges of the nuclear chain fibres. The shaded area is the key to figure 91, plate 51.

FIGURE 24. *Type PS_1 spindle; soleus muscle, de-afferented 6 days; cat 5.* This spindle has two nuclear bag fibres and three or four nuclear chain fibres. The primary sensory ending and a secondary sensory ending in the S_1 region to the right of the nuclei (not shown) had completely disappeared, but traces of the group I*a* and group II axons remained. The shaded area is the key to figure 90, plate 51.

Two γ_1 axons enter the S_1 region, cross the spindle and pass along the lower edge to the S_4 region (not shown) where their endings were unstained. Two γ_2 axons branch repeatedly to form a γ_2 network of fine axons and about thirteen γ_2 endings in the S_1 and S_2 regions. One nuclear bag fibre is separate from the other intrafusal fibres in the P and S_1 regions, and has no motor innervation in the S_1 and S_2 regions. The γ_2 network presumably lies on the nuclear chain fibres, though a nuclear bag fibre is present somewhere in the group of intrafusal fibres in the lower part of the spindle.

PLATE 53

FIGURES 102 to 112. *Motor nerve endings in normal spindles (gold chloride staining).*

FIGURE 102. *Interosseous spindle, type P.* The S_1 region of the spindle drawn in figure 25 is shown. A group of γ_1 motor axons crosses the field at the top. A group of much finer γ_2 motor axons traverse the primary sensory ending, part of which is shown on the right; one of these turns back to supply a γ_2 ending close to the primary sensory ending.

FIGURE 103. *Tenuissimus spindle, type P.* Two γ_2 endings, joined together in a network, lie on different nuclear chain fibres close to the primary sensory ending, part of which is visible on the right.

FIGURE 104. *Interosseous spindle, type* S_1PS_1. Network of γ_2 motor axons and γ_2 endings in the S_2 region. The primary afferent axon crosses the top right hand corner of the field.

FIGURE 105. *Soleus spindle, type* $S_1PS_1S_2$. The S_3 region of the spindle drawn in figure 22 is shown. A large γ_1 end-plate and a number of small γ_2 endings in the same region produce an appearance not unlike a secondary sensory ending of spray form. A bundle of afferent and motor axons to this spindle crosses the field below the spindle itself.

FIGURE 106. *Interosseous spindle, type* PS_1. Network of γ_2 motor axons and γ_2 endings in the S_2 region. Above is a bundle of afferent and motor axons to this spindle.

FIGURE 107. *Soleus spindle, type* S_1PS_1. A γ_1 end-plate on a nuclear bag fibre in the S_3 region. A small accessory end-plate, supplied by the same γ_1 axon, lies further along the same muscle fibre.

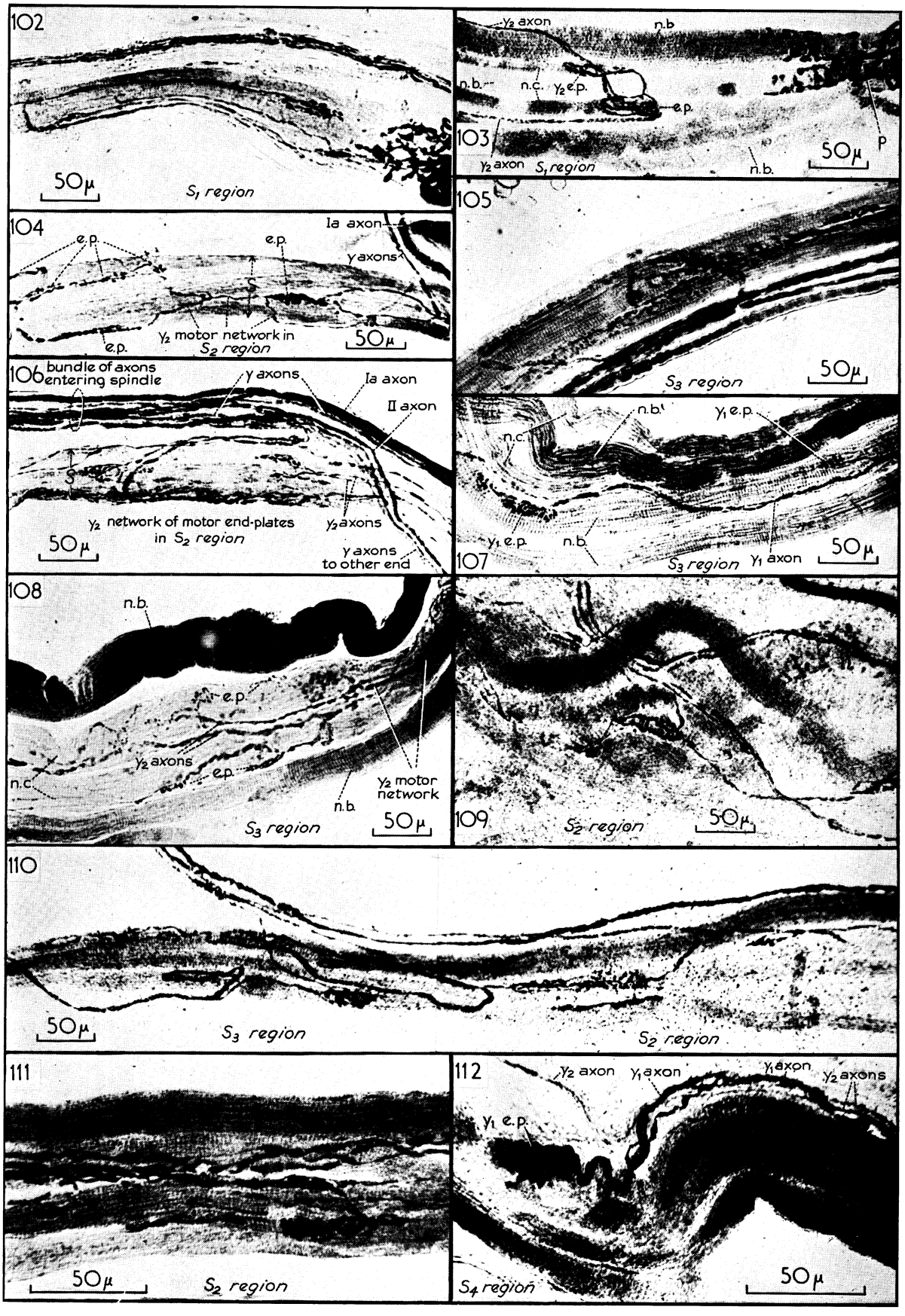
FIGURE 108. *Interosseous spindle, type* PS_1. Network of γ_2 motor axons and multiple γ_2 endings on two out of four intrafusal muscle fibres in the S_3 region. The outer two fibres are nuclear bag fibres.

FIGURE 109. *Tenuissimus spindle, type* S_1PS_1. The S_2 region of the spindle drawn in figure 20 is shown. Part of a secondary sensory ending is visible on the right. One relatively large motor ending and several smaller ones form part of the γ_2 network on nuclear chain fibres. The nuclear bag fibres have no motor innervation in this region.

FIGURE 110. *Tenuissimus spindle, type* S_1PS_1. The S_2 and S_3 regions of the spindle drawn in figure 26 are shown. A number of relatively large motor endings lie on both nuclear chain and nuclear bag fibres, and are connected in a network by small motor axons.

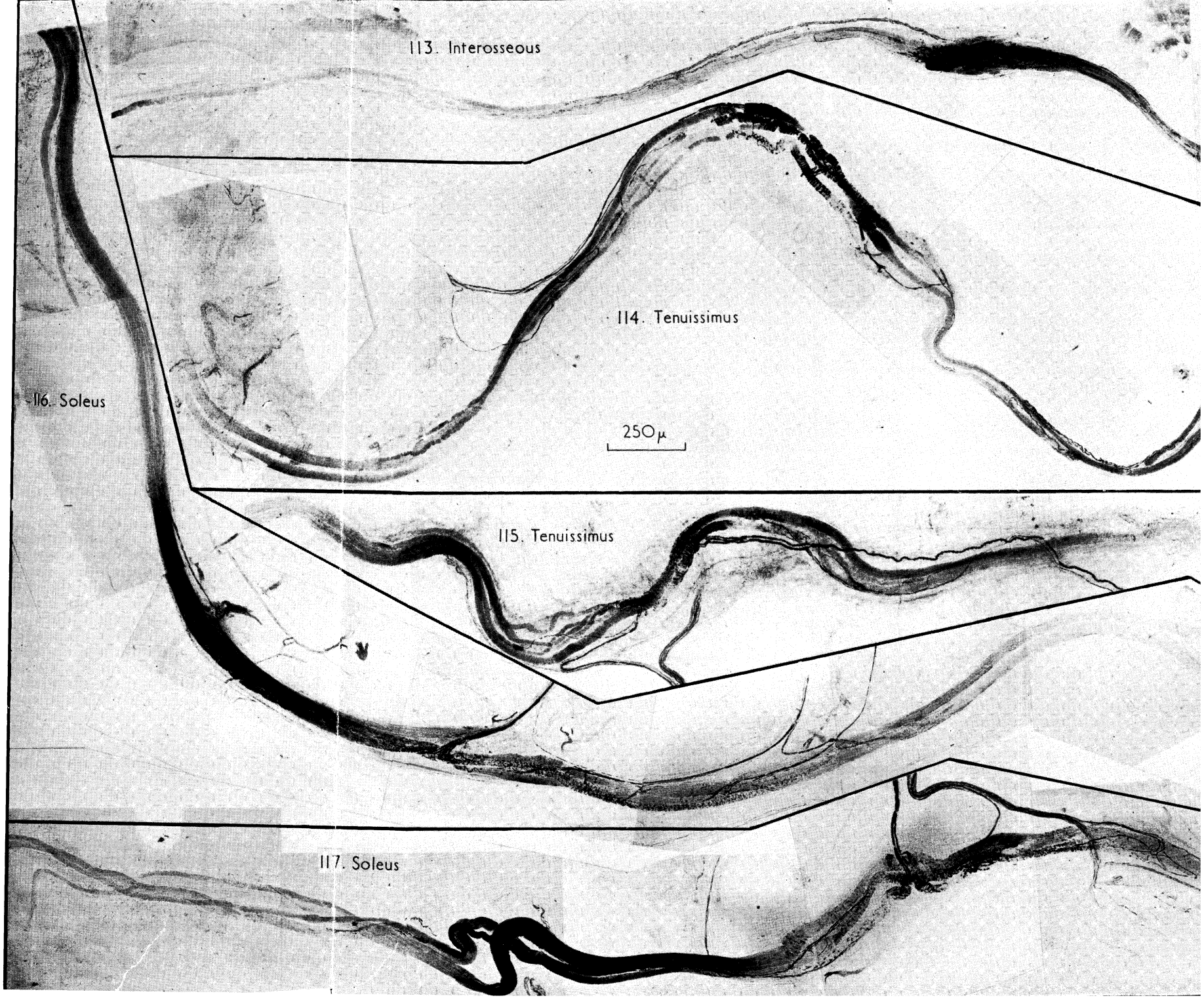
FIGURE 111. *Interosseous spindle, type* PS_1. The S_2 region of the spindle drawn in figure 30 is shown. A large γ_1 motor end-plate and a small γ_2 ending lie on the same intrafusal muscle fibre, probably a nuclear bag fibre.

FIGURE 112. *Tenuissimus spindle, type* PS_1S_2. A large γ_1 motor end-plate in the S_4 region. It has a relatively large γ_1 axon, and two fine γ_2 axons are also present.



FIGURES 102 TO 112

113. Interosseous
114. Tenuissimus
250μ
115. Tenuissimus
118. Interosseous


113. Interosseous
114. Tenuissimus
116. Soleus
250μ
115. Tenuissimus
117. Soleus

(*Facing p.* 113)

FIGURE 25 and FIGURE 113, PLATE 54. *Type P spindle; interosseous muscle.* This spindle has a primary sensory ending but no secondary sensory endings. The intrafusal fibres are numerous and about the same size, so that it is impossible to tell on which type of intrafusal fibre the motor nerve endings are situated. The motor axons are of two distinct sizes, however, and the site and form of the endings indicate that the γ_1 and γ_2 innervation found in other spindles is present here, also.

Three γ_1 axons supply five discrete end-plates in the S_3 and part of the S_2 regions on the left. Three γ_2 axons pass through the primary ending to the lower edge of the spindle, and divide to supply a network of about seven γ_2 endings in the S_1 and part of the S_2 regions. One of these γ_2 endings is very close to the primary sensory ending. The γ_1 axons are much larger than the γ_2 axons. The area within the rectangle is the key to figure 102, plate 53.

At the other end, five very fine γ_2 axons supply about seven very small γ_2 endings in the S_1 and S_2 regions, intermingled with five larger end-plates innervated by two γ_1 axons. A γ_1 axon, which accompanies two axons to extrafusal end-plates, supplies a typical γ_1 end-plate in the S_3 region.

FIGURE 26 and FIGURE 114, PLATE 54. *Type S_1PS_1 spindle; tenuissimus muscle.* This spindle has two large nuclear bag fibres which can be traced from end to end, and four small nuclear chain fibres traceable for most of their length. The primary sensory ending consists of two large and four small spirals, each spiral surrounding one of the intrafusal fibres. Both secondary sensory endings consist of spiral terminations round the individual nuclear chain fibres and sprays on the nuclear bag fibres. Both the S_1 afferent axons enter the spindle separately from the primary axon.

On the right, two γ_2 axons enter the spindle with the S_1 afferent axon and supply at least four small γ_2 endings definitely lying on the nuclear chain fibres in the S_2 region. The nuclear bag fibres have no innervation in this region, but two γ_1 axons enter the spindle in the S_4 region and end in two much larger end-plates of coarser structure on each nuclear bag fibre in the S_3 region.

On the left the motor innervation is atypical, and is all in the S_2 and S_3 regions. Four motor axons of similar size terminate in a group of endings on both nuclear bag and nuclear chain fibres. The area within the rectangle is the key to figure 110, plate 53. In the S_2 region the endings are on the nuclear chain fibres. In the S_3 region one ending appears to lie on each of the nuclear bag fibres, and both endings extend over a long length of muscle fibre. Further, all the six endings are linked in a network, which is typical of γ_2 innervation but the axons are larger than usual.

FIGURE 27 and FIGURE 115, PLATE 54. *Type S_1PS_1 spindle; tenuissimus muscle.* This spindle contains two large nuclear bag fibres and four small nuclear chain fibres, clearly separated from each other in the S_2 region to the left of the primary region. The primary sensory ending consists of two large and four small spirals, each of which encircles one intrafusal fibre. The branching of the group I*a* axon, its myelin sheath, and the position of the nodes, are particularly clear. Both S_1 sensory endings consist of spiral terminations round the nuclear chain fibres, and small accessory sprays on the nuclear bag fibres.

On the right, four motor axons enter with the group I*a* and group II axons and terminate in about seven small endings in the S_2 region, most of which definitely lie on the nuclear chain fibres and are probably γ_2 endings. There are no typical γ_1 end-plates at this end of the spindle.

At the other end, each of the nuclear bag fibres has one typical large γ_1 end-plate in the S_3 region, and two γ_1 axons to these enter the spindle with the S_1 sensory axon. Two fine γ_2 axons enter at the same point; one of them supplies a small ending probably on a nuclear chain fibre in the S_3 region. The other γ_2 axon supplies two γ_2 endings on nuclear chain fibres at the far end of the S_2 region. A larger axon, probably a γ_2 axon, supplies two endings, one definitely on a nuclear chain fibre, the other on a nuclear bag fibre, in the S_2 region.

FIGURE 28 and FIGURE 116, PLATE 54. *Type $S_2S_1PS_1S_2$ spindle; soleus muscle.* This spindle contains two large nuclear bag fibres and a bundle of four or five small nuclear chain fibres. At one end the group II axons enter together; at the other end they enter at separate points. The group I*a* axon has spiral terminations on both nuclear bag and nuclear chain fibres. The secondary sensory terminations lie almost exclusively on the bundle of nuclear chain fibres, and are of spiral form. The sensory terminations cover the nuclear chain fibres along much of their whole length, and outline their course through the spindle. The area within the rectangle is the key to figure 83, plate 50.

One end of the spindle is darkly stained in the S_2 and S_3 regions and poorly stained beyond, so that the motor endings are not visible. The motor axons are classified in terms of size only. Three γ_1 axons terminate in the S_3 and S_4 regions. Three fine γ_2 axons enter at the same point, while two fine γ_1 axons enter with the group I*a* axon. All five γ_2 axons travel to the S_2 region where the terminations are not visible.

Motor axons to the other end enter at four points, and the innervation is very complex. Three γ_1 axons supply about six large end-plates in the S_3 region, probably on the nuclear bag fibres, and a fourth γ_1 axon innervates a γ_1 end-plate on a nuclear bag fibre in the S_4 region. A total of six γ_2 axons enter at various points and form a network of fine axons and numerous endings, associated with the bundle of nuclear chain fibres, not only in the S_3 and S_4 regions but also beneath the secondary sensory endings in the S_1 and S_2 regions.

FIGURE 29 and FIGURE 117, PLATE 54. *Type $S_1PS_1S_2$ spindle; soleus muscle.* This spindle has two large nuclear bag fibres and a bundle of four small nuclear chain fibres. At one end both the group II axons enter with the group I*a* axon. The group II axon at the other end enters separately. The primary ending has two large spirals and four small spirals, each encircling an intrafusal fibre. Both S_1 sensory endings consist of spiral terminations round each of the nuclear chain fibres in the middle of the spindle and endings of spray form on the nuclear bag fibres at the edges. The S_2 sensory ending lies almost entirely on the nuclear chain fibres and extends for some distance along them. The area within the rectangle is the key to figure 79, plate 50.

Two fine γ_2 axons approach with the group I*a* axon and one passes to each S_1 region; their terminations are not visible amid the extensive sensory nerve endings. On the left, two fine γ_2 axons enter with the S_1 afferent axon and end in very small γ_2 endings in the S_2 region of which only two are visible, though more are probably present. The staining at this end is very dark. Four γ axons enter the S_3 region and supply several end-plates. They are probably γ_1 end-plates but they cannot be classified with certainty.

At the other end, two γ_2 axons enter with the S_2 afferent axon and end in about eight well stained γ_2 endings. Four γ_1 axons cross the spindle and pass down the lower edge to four γ_1 end-plates in the S_4 region; one axon continues towards the end of the spindle. All of these γ_1 end-plates probably lie on nuclear bag fibres, though only two definitely do so.

FIGURE 30 and FIGURE 118, PLATE 54. *Type PS_1 spindle; interosseous muscle.* One end of this spindle is continuous with a slip of tendon and the motor endings are not stained in this region. At the other end there are five intrafusal fibres of about the same diameter. The S_1 sensory ending consists of sprays lying on most, if not all, of the intrafusal fibres.

Four fine γ_2 axons enter in the S_2 region at the other end and supply a network of fine axon branches and about nine γ_2 endings scattered throughout the S_1 and S_2 regions. Two additional endings lie on fibres in the middle of the spindle in the S_3 region; they seem to be supplied by the γ_2 axons also. The intrafusal muscle fibre on the inner edge is the largest and longest in the spindle, and has no innervation in the S_2 and S_3 regions, and perhaps none in the S_1 region; it is probably a nuclear bag fibre. A large γ_1 axon ends in a large end-plate on the muscle fibre on the other edge of the spindle in the S_2 region adjacent to a very small γ_2 end-plate on the same muscle fibre. The area within the rectangle is the key to figure 111, plate 53.

which their diameter was measured, i.e. within about 1 mm of the spindle, so that intramuscular branching had probably already taken place.

If the total number of fibres in each of the histograms of figure 10*a–c* is divided by the corresponding number of spindles, values of 5·6, 9·0 and 7·5 are obtained for the number of motor fibres per spindle in the tenuissimus, soleus and interosseous muscles, respectively. However, some measurements from incomplete spindles, or ones in which not all the nerve fibres were stained, are included in the histograms. Therefore, in a total population of almost a hundred de-afferented spindles the true mean number of motor fibres per spindle in each of the different muscles was at least as great as the value given above. More accurate values were obtained by counting the number of nerve fibres to about 40 de-afferented spindles which were more or less complete, and in which all the nerve fibres were well stained. The number of motor fibres ranged from 7 to 16 in tenuissimus spindles, from 7 to 23 in soleus spindles, and from 8 to 15 in interosseous spindles. *Most tenuissimus spindles have from* 9 *to* 12 *motor fibres, which is definitely less than is the case in soleus and interosseous spindles most of which have from* 10 *to* 15 *motor fibres.*

If γ_1 fibres and γ_2 fibres are to be distinguished with certainty, and the number of motor nerve endings and their relation to individual intrafusal muscle fibres is to be determined, it is necessary to have spindles which are complete and uniformly stained from end to end. The staining must also be such that the individual intrafusal muscle fibres are visible, but are not so densely stained that they obscure the nerve endings situated on them. With gold chloride staining these conditions are very difficult to achieve, and it was necessary to include some normal as well as de-afferented spindles to obtain a population large enough for analysis of the details of the γ_1 and γ_2 motor innervation.

The distribution of motor fibres and nerve endings in spindles may best be appreciated by studying the projection tracings of spindles in figures 15 to 30. The number of nerve fibres of each type in the small nerve branches to the spindles is given beside each branch in the tracings and a detailed description of the innervation of each spindle is given in the legends. With the exception of figures 17 and 24, the complete motor innervation of at least one half of each of the spindles was well stained, though only parts of some of the spindles are shown. In these 14 spindles together there is an average of 2 or 3 γ_1 fibres and 4 γ_1 end-plates, and 3 or 4 γ_2 fibres and 9 γ_2 endings, per half spindle. The actual ratio of nerve endings to fibres is 1·4 to 1 for the γ_1 system and 2·6 to 1 for the γ_2 system, but the latter figure is only approximate since it is often difficult to decide where one γ_2 ending finishes and another begins in the γ_2 network, especially in soleus spindles. In spindles in which both ends are well stained the number of motor nerve fibres and endings at the two ends are approximately the same. *Hence, on the average, each spindle receives* 5 γ_1 *fibres and* 7 γ_2 *fibres supplying* 8 γ_1 *end-plates and* 18 γ_2 *endings, respectively.* Since all these spindles, except the one in figure 20, contain two nuclear bag fibres and either four or five nuclear chain fibres, *there are* 4 γ_1 *end-plates per nuclear bag muscle fibre and* 4 γ_2 *endings per nuclear chain muscle fibre.* This conclusion is surprising since at first sight the number of γ_2 endings on the nuclear chain fibres appears to be much greater than the number of γ_1 end-plates on nuclear bag fibres. This is to some extent due to the larger number and shorter length of the nuclear chain fibres. Spindles from the soleus muscle, however, frequently have 6 or 8 γ_2 endings per nuclear chain fibre.

In general, slightly less than half of the motor fibres to any spindle belong to the γ_1 group; the remainder belong to the γ_2 group. Many γ_1 fibres end in a single γ_1 end-plate, while some supply two end-plates either on the same or on different nuclear bag fibres; occasionally a γ_1 fibre supplies a group of more than two end-plates. Some γ_2 fibres end in a single small γ_2 ending, but most of them branch and join the γ_2 network in which there may be from two to four times as many endings as there are γ_2 fibres entering the spindle.

(15) *Motor innervation of nuclear bag muscle fibres*

Nuclear bag fibres never receive any motor innervation in either of the S_1 regions even though sensory endings are absent in this area, and in most spindles they have no motor innervation in the S_2 regions either (figures 20, 21, 23, 24, 26; figure 103, plate 53). In some shorter spindles, however, especially those from the interosseous muscles, there may be a few γ_1 end-plates on the nuclear bag fibres in the S_2 region (figures 19, 25, 30).

The γ_1 end-plates are usually situated on the nuclear bag fibres in the S_3 region (figures 15, 19, 20, 27); in very long spindles they extend into the S_4 region (figures 16, 28, 29). The γ_1 fibres to the main group of γ_1 end-plates sometimes enter the spindle with the group I*a* afferent fibre, but it is more common for them to enter with a group II afferent fibre or in small bundles completely independent of afferent fibres, especially in complex spindles. There may be as many as five separate points of entry of nerve fibres into a spindle (figure 28). One or two tenuissimus spindles have γ_1 end-plates at one end only, but this is rare. In many spindles, particularly in the tenuissimus muscle, each nuclear bag fibre has two γ_1 end-plates, one at each end of the spindle in the S_3 region. In some soleus and interosseous spindles γ_1 end-plates are more numerous which accounts for the average number of four γ_1 end-plates per nuclear bag fibre estimated earlier. Two plates close together on the same muscle fibre may have a common γ_1 fibre, in which case they may be considered to form a single end-plate from the functional point of view (figure 107, plate 53), or they may have different γ_1 fibres as though the muscle fibre belongs to two different intrafusal motor units.

In addition to the principal group of γ_1 end-plates, quite often there is a γ_1 end-plate on one of the nuclear bag fibres at the distal end of the S_4 region or even well beyond the end of the nuclear chain fibres in leg muscle spindles (figures 92, 93, 94, plate 51). The γ_1 fibre to this plate may traverse a long length of spindle to reach it (figure 16) or it may leave a small bundle of α fibres to extrafusal end-plates as the bundle passes near to the end of the spindle, in which case the γ_1 fibre enters the spindle close to the plate which it supplies (figures 18, 22).

In general, then, nuclear bag fibres have γ_1 end-plates on both sides of the nuclear region. They are not scattered at equal intervals along the fibres, however, but occur in two groups, one group in or near each of the S_3 regions, with the odd plate much further towards the ends. Long lengths of the nuclear bag fibres (2 to 3 mm in some cases) are devoid of motor innervation.

(16) *Motor innervation of nuclear chain muscle fibres*

In contrast to the nuclear bag fibres, the nuclear chain fibres almost always have motor innervation in any S_1 region which is free of sensory nerve endings. Thus, in spindles which have no secondary sensory endings, or in which all the secondary sensory endings lie on the

same side of the primary ending, motor nerve endings which form part of the γ_2 network are usually found on the nuclear chain fibres in the S_1 region, often very close to the primary sensory ending (figure 71, plate 49; figures 102, 103, plate 53; figures 18, 23, 24). If the spindle has an S_1 secondary sensory ending then this S_1 region is free of motor innervation altogether. This can best be seen in spindles in which the secondary sensory endings have degenerated, but in which the presence of the degenerating group II afferent fibre indicates the site which was occupied by the sensory ending (figures 16, 23).

Most of the nerve endings of the γ_2 network are situated on the nuclear chain fibres in the S_2 regions at both ends of the spindle (figures 104, 106, plate 53) and frequently extend into the S_3 region (figure 108, plate 53), particularly if the S_1 region is occupied by a sensory ending. The extent of the γ_2 innervation varies from a single γ_2 ending on each nuclear chain fibre in the S_2 regions of some tenuissimus spindles (figure 26), to an extensive network, in which individual endings can scarcely be distinguished, covering much of the length of the nuclear chain fibres in the most complex soleus and interosseous spindles (figures 23, 24). There seem to be γ_2 endings in the S_2 region even though there is an S_2 secondary sensory ending in the same region. Thus, in the spindle of figure 16 there are γ_2 endings in the S_2 region in which a degenerating group II fibre also ends, indicating that there was a sensory ending here; also, in the normal spindle in figure 28 there are a number of γ_2 fibres which appear to end in the S_2 regions where secondary sensory endings are situated. In longer spindles in which the nuclear chain fibres extend through the S_4 region they appear to have no motor endings in this area (figures 16, 18, 26).

The γ_2 fibres to nerve endings in the S_1 region usually enter the spindle with the group I*a* afferent fibre (figures 95, 96, plate 51). Those which join the γ_2 network in the S_2 and S_3 regions may enter either with the group I*a* fibre, or with a group II afferent fibre, or in a purely motor bundle with γ_1 fibres.

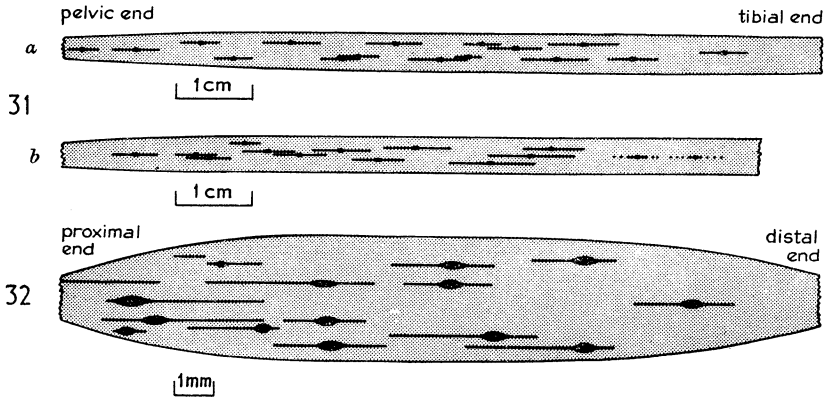
In general, the nuclear chain fibres have γ_2 endings in the S_1, S_2 and part of the S_3 regions at both ends of the spindle. The actual position of the γ_2 endings depends on the distribution of the secondary sensory endings. The γ_2 endings may lie at any point where sensory endings are absent. If, however, the sensory endings occupy a length of nuclear chain fibre greater than about 700 μ, then γ_2 endings may lie on the fibres beneath the sensory endings in any site except the *P* region and an adjacent length of fibre corresponding to the length of one secondary sensory ending.

Part III. Arrangement of spindles in certain muscles

Muscle spindles lie in greatest number in close proximity to the branches of the intramuscular nerves. The number and precise distribution of spindles in many cat muscles, including the soleus muscle, are described elsewhere (Barker & Chin 1960; Swett & Eldred 1960*a*; for other references see Cooper 1960). The arrangement of the spindles in the tenuissimus muscle and in the adductor digiti minimi longus muscle (the most superficial member of the interosseous group in the hind limb of the cat) is now described. In the diagrams no attempt is made to orientate the spindles correctly in relation to the muscle or its intramuscular nerves. The diagrams show the length of each spindle, its relationship to the other spindles and to the length of the muscle, and the extent and position of the lymph space in each spindle.

(17) *Tenuissimus muscle*

The nerve to the tenuissimus muscle divides as it approaches the muscle into proximal and distal branches which enter it about one third of the way down its length. The proximal branch passes up the centre of the muscle towards its point of emergence from the sciatic notch, and the distal branch, which is the larger, passes down the centre of the muscle towards its insertion in the fascial sheath of the gastrocnemius muscle near the Achilles tendon. The spindles lie in close relation to the intramuscular nerves, except in the region between the points of entry of the two nerve branches where they are scattered throughout the width of the muscle. The spindles are orientated parallel to the extrafusal muscle fasciculi, i.e. parallel to the length of the muscle.



FIGURES 31 and 32. Diagrams reconstructed from serial transverse sections of complete muscles to show the number and length of the spindles they contain, and the position of the the lymph space in each spindle. Only the longitudinal scale is accurate; note different scale in figure 32. No attempt has been made to show the exact orientation of each spindle in the muscle.

FIGURE 31*a*, *b*. Two different tenuissimus muscles.

FIGURE 32. An interosseous muscle from the hind foot (add. dig. long. V).

Two tenuissimus muscles in different cats were fixed *in situ* by perfusion with Susa fixative, with the leg almost fully extended. The part of the muscle between the sciatic notch and the expansion of the muscle into the sheath of the gastrocnemius muscle was removed and serially sectioned at 10 μ from end to end. The muscle is ribbon-like in shape, and the part removed was 10 to 12 cm long. No tendon organs were encountered in any of the tenuissimus muscles used in this investigation, but any which are present might be expected to lie at the origin or insertion in the small parts of the muscle not removed; one or two spindles may also have been present in these portions. The two muscles contained 14 and 16 spindles arranged as shown in figure 31*a*, *b*, in which the muscles and spindles are drawn to scale longitudinally only. Several other muscles, stained with gold chloride, each contained between 12 and 16 spindles, but never less than 12.

The spindles are arranged in a chain down the centre of the muscle so that at most points along its length a single transverse section contains the intrafusal fibres of one spindle, not always recognizable unless the section passes through the lymph space, as in figures 34, 35, plate 42, which are transverse sections of two complete tenuissimus muscles. Towards the ends of the muscle (figure 31) the spindles are long and are completely separated both

laterally and longitudinally so that some tranverse sections of the muscle contain no intrafusal fibres at all. Near the point of entry of the nerve the spindles tend to be shorter and their ends overlap more longitudinally, so that a transverse section may contain the intrafusal fibres of two spindles.

The ends of the spindles frequently overlap and are bound together to form chains of two or three spindles, though the intrafusal fibres are not continuous. If the spindles are numbered from the pelvic end of the muscle, then in muscle *a* of figure 31 spindles 6 and 7, 9 and 10, and 11 and 12 are arranged in pairs, while in muscle *b*, spindles 2 and 3 form a pair, and spindles 5, 6 and 7 form a trio. Neither of these muscles contained any true tandem spindles, in which the intrafusal fibres of two spindles are continuous, but many tenuissimus muscles do contain one tandem spindle.

Tenuissimus spindles are more or less symmetrical, with the lymph space about halfway along their length, as is the case also in soleus muscle spindles. The structure and number of spindles in different tenuissimus muscles is relatively constant, but the number of extrafusal fibres varies greatly (Boyd, 1956). In the tenuissimus muscles in figures 34, 35, plate 42, in which the magnification is the same, the total cross-sectional area of the two muscles is widely different. The number of α motor axons to the extrafusal fibres varies with the cross-sectional area of the muscle, and in very small muscles the nerve fibres to the spindles form a very large proportion of the total number of fibres in the nerve.

(18) *Interosseous muscle of the hind foot (add. dig. long. V)*

The precise distribution and orientation of the spindles in this muscle is similar to that in the fifth interosseous muscle of the forelimb, described by Barker & Chin (1960). One interosseous muscle, fixed after removal from the cat, was serially sectioned transversely at 6 μ from end to end; the position of the 14 complete spindles it contained, relative to each other and to the length of the muscle, is shown in figure 32 (note the different scale from that of figure 31). In addition, this muscle contained, near its origin, one spindle only part of which was removed, and one bundle of short fibres of intrafusal type, contained in the usual sheath, but without any region in which the fibres contained nuclear bags or chains.

Most of the spindles are very asymmetrical, the lymph space being situated near one end. The long ends of the spindles are not all directed towards the same end of the muscle, but in the spindles situated near the origin or insertion of the muscle the long ends are mostly directed away from the tendon. No tandem spindles were present in this muscle but the ends of two spindles were dovetailed together; they are shown close together near the proximal end of the muscle in figure 32. The long ends of most of the spindles were attached deep in the muscle while the short ends were attached to the epimysium as described in § 8 of the Results.

Discussion

From this work it is quite certain that mammalian muscle spindles contain two distinct types of intrafusal muscle fibre. The evidence for this rests on differences in structure, and in sensory and motor innervation. The relation of these results to the findings of other authors will now be discussed.

Structure

(1) *Nuclear bag and nuclear chain intrafusal muscle fibres*

The existence of nuclei in intrafusal fibres, other than peripheral nuclei similar to those present in extrafusal fibres, was one of the principal findings which gave rise to the now outdated concept that spindles are growth centres in muscle, since the central nuclei in the equatorial region resemble those in the myotubes of developing muscle fibres. The term 'nuclear bag' was applied to the aggregate of 40 to 50 nuclei in some intrafusal fibres by Barker (1948) who stated that each intrafusal fibre in the quadriceps femoris muscle of the rabbit contained a nuclear bag. The fact that some intrafusal fibres did not have a nuclear bag, but had fewer nuclei arranged in a single central row, was observed by Cooper & Daniel (1956), who termed them 'myotubes', by Boyd (1956, 1958*a*) and by Barker & Gidumal (1960), who called the fibres 'nuclear chain fibres', and by Swett & Eldred (1960*b*) who stated that the nuclei were 'stacked rouleaux-fashion'. The spindles studied by Barker (1948) may have contained nuclear bag fibres only, but in view of the fact that he described fine nerve fibres which correspond with the γ_2 fibres in this paper (see §13 below) it is more likely that in his earlier investigations he failed to identify the nuclear chain fibres as separate entities because of their small size.

(2) *Diameter and length of intrafusal muscle fibres*

A wide variation in the diameter of intrafusal muscle fibres was noted by a number of authors. Kölliker (1862) gave values of 38 to 53 μ for the diameter of 'parent' fibres and 19 to 22 μ for the diameter of 'daughter' fibres in rabbit spindles; these two groups probably correspond to the nuclear bag and nuclear chain fibres of this paper, respectively. Sherrington (1894) gave a range of intrafusal fibre diameter of 6 to 28 μ in transverse sections. Barker & Gidumal (1960) described three sizes of intrafusal fibre within the ranges 15 to 25 μ, 10 to 15 μ and 4 to 9 μ in transverse sections of cat spindles from a number of muscles. Walker (1958) noted that the distribution of diameters of intrafusal fibres in spindles from the tibialis anterior and intercostal muscles of the dog was bimodal. Swett & Eldred (1960*b*) also found that histograms of the diameter of intrafusal fibres in transverse sections of the soleus and medial gastrocnemius muscles were bimodal, with peaks at about 14 and 26 μ for soleus spindles fixed *in situ*; these values were corrected for shrinkage during fixation.

The mean values for intrafusal fibre diameter obtained in this investigation (see table 2) were 30 μ for the nuclear bag fibres, and 14 μ for the nuclear chain fibres, of normal soleus spindles. These values are similar to the means of the two groups of fibres given by Swett & Eldred. It is clear from table 2 of this paper that intrafusal fibre diameter varies from muscle to muscle, as does the diameter of extrafusal muscle fibres.

Values for spindle length in the literature often refer to the length of the spindle sheath, and the writers state that the 'parent' intrafusal fibres project beyond the ends of the spindle. Kölliker (1862) gives a range of length of 4 to 7 mm, which probably refers to the total length, while Sherrington (1894) gives a range of 0·75 to 4 mm, no doubt the length of the sheath only. The mean value of 2·6 mm for the length of soleus spindles given by Hagbarth & Wohlfart (1952) is close to the value of 2·3 mm for the length of the nuclear

chain fibres in soleus spindles, fixed in the relaxed state and without correction for shrinkage, given in table 3 of this paper; presumably these authors measured the length of the spindle sheath. The total length of spindles in the cat rectus femoris muscle, according to Barker, Cope & Ip (1960), varies from about 3 to 14 mm, with a mean of 7 mm, which agrees with the mean of 7·5 mm for the length of leg muscle spindles obtained in the present study. The mean length of spindles in the small muscles of the foot is less than 7·5 mm, however (about 5 mm; table 3).

Swett & Eldred (1960*b*) found the mean length of spindles in the soleus and medial gastrocnemius muscles to be 5·8 and 4·8 mm, respectively. Measurements of the half-length of individual intrafusal fibres in soleus spindles showed that the fibres fell into two distinct groups. If it is assumed that the intrafusal fibres are symmetrical about the nuclear region, which is true approximately for spindles in the leg muscles, then the mean total lengths of their two groups of fibres were 6 and 2 mm. These values are smaller than those obtained in this investigation for the nuclear bag fibres (7 mm) and the nuclear chain fibres (4 mm) in isolated whole soleus spindles (table 3) but their results clearly support the concept of two distinct types of intrafusal muscle fibre.

(3) *Structure of intrafusal fibres in transverse section*

It was shown in the Results that nuclear bag intrafusal fibres have a large number of myofibrils per unit area and relatively little sarcoplasm. The myofibrils are of fairly uniform size and presumably each contains about the same number of myofilaments which cannot be resolved under the light microscope. The distribution of myofibrils through the sarcoplasm is also uniform. The nuclear chain fibres, on the other hand, contain fewer myofibrils per unit area. The myofibrils are of greatly varying size, some of them much larger than those in the nuclear bag fibres and presumably containing very large numbers of myofilaments. These myofibrils of variable size are scattered irregularly throughout a relatively large amount of sarcoplasm.

In the interosseous muscles the nuclear bag fibres contain many more myofibrils per unit area than the extrafusal fibres and are packed so full of myofibrils that in transverse sections they frequently stain uniformly dark. In the soleus muscle the nuclear bag fibres also stain densely but are rarely uniformly dark.

Kruger (1952) describes two types of skeletal muscle fibre: (1) Fibres with 'Fibrillenstruktur', i.e. with myofibrils uniformly distributed in transverse sections, and usually, but not always, with relatively little sarcoplasm. These fibres occur typically in phasic (or tetanic) muscles. (2) Fibres with 'Felderstruktur', i.e. with areas of contractile elements irregularly distributed in a relatively large amount of sarcoplasm. These fibres occur typically in tonic muscles. From his description of the electrophysiological properties of 'tonic' fibres it is clear that Kruger is referring to fibres similar to the 'slow' fibres of the frog, which have a multiple motor innervation, no propagated action potentials, and respond to prolonged depolarization with prolonged contraction (Kuffler & Vaughan Williams 1953).

A classification of all skeletal muscle into two types only is inadequate, however, for at least two other types exist, and perhaps numerous gradations in between. The 'red' or 'tonic' extrafusal fibres in avian muscle are like 'slow' fibres except that they have a

propagated action potential (Ginsborg 1960). The 'red' or 'tonic' extrafusal fibres in mammalian muscle are not like 'slow' fibres; these mammalian fibres have a propagated action potential, focal innervation, are capable of tetanic contraction, and do not respond to prolonged depolarization with prolonged contraction, i.e. they are much more like 'phasic' fibres than 'slow' fibres.

While it is tempting, therefore, to equate the structure of the nuclear bag fibres with 'Fibrillenstruktur' (and 'phasic' activity), and the structure of the nuclear chain fibres with 'Felderstruktur' (and 'slow' activity), this is probably not correct. The nuclear chain fibres may be 'slow' fibres, but other evidence given below indicates that the nuclear bag fibres are quite different from mammalian extrafusal fibres, phasic or tonic.

Kruger (1960) states that a distinction should be made between 'phasic spindles' in phasic muscles and 'tonic spindles' in tonic muscles, and spindles with a double character in mixed muscles. In support of this view transverse sections of a human lumbrical (phasic) muscle spindle (Kruger 1952) and of a cat soleus (tonic) muscle spindle (Kruger 1960) are shown. Both spindles appear to contain two types of fibre, however, and the photographs are similar to the transverse sections of interosseous and soleus spindles obtained in the present work in which it has been shown that all spindles contain some intrafusal fibres of each of the nuclear bag and nuclear chain types. Swett & Eldred (1960*b*) also state that both large and small intrafusal muscle fibres occur in phasic (medial gastrocnemius) and tonic (soleus) muscles. Kruger is probably correct, however, to the extent that both types of intrafusal fibre show a gradation in activity which is related to the nature of the extrafusal fibres of the muscle in which they lie.

(4) *Atrophy of intrafusal fibres after transection of ventral roots*

The literature contains conflicting evidence on this point. Sherrington (1894) stated that 150 days after degeneration of the muscle nerves the extrafusal fibres in muscles from the hind leg of the cat were grossly atrophied and degenerated while the intrafusal fibres were not obviously altered. The spindles were very obvious amid the atrophied extrafusal muscle bundles. Spindles are also very prominent in muscles which are wasted for pathological reasons (Batten 1897; Forster 1894). Batten found no noticeable reduction in diameter of intrafusal fibres in the gastrocnemius muscle of cats within 3 months of complete transection of the sciatic nerve; but in a case of injury to the brachial plexus of 1 year's standing in a human subject he found the intrafusal fibres in spindles in the forelimb muscles very atrophied. He deduced that atrophy of intrafusal fibres does take place after they are denervated but that the rate of atrophy is much less than that of extrafusal fibres.

Tower (1932) studied this point in some detail; she observed the reaction of the extrafusal and intrafusal muscle fibres of the interosseous muscles of the forelimbs of young adult cats after cutting the peripheral nerves and after cutting the appropriate ventral spinal roots. She found that intrafusal and extrafusal fibres both atrophied to the same degree, the atrophy being pronounced 4 months after operation.

It has been shown in this paper that the intrafusal fibres do atrophy after the ventral roots are cut, but that the two types do so to a different degree. The nuclear bag fibres show only a slight reduction in diameter after several months and it seems clear that these were the muscle fibres to which Sherrington and Batten referred. Since the nuclear chain fibres

are small in limb muscle spindles it is not surprising that they were overlooked, especially if they had atrophied. The nuclear chain fibres atrophy nearly as rapidly as the extrafusal fibres. Since in normal interosseous spindles the nuclear chain fibres may be as large as the nuclear bag fibres and more numerous, the whole spindle appears to have atrophied considerably as observed by Tower. Thus, the apparent discrepancies in previous descriptions are explained.

The difference in the rate of atrophy of nuclear bag intrafusal fibres and nuclear chain intrafusal fibres after ventral root transection is additional confirmation of the fact that they represent two distinct types of muscle fibre. Extrafusal muscle fibres atrophy rapidly after denervation and phasic fibres are usually considered to do so more rapidly than tonic fibres. The nuclear bag fibres, however, atrophy much more slowly than either nuclear chain fibres or extrafusal fibres, yet other evidence indicates that it is the nuclear chain fibres which most probably show true 'slow' activity, not the nuclear bag fibres. The relation of rate of atrophy to type of behaviour cannot be a simple one. The pronounced difference between nuclear bag intrafusal fibres and extrafusal fibres in this respect, however, makes it unlikely that nuclear bag fibres are similar in behaviour to extrafusal fibres.

(5) *Branching of intrafusal muscle fibres*

In much of the early literature about spindles opinions were clearly divided on this point. Many authors believed that the larger intrafusal fibres found beyond the ends of the spindle capsule divided to form smaller daughter fibres in the equatorial region (Kühne 1863; Sherrington 1894; Batten 1897) and some said that branching and re-uniting of the intrafusal fibres was extensive (Forster 1894). Other authors stated that the intrafusal fibres could be traced right through the spindles without any branching at all (Kerschner 1888; Baum 1900; Cuajunco 1927) and that the varying number of intrafusal fibres seen in transverse sections was due to the fact that the fibres were of different lengths. With the definite statement of Barker (1948), after a detailed study of normal rabbit spindles in serial longitudinal sections, that division of intrafusal fibres did not occur, the matter appeared to be settled. All the evidence up to this point, however, depended on observation and description alone; no photographic evidence in support of either point of view was given.

More recently the matter has again been raised. Some authors still maintain that intrafusal branching, if it occurs at all, is a rarity (Boyd 1958*a*; Cooper 1960; Swett & Eldred 1960*b*). But Barker (1959) now holds that extensive branching and re-uniting of some intrafusal muscle fibres occurs both towards the poles and at the ends of the equatorial region, though the largest of the intrafusal fibres do not divide. It has been shown in the present work that in many spindles neither the nuclear bag fibres nor the nuclear chain fibres divide at all and each can be traced as a discrete entity from end to end. It seems clear that Sherrington's statement that large parent muscle fibres divide to form small daughter fibres as they enter the capsule was incorrect. The small nuclear chain fibres in leg muscle spindles are attached to the endomysium of the large nuclear bag fibres near to the point at which the capsule begins, but they are not branches of the nuclear bag fibres. The presence in some spindles of short nuclear chain fibres accounts for the fact that the number of them in transverse sections from opposite halves of the spindle may be different.

Nevertheless, Barker & Gidumal (1960) have produced unequivocal evidence that intrafusal fibres do sometimes divide. This has, in fact, been definitely demonstrated for one nuclear bag fibre in the present study. The author belives that division of nuclear bag fibres is so rare as to be negligible, while the degree of branching of the nuclear chain fibres may vary in spindles from different sites. The extensive branching and re-uniting of the nuclear chain fibres to form a network of muscle fibres, as described by Barker, has never been observed in any of the spindles studied in this investigation. This point is probably not of great functional importance since the nuclear chain fibres have a common motor innervation and presumably behave as a single functional unit.

It is of importance, however, to know whether there is any branching which connects the muscle fibres of the nuclear bag system to those of the nuclear chain system. This has never been observed in this study, and is most unlikely in view of the other differences between them besides those of size and nuclear arrangement; there are differences in structure in cross-sections and in the rate of atrophy after the ventral roots are cut, and also differences in their sensory and motor innervation.

(6) *Simple spindles*

Simple (type *P*) spindles have no secondary sensory innervation. In the early stages of this investigation (Boyd 1959) it was thought that these spindles contained only one of the two types of intrafusal fibre which have been described in this paper, probably nuclear bag fibres, whereas other spindles were compound in the sense that they contained both nuclear bag and nuclear chain systems. The interosseous muscles were thought to contain more simple spindles than other muscles, for in many of them all the intrafusal fibres were the same size. It has been shown in this paper, however, that simple spindles contain both nuclear bag and nuclear chain intrafusal fibres, and receive both γ_1 and γ_2 motor innervation as do other spindles (figures 14, 19, 25; figure 68, plate 48; figure 71, plate 49).

The proportion of simple spindles out of the total number of spindles in the interosseous muscles is 19%, which is greater than it is in the tenuissimus (16%) and soleus (11%) muscles (table 5). The soleus muscle in the cat is a tonic muscle, whereas the tenuissimus and interosseous muscles are mixed muscles. In phasic muscles the proportion of simple spindles is higher (Cooper 1960). In the rectus femoris muscles in the cat, for example, Barker (1959) found that about 30% of the spindles were simple.

(7) *Tandem spindles*

True tandem spindles, in which at least some of the nuclear bag intrafusal fibres are continuous through two or more nuclear regions, were found infrequently in this investigation, though spindles with the ends of their nuclear bag fibres dovetailed together were quite common, especially in the tenuissimus muscle. Tandem spindles usually consist of a complex spindle with a simple spindle in series with it. Two such spindles from the soleus muscle are described in this paper (figure 1, spindle II; figure 17).

A value of 16 to 20% for the proportion of spindles of tandem type in the rectus femoris muscle of the cat was given by Barker, Cope & Ip (1960). Corresponding values obtained by Swett & Eldred (1960*a*) were 44% for the medial gastrocnemius and 21% for the soleus muscles. The latter figure seems high in relation to the number of tandem spindles

encountered in the soleus muscle in the present study. It is difficult to assess the proportion of spindles of tandem type from isolated preparations since the nuclear bag fibres sometimes break near their ends during the teasing process. However, in two tenuissimus muscles and one interosseous muscle which were serially sectioned transversely (figures 31, 32) no tandem spindles were found.

In the estimation of numbers of nerve fibres or nerve endings in spindles in this investigation, the two spindles making up a tandem spindle were considered to be separate entities.

Innervation

(8) *Primary and secondary sensory endings*

Every spindle has a primary sensory ending whose spiral terminations surround the nuclear regions of each intrafusal fibre. The observation of Ruffini (1898) that each intrafusal muscle fibre has a riband-like annulo-spiral wrapped round it has been confirmed. Since the nuclear chain fibres are always much smaller than the nuclear bag fibres, there are two distinct sizes of spiral termination. No spiral includes more than one intrafusal muscle fibre within it and all the spirals are supplied by branches of the one group I *a* fibre. The length of the intrafusal muscle fibres occupied by the primary sensory terminations varies from 200 to 400 μ in the cat. Barker (1948) gives a comparable value of 200 μ for the rabbit. Thus, the primary sensory ending and its group I *a* afferent fibre provide an afferent pathway which is common to both the nuclear bag and nuclear chain intrafusal systems.

The number of secondary sensory endings in a spindle varies from zero to five. Ruffini (1898) and Barker (1948) gave the number as zero to two. Sherrington (1894) found three to four afferent fibres per spindle, which implies that some had three secondary sensory endings. Spindles with one secondary sensory ending are the most common; in spindles with two secondary endings, they may lie one on each side of the primary ending or both on the same side of it. If a spindle contains more than one secondary sensory ending, then γ_2 motor endings may lie on the same region of nuclear chain intrafusal fibres as the secondary sensory terminations. The secondary sensory terminations lie predominantly on the nuclear chain intrafusal fibres; they are usually of spiral or annular form encircling each nuclear chain fibre. Any terminations on the nuclear bag fibres have a spray form and their extent varies from muscle to muscle. In many soleus spindles the inflow in group II afferent fibres must arise almost entirely in the nuclear chain system. An individual secondary ending occupies a length of the bundle of nuclear chain fibres between 300 and 500 μ. Barker & Ip (1960) also stated that the secondary terminations in the cat were annulo-spiral in form and Barker (1948) found that secondary endings in rabbit spindles were about 500 μ in length.

(9) *Diameter and branching of afferent nerve fibres*

In the present study the mean total diameters of group I *a* and group II afferent fibres, measured about 1 mm from the spindles, were 12 and 6 μ, respectively. These values are consistent with those given by Barker (1948) for rabbit spindles. As observed by Barker (1959), the afferent nerve fibres from spindles in muscles near to the spinal cord are slightly larger than those from muscles distant from the cord.

Eccles & Sherrington (1930) reported that there was a minor degree of splitting of large diameter afferent fibres in the gastrocnemius nerve. From the present study branching of group I*a* fibres is very rare. Two or three tendon organs, however, quite often have a common group I*b* fibre. The soleus nerve contains approximately 80 group I fibres (Hagbarth & Wohlfart 1952; Boyd & Davey 1962). The soleus muscle contains about 54 spindles and 45 tendon organs (Hagbarth & Wohlfart 1952; Swett & Eldred 1960*a*). If each spindle receives one group I*a* fibre, then there are 1·8 tendon organs per group I*b* fibre.

Some branching of group II fibres definitely occurs, the branches supplying two secondary sensory endings either in the same spindle, or in different spindles lying near to each other in the muscle. These histological observations agree with the electrophysiological findings of Swett & Eldred (1959). The number of secondary sensory endings per spindle is 1·5 in the soleus muscle and 1·6 in the tenuissimus muscle. The nerves contain about 50 and 20 group II fibres, respectively, and the tenuissimus muscle contains about 15 spindles. Hence, there are about 1·6 and 1·2 secondary sensory endings per group II fibre in the soleus and tenuissimus muscles, respectively.

(10) *Motor innervation of the spindle as a whole*

It is has been shown in the Results that, in general, the nuclear bag intrafusal fibres are innervated by γ_1 fibres, and that the γ_1 end-plates are situated mostly in the S_3 regions and beyond, so that long lengths of the nuclear bag fibres have no motor innervation. The nuclear chain fibres are innervated by γ_2 fibres whose terminal branches connect a number of γ_2 endings in a communicating network. The γ_2 endings may lie anywhere on the nuclear chain fibres except in the nuclear region.

Thus, in the spindle as a whole any motor innervation in the S_1 and part of the S_2 regions is part of the γ_2 network on the nuclear chain fibres. Most of the motor innervation in the S_3 region, and all of that beyond the S_3 region, consists of γ_1 end-plates on nuclear bag fibres. In between the two motor systems overlap to a varying degree. If one or other half of any spindle is free of secondary sensory endings, then the γ_2 and γ_1 motor innervations in this half may be quite separate, occupying the S_1 and S_2 regions, and the S_3 region and beyond, respectively. If an S_1 secondary sensory ending is present the γ_2 innervation is displaced towards the end of the spindle and overlaps the γ_1 innervation, though on different muscle fibres, producing a complex collection of motor nerve fibres and nerve endings in the S_2 and S_3 regions (figure 22). This is the 'diffuse ending' of Cooper (1960) and probably also the 'polar ending' of Hines & Tower (1928), and the appearance is not unlike some secondary sensory endings.

Coers & Durand (1956) studied the distribution of foci of cholinesterase in spindles in the rectus abdominis muscle of the cat and the rat using histochemical methods. They also stained normal spindles with methylene blue for comparison. No cholinesterasic activity was found in the equatorial region, but diffuse cholinesterasic activity was found scattered throughout the rest of the spindle. The density of the activity was greatest close to the equatorial region and diminished towards the poles. Coers & Wolff (1959) summarize the results. The conclusion these authors reach that intrafusal fibres receive multiple motor innervation of two types is undoubtedly correct, but the conclusion that the flower-spray

(secondary sensory) endings of Ruffini (1898) are mainly motor is definitely not correct. As has been shown in the present work, if there is more than one secondary ending, some of the γ_2 network lies on the same regions of the nuclear chain fibres as the secondary sensory terminations.

Coers & Durand found that the length of spindle at the equator free of cholinesterasic activity was between 250 and 660 μ, and was more than 600 μ in many spindles. The smaller value corresponds with the length of the primary sensory ending in a simple spindle (250 to 400 μ) given in this paper and the larger value with the combined lengths of one primary (about 300 μ) and one secondary (about 400 μ) sensory ending. Their results, therefore, agree with the conclusion of the present study that in simple spindles only the *P* region is free of motor nerve endings, while in complex spindles with any number of secondary sensory endings between one and five, the length of spindle without motor endings (i.e. the length of nuclear chain fibres free of γ_2 nerve endings) is approximately equal to 700 μ, the length of the primary ending plus one secondary sensory ending.

Neither Coers & Durand (1956) nor Hess (1961), using techniques for demonstrating the distribution of sites of cholinesterasic activity, were able to determine definitely whether the two types of motor ending they found were located on the same or on different intrafusal fibres. Kupfer (1960) studied spindles in human extraocular muscles and found thin intrafusal muscles fibres with numerous discrete loci of cholinesterastic activity, and larger intrafusal fibres having both typical end-plates and discrete loci.

It has been shown in this paper that in a few spindles one of the nuclear bag fibres may have a γ_2 ending in the S_2 region in addition to the usual γ_1 end-plates in the S_3 region. In many spindles, however, the nuclear bag fibres definitely have no γ_2 innervation. At present the author feels that the presence of γ_1 and γ_2 nerve endings on the same nuclear bag fibre is perhaps an anatomical peculiarity without special physiological significance.

(11) *Groups of origin of γ_1 and γ_2 fusimotor fibres in the muscle nerves*

The γ_1 and γ_2 motor fibres found in the spindles cannot be directly correlated with the groups of motor fibres in the muscle nerves because the exact nature of intramuscular branching of motor fibres is not known.

There are three obvious possibilities: (1) Both γ_1 and γ_2 fibres may be branches of the one type of γ-efferent fibre in the nerve to the muscle. This seems very unlikely in view of the characteristic difference in the branching and diameter of the γ_1 and γ_2 fibres near to and in the spindles, and in the site and nature of their terminations on the intrafusal muscle fibres. (2) The γ_1 fibres may be branches of α-efferent stem fibres while the γ_2 fibres are branches of γ-efferent stem fibres. (3) The γ_1 and γ_2 fibres may be branches of two different types of stem fibre contained within the traditional γ-efferent group in the muscle nerves.

The histological evidence for or against possibilities (2) and (3) may be listed as follows:

(*a*) Previous workers, e.g. Barker (1948), described spindles in which one large motor fibre branched in the spindle to supply all the end-plates at one pole. These 'large' motor fibres had a total diameter of about 5 μ. He stated, however, that in many spindles both poles were innervated by a number of small nerve fibres. In the present study only a few spindles were found in which the γ_1 end-plates at one pole were all supplied by a single γ_1 fibre with an axon diameter of 4 to 5 μ. As Barker (1959) himself has pointed out, none

of the motor fibres at the spindle is too large to be derived from a γ-efferent stem fibre, the largest of which have a total diameter of 7 or 8 μ.

(*b*) Occasionally a γ_1 end-plate towards the end of a nuclear bag fibre receives its γ_1 fibres from a bundle of nerve fibres the rest of which innervate extrafusal muscle fibres near by. Such γ_1 fibres might be branches of α fibres. A number of these γ_1 fibres were traced back into the intramuscular nerve branches for a considerable distance, in one case more than 4 mm, without any of them joining another nerve fibre or increasing significantly in diameter. Ruffini (1898), and Barker & Chin (1961), stated quite definitely that nerve fibres innervating surrounding extrafusal muscle never innervated the intrafusal fibres. This does not, of course, prove that spindles do not receive α fibres; it merely proves that the fusimotor fibres are independent of α fibres to extrafusal muscle.

(*c*) If α-innervation of spindles exists, then the intrafusal muscle fibres might be expected to have a structure and innervation similar to extrafusal muscle fibres. The intrafusal fibres concerned are the nuclear bag fibres since the largest fusimotor fibres innervate them. The nuclear bag fibres, however, differ from extrafusal fibres in several ways. They contain more myofibrils per unit area than extrafusal fibres, they atrophy much more slowly than extrafusal fibres after the ventra roots are cut, and there are several motor end-plates on each nuclear bag fibre.

(*d*) Boyd & Davey (1962 and unpublished) examined histologically the fibres which make up the traditional γ-efferent group in the nerves to many de-afferented hind limb muscles in cats. They found, in most nerves, two groups of fibres in addition to the α group; thickly myelinated fibres with total diameters between about 3 and 6 μ and thinly myelinated fibres with total diameters between 1 and 3 μ. Histograms of fibre-size showed that in some muscles the two groups overlapped in diameter, while in others they formed two separate peaks at 2 to 3 μ and 5 to 6 μ. It is possible that the groups of larger and smaller diameter in the nerve were the stem fibres of the γ_1 and γ_2 fibres at the spindles.

(*e*) If the γ_1 fibres are branches of α stem fibres then every spindle has extensive α-innervation, since an average of five γ_1 fibres enters each spindle. Hunt & Kuffler (1951) stimulated single fibres in the ventral roots while recording from spindle afferent fibres in the dorsal roots. Only on rare occasions did stimulation of an α fibre affect a spindle.

Most of the histological evidence, therefore, supports the view that mammalian fusimotor fibres of two types, neither of which are contained in the α group, are present in nerves to skeletal muscle.

(12) *Branching of fusimotor fibres and number of motor nerve endings*

The average number of motor fibres about 1 mm from each soleus spindle has been shown to be 14, of which 6 are γ_1 fibres and 8 are γ_2 fibres, while each tenuissimus muscle spindle receives 10 fibres, of which 4 are γ_1 fibres and 6 are γ_2 fibres. The soleus nerve contains about 115 fibres in the γ group of which 80 are thickly myelinated and 35 are thinly myelinated; the tenuissimus nerve contains about 10 thickly myelinated and 10 thinly myelinated γ fibres (Boyd & Davey 1962). If the thickly and thinly myelinated fibres are the stem fibres of the γ_1 and γ_2 fibres found at the spindles, respectively, then it may be calculated that, on the average, each γ_1 stem fibre may innervate up to about five spindles, while each γ_2 stem fibre may innervate as many as twelve spindles. Hunt &

Kuffler (1951) showed that the discharge in a single spindle afferent fibre could be affected by stimulation of three to five different γ-efferent fibres isolated separately from the ventral roots. The histological evidence suggests that these workers were stimulating γ_1 stem fibres.

While many γ_1 fibres do not branch close to or after entering the spindle, some of them undoubtedly do branch, for there are about three γ_1 end-plates to every two γ_1 fibres approaching the spindle. The γ_2 fibres branch even more extensively, and there are two to four times as many γ_2 endings as there are γ_2 fibres approaching the spindle. The total number of motor nerve endings varies from about 15 in some tenuissimus spindles to about 40 in the most complex soleus spindles, values which are consistent with the figure of 20 or more plates per spindle given by Ruffini (1898).

Barker (1948) found that there were about two motor end-plates per intrafusal muscle fibre in spindles from the quadriceps femoris muscle of the rabbit, and the number of plates at each pole was approximately the same. It is clear from his description that Barker was referring to γ_1 end-plates on nuclear bag muscle fibres, and a similar arrangement of one γ_1 end-plate at each end of each nuclear bag fibre was seen in many tenuissimus spindles in the present investigation. On the average, each tenuissimus spindle contains 5 γ_1 end-plates and 14 γ_2 endings, while each soleus spindle has 10 γ_1 end-plates and 22 γ_2 endings.

It is impossible to assess the actual number of intrafusal muscle fibres in a γ_1 or a γ_2 motor unit since the number of motor nerve endings per muscle fibre is very variable. It is quite likely that each nuclear bag fibre belongs to several γ_1 motor units, and it has several end-plates for this reason rather than for the production of local non-propagated potentials. This would account for the fact that the γ_1 end-plates usually occur in two groups, one at each pole of the spindle, instead of lying at regular intervals along the nuclear bag fibres. The γ_2 network forms a 'motor pool', involving all the nuclear chain muscle fibres, with which a considerable number of γ_2 stem fibres are connected. Recruitment of more γ_2 fibres may increase the general output of transmitter substance from this motor pool, the contraction of all the nuclear chain fibres as a group being graded according to the amount of transmitter released.

(13) *Sympathetic innervation of spindles*

Very fine nerve fibres were observed by a number of workers to take part in spindle innervation, and were sometimes assumed to be sympathetic in origin because of their small diameter and because they were usually non-myelinated fibres. Perroncito (1902) described very fine fibres running to normal spindles in the Henle's sheath of large myelinated fibres and also in association with their terminal branches. These fine fibres were quite independent of the blood vessels, but he could not be certain that they had contact with the intrafusal muscle fibres. His drawings show an extensive network of very fine nerve fibres in the *P* region associated with the primary sensory ending. Tello (1922) saw very fine nerve fibres ending on the intrafusal muscle fibres, but the terminations were obscure. Creed, Denny-Brown, Eccles, Liddell & Sherrington (1932) state that unmyelinated fibres enter the spindle with the primary sensory fibre and end in the region of the primary ending. Barker (1948) observed very fine fibres (diameter $< 0{\cdot}5\,\mu$) which were only detectable with silver staining, forming an anastomosing network in the polar

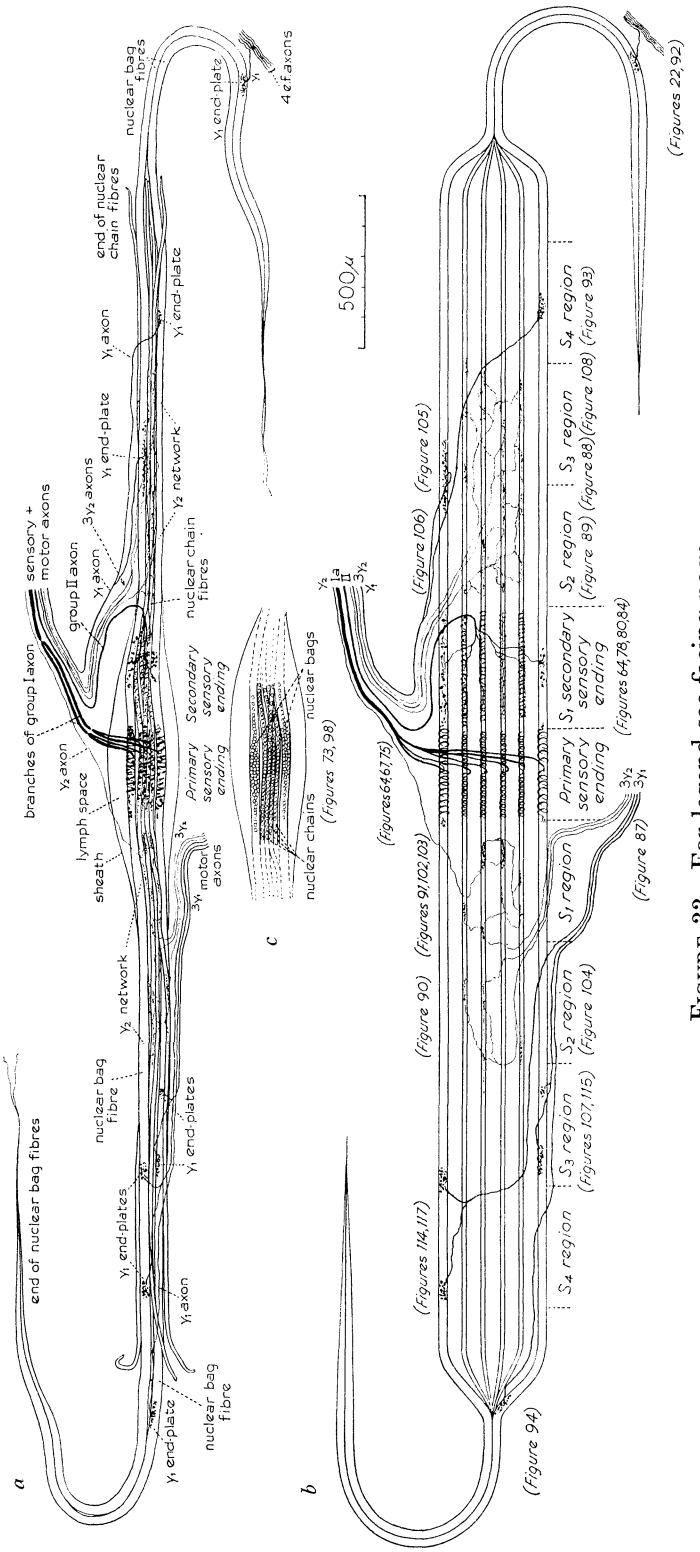


FIGURE 33. For legend see facing page.

FIGURE 33. A representative mammalian muscle spindle. *a*, as seen in isolated gold chloride preparations. *b*, expanded scale diagram incorporating the mean values of all the series of measurements made in this investigation.

The spindle has two nuclear bag fibres, each 26 μ in diameter and 7·5 mm in length, and four nuclear chain fibres, each 12 μ in diameter and 4 mm in length. The nuclear bags and chains which lie beneath the sensory endings are shown in *c*. This is the appearance of the nuclear region in isolated whole spindles in which the sensory nerve fibres and endings have completely degenerated. The nuclei are each 10 μ in diameter. The ends of the nuclear chain fibres are attached to the nuclear bag fibres and both ends of the spindle are attached to extrafusal muscle fasciculi. The ends of the nuclear bag fibres are looped back so that the magnification of the diagram can be as large as possible: the spindles are normally straight.

There is a primary sensory ending with a large myelinated group I*a* nerve fibre of total diameter (axon + myelin sheath) 12 μ at this point. The spiral terminations encircle each of the nuclear bag and each of the nuclear chain fibres; they occupy a length of spindle of 300 μ. There is one secondary sensory ending with a group II myelinated nerve fibre, 6 μ in total diameter, which enters with the group I*a* fibre. The secondary sensory terminations lie mostly on the nuclear chain fibres, but there are small accessory sprays on the nuclear bag fibres also. The endings on the nuclear chain fibres are spiral in form, though less regular than those in the primary ending, and the spirals or semi-spirals are linked by a fine axon running along the surface of each muscle fibre. The secondary sensory ending occupies a length of 400 μ.

At the pole at which there is no secondary sensory ending the γ_1 and γ_2 motor innervations do not overlap. The γ_1 end-plates lie on the nuclear bag fibres in the S_3 region and beyond. Three γ_1 motor fibres, each with an axon diameter of 3 μ, and three γ_2 motor fibres, with an axon diameter of about 1 μ, enter the spindle together but at a different point from the afferent nerve fibres. The upper nuclear bag fibre has two γ_1 end-plates in the S_4 region, supplied by the same γ_1 fibre. The lower nuclear bag fibre has a γ_1 end-plate, with a small accessory plate from the same γ_1 fibre, in the S_3 region. It has, also, another γ_1 end-plate just beyond the end of the nuclear chain fibres; this plate is supplied by a separate γ_1 fibre which travels for some distance inside the spindle to reach it. The γ_2 innervation consists of a network of eleven γ_2 endings on the nuclear chain fibres some of which lie in the S_2 region, and some of which lie in the S_1 region close to the primary sensory ending. The nuclear bag fibres have no motor innervation in either the S_1 or S_2 region. The γ_2 network at this end of the spindle is joined by the three γ_2 fibres already mentioned, plus a fourth γ_2 fibre which enters with the afferent fibres.

At the other pole the S_1 region is occupied by the secondary sensory ending and the γ_2 network is displaced, so that it occupies the S_2 and S_3 regions. It consists of thirteen γ_2 endings on the nuclear chain fibres, some close to the secondary sensory ending, others extending to the end of the S_3 region. The upper nuclear bag muscle fibre has a large γ_1 end-plate between the S_2 and S_3 regions, so that in this area the γ_1 and γ_2 innervations overlap, though on different muscle fibres. The γ_2 network is supplied by three γ_2 fibres which enter the spindle with the afferent nerve fibres. One of these γ_2 fibres is larger than the others and becomes thin at intervals before it joins the network. The lower nuclear bag muscle fibre has only one γ_1 end-plate, which is in the S_4 region; its nerve fibre is a branch of the same γ_1 fibre which supplies the plate on the upper nuclear bag fibre. This upper nuclear bag fibre has, in addition, a second γ_1 end-plate, situated well beyond the end of the nuclear chain fibres; its γ_1 nerve fibre approaches the spindle with a bundle of extrafusal motor nerve fibres.

Thus, the γ_1 motor innervation of the whole spindle consists of five γ_1 fibres to eight γ_1 end-plates, four plates lying on each nuclear bag muscle fibre. The γ_2 motor innervation consists of seven γ_2 fibres to twenty-four γ_2 endings, i.e. six endings per nuclear chain muscle fibre.

regions. These fibres sometimes passed from one pole to the other, but none was seen to end among sensory endings. He was not able to tell whether they ended in contact with the intrafusal muscle fibres. He suggested that they might be somatic afferent (pain) fibres.

Since all these observations were made on normal spindles, there is no evidence as to whether these very fine fibres were sympathetic, or somatic, in origin. Hinsey (1927), however, after removing the dorsal root ganglia and short lengths of each of the ventral roots, taking care to leave the grey rami intact, found no nerve fibres innervating the intrafusal muscle fibres, though he found groups of unmyelinated fibres associated with blood vessels within the capsular wall of the spindles. Hines & Tower (1928) observed no loss of spindle innervation following sympathectomy, and found that no innervation remained in the spindles after cutting dorsal and ventral spinal roots distal to the dorsal root ganglia. They did, however, describe axons of 'sympathetic type' in de-afferented material. These axons had slender, non-myelinated parts at intervals along their length, alternating with myelinated regions. The results of Hinsey, and of Hines & Tower, are frequently misquoted.

It is clear that the fine fibres observed by Barker, and probably those seen by the earlier workers, too, were the terminal branches of the γ_2 motor fibres to the nuclear chain muscle fibres described in this paper. These γ_2 nerve fibres frequently enter the spindle with the group I*a* afferent nerve fibre and often transverse the sensory endings though they do not terminate in the *P* region (figures 68, 71). They are somatic motor fibres since they are present after removal of the dorsal root ganglia but disappear following transection of the appropriate ventral roots. The appearance described by Hines & Tower (see above) is typical of γ_2 fibres which travel a long distance in the spindle before terminating.

Hunt (1960) and Eldred, Schnitzlein & Buchwald (1960) reported that stimulation of the sympathetic trunk, while recording from dorsal root filaments in cats, produced an alteration in the discharge in limb muscle spindle afferent fibres. It is possible that transmitter substances, released from the terminals of the sympathetic fibres to the blood vessels in the spindle capsule, may produce some direct alteration of sensitivity of the receptor terminals. There is no histological evidence to support the view that spindles receive sympathetic innervation other than that associated with the blood vessels.

(14) *A representative mammalian muscle spindle*

A drawing of a muscle spindle is shown in figure 33*a*, and the components of it are drawn to scale in the diagram in figure 33*b*. This drawing incorporates the mean values of all the various series of measurements made in this investigation. A detailed description is given in the legend. Figure 33*b* also contains references to photographs in the plates which illustrate the features shown in the diagram. The principal features of this spindle apply to all spindles in the limb muscles, though the number of motor endings is typical of spindles in the soleus and interosseous muscles. It should be remembered that there is great variation in detail in different spindles in the same muscle, and in spindles from different sites.

(15) *Physiology of the nuclear bag and nuclear chain intrafusal systems*

A consideration of the spindle in figure 33 shows that activity in one intrafusal system must influence activity in the other, and that there can be no simple explanation of the

manner in which the two systems operate. The group I*a* afferent pathway is common to both systems while the group II afferent inflow arises primarily in the nuclear chain system.

The histological evidence suggests that neither the γ_1 motor fibres nor the γ_2 fibres are derived from α stem fibres and that there are probably two types of nerve fibre within the traditional γ-efferent group in the muscle nerves.* Electrophysiological evidence on this point is at present controversial (Granit, Pompeiano & Waltman 1959*a*, *b*; Rutledge & Haase 1961; review by Hunt & Perl 1960). Information obtained directly from mammalian spindles is very limited. Eyzaguirre (1960*a*, *b*), recording from spindles externally, has shown that propagated action potentials can be produced in some intrafusal fibres. Boyd (1958*b*, *d*; 1959) observed, on the few occasions on which the experiment proved possible, that the spindles in the tenuissimus muscle twitched in response to single stimuli applied to the muscle nerve when the α fibres were blocked anodally so that the extrafusal muscle did not respond. The inference is that twitches, and presumably propagated action potentials, may be produced in intrafusal fibres by impulses in nerve fibres other than those in the α group. If so, then the histological evidence makes it very probable that it is the nuclear bag fibres which are concerned.

Thus, the nuclear bag fibres may be similar to certain intrafusal fibres in frog and toad spindles (Eyzaguirre 1957; Koketsu & Nishi 1957*a*, *b*) and to 'red' avian extrafusal fibres (Ginsborg 1960), both of which have propagated action potentials and yet respond to prolonged depolarization with sustained contraction. The nuclear bag fibres contain a large number of myofibrils uniformly distributed in cross-sections yet they atrophy slowly when denervated; they have more than one end-plate yet have no motor innervation over much of their length.

The nuclear chain fibres may be similar to frog 'slow' fibres in which local non-propagated potentials are produced at multiple neuromuscular junctions, and the fibres are capable of sustained contraction when maintained depolarized (Kuffler & Vaughan Williams 1953). The γ_2 network on the nuclear chain fibres suggest a similar mechanism. The bundle of nuclear chain fibres probably behaves as a single functional unit, the degree of contraction depending on the frequency of discharge in individual γ_2 fibres and on the number of γ_2 fibres which are activated.

It is probable that both the nuclear bag and the nuclear chain intrafusal fibres, which occur in all spindles, show a gradation in activity which is related to the nature of the extrafusal fibres of the muscle in which they lie. Histologically there are more motor nerve endings on both types of intrafusal fibre in tonic muscles than there are on intrafusal fibres in other muscles. The author suggests that the nuclear chain system is functionally 'slower' than the nuclear bag system in all spindles, but that both types will be found to be relatively 'slower' in tonic muscles than in phasic muscles.

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* *Note added in proof* 26 *March* 1962. The presence of separate groups of fast and slow motor fibres within the traditional gamma group in nerves to skeletal muscle has recently been confirmed electrophysiologically by the author.

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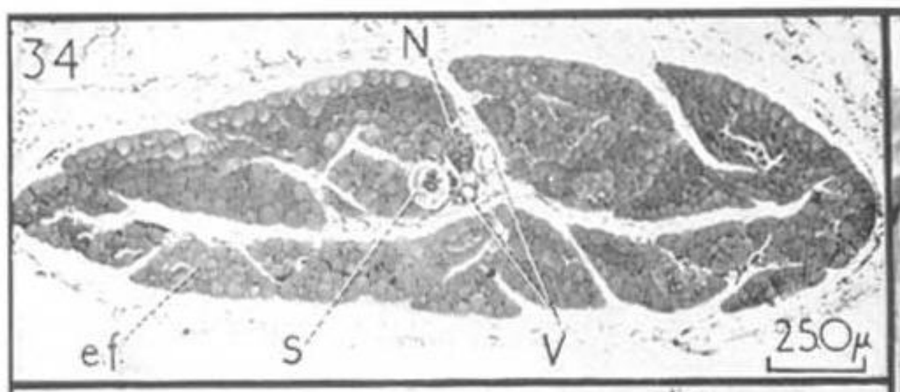
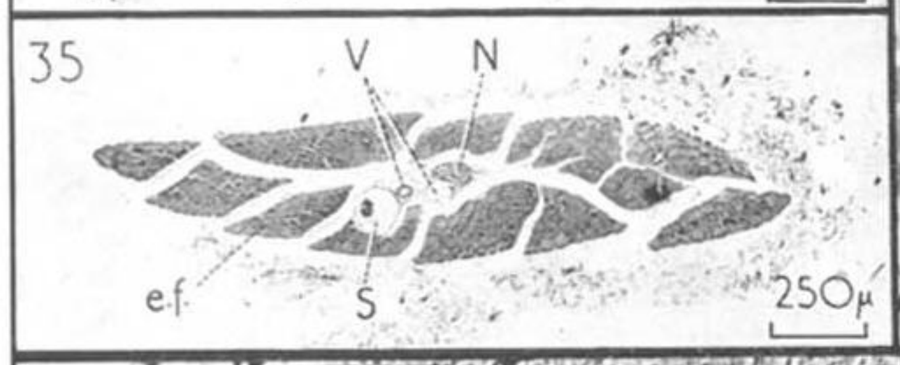
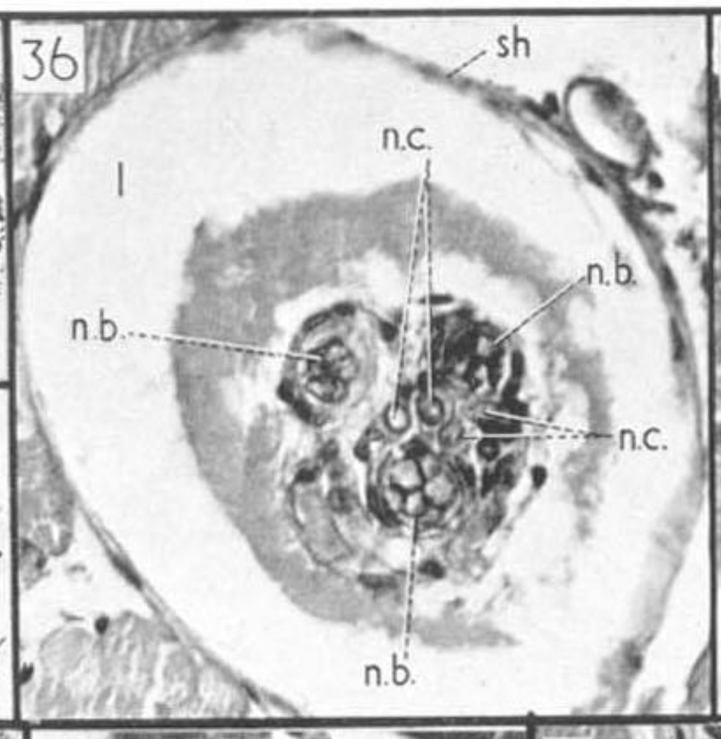
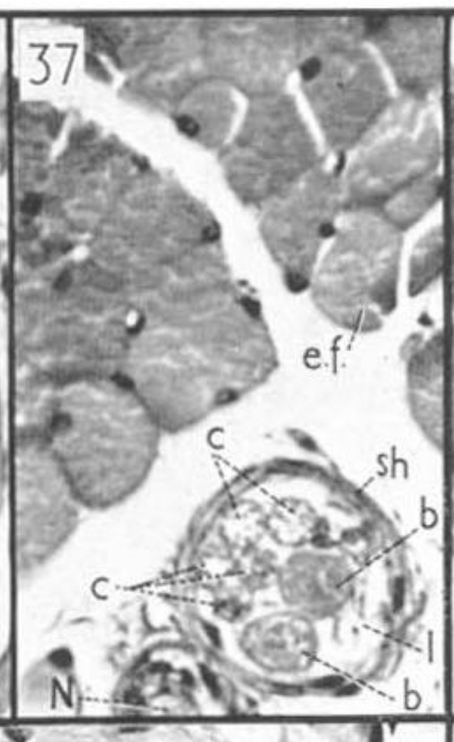
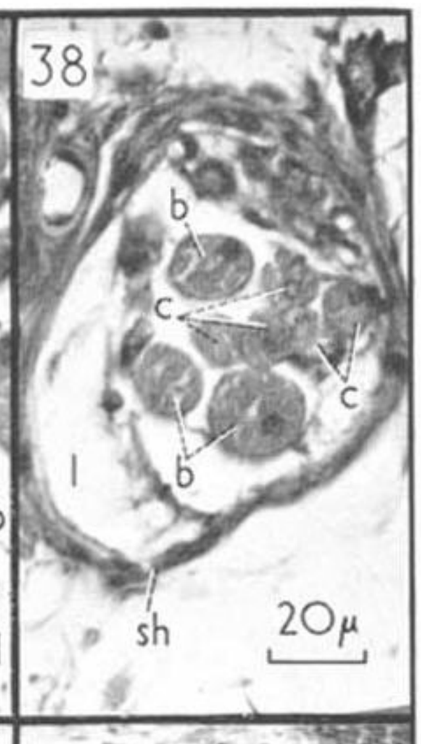
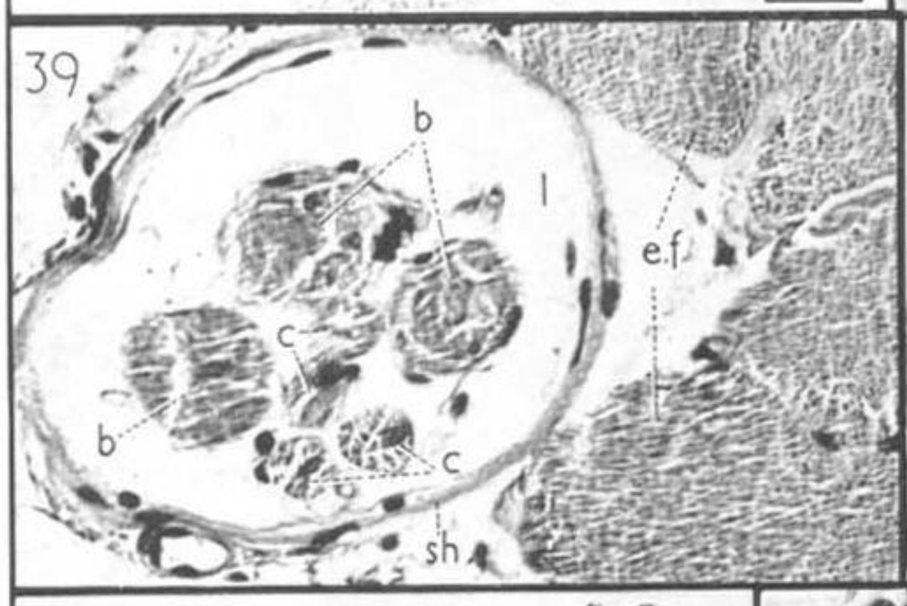


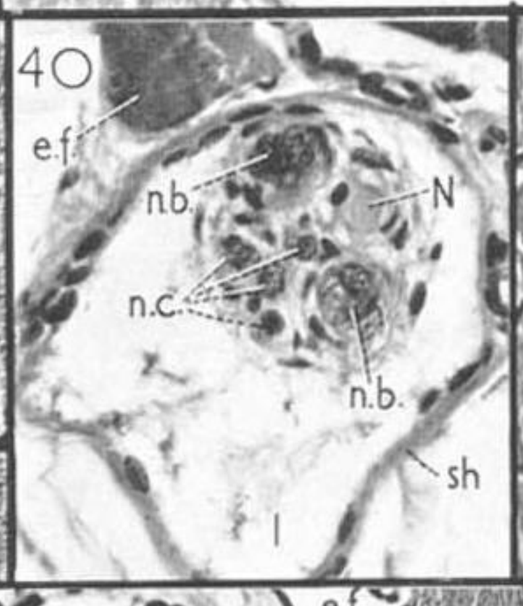


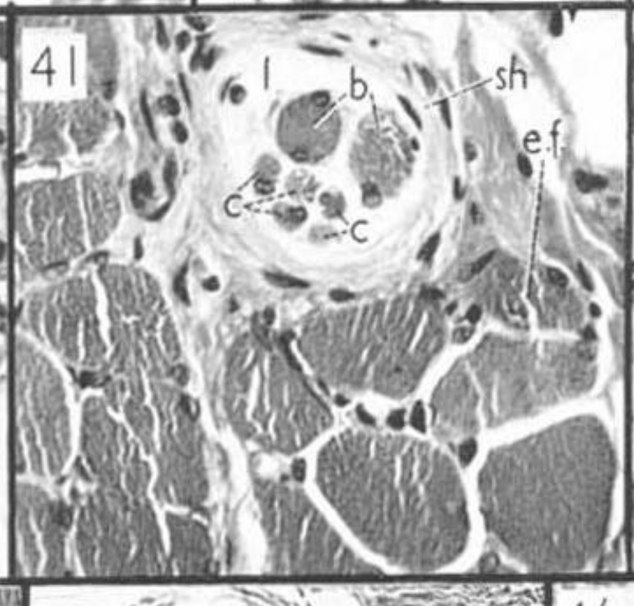


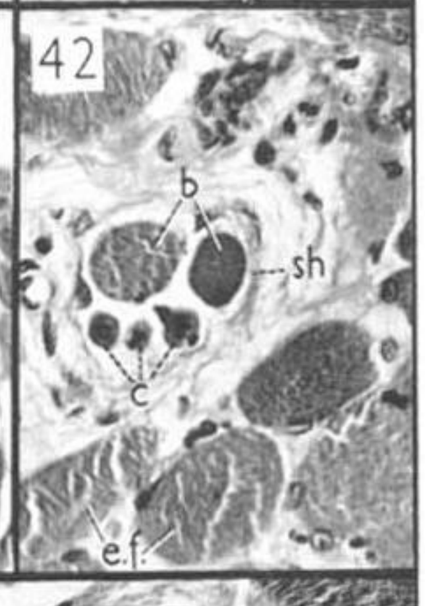


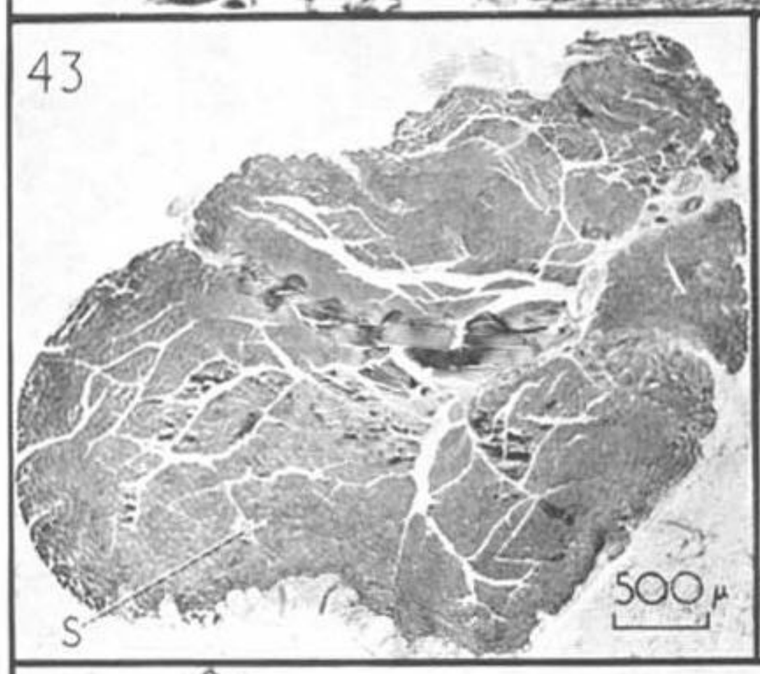


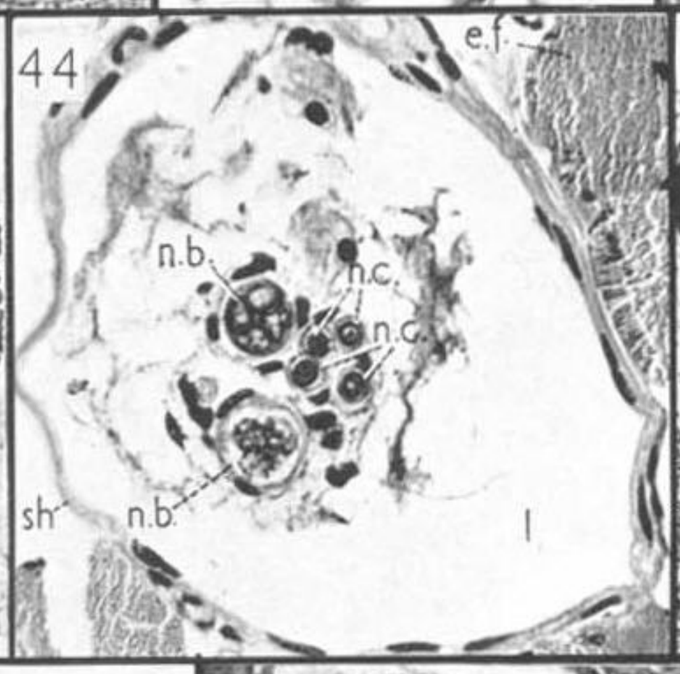


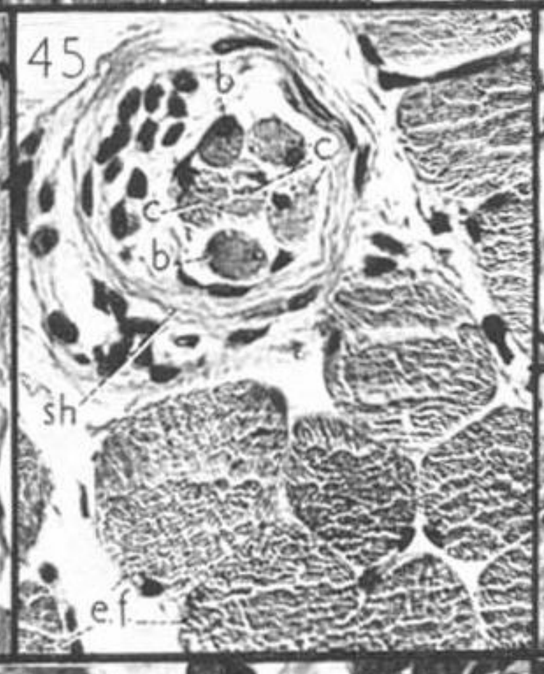


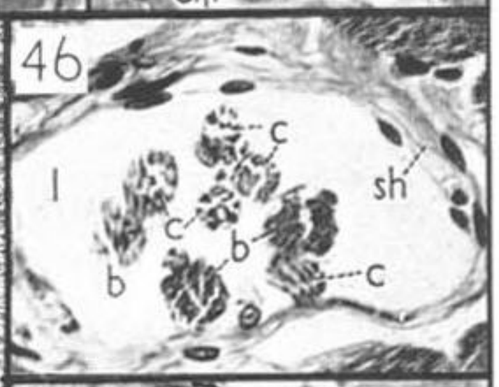


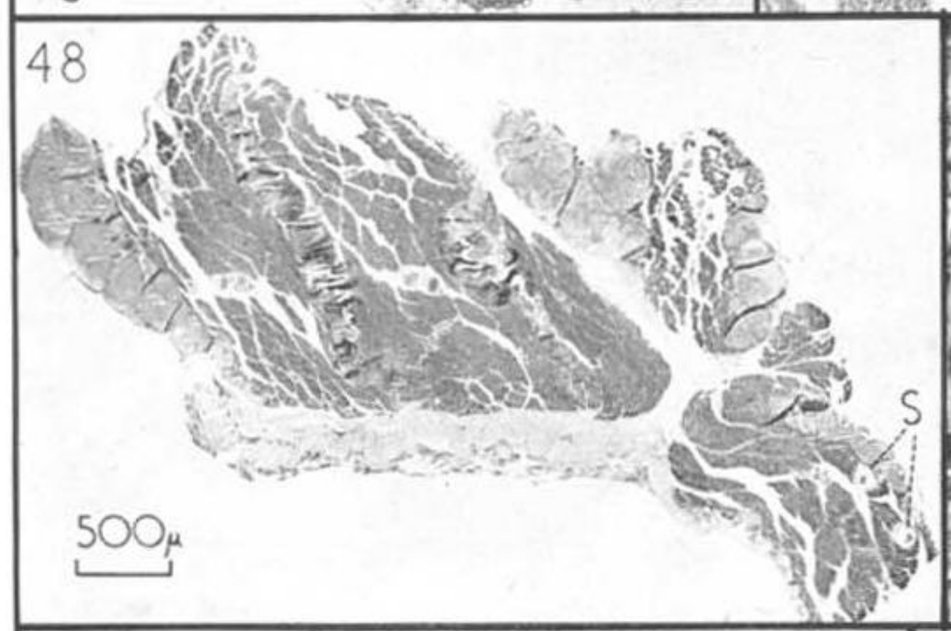


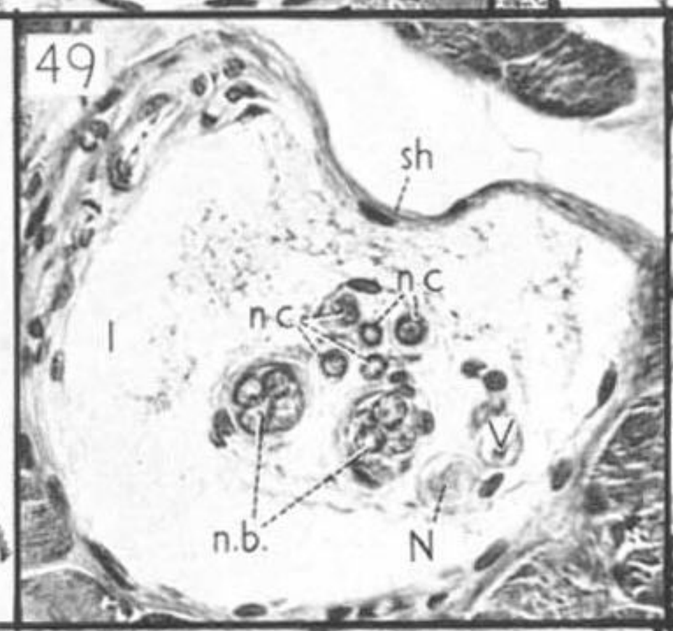


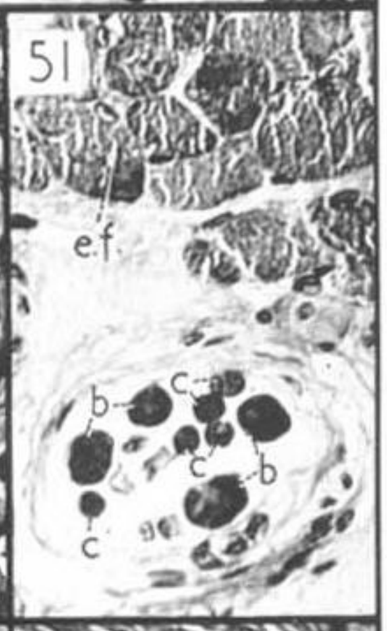


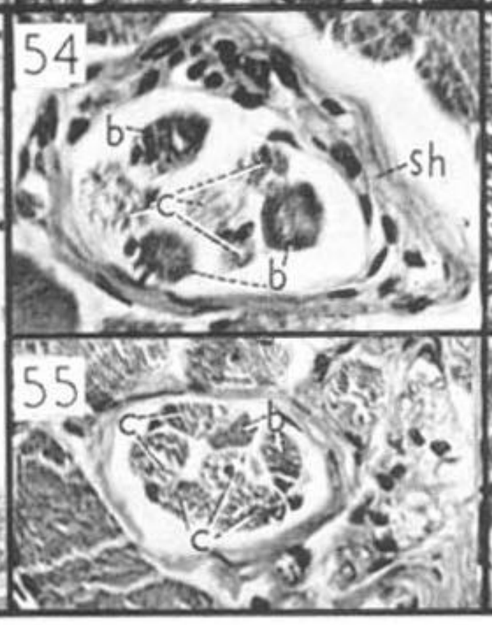


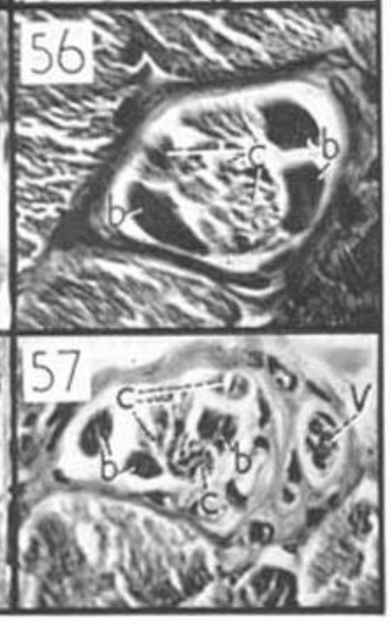












FIGURES 34 TO 57

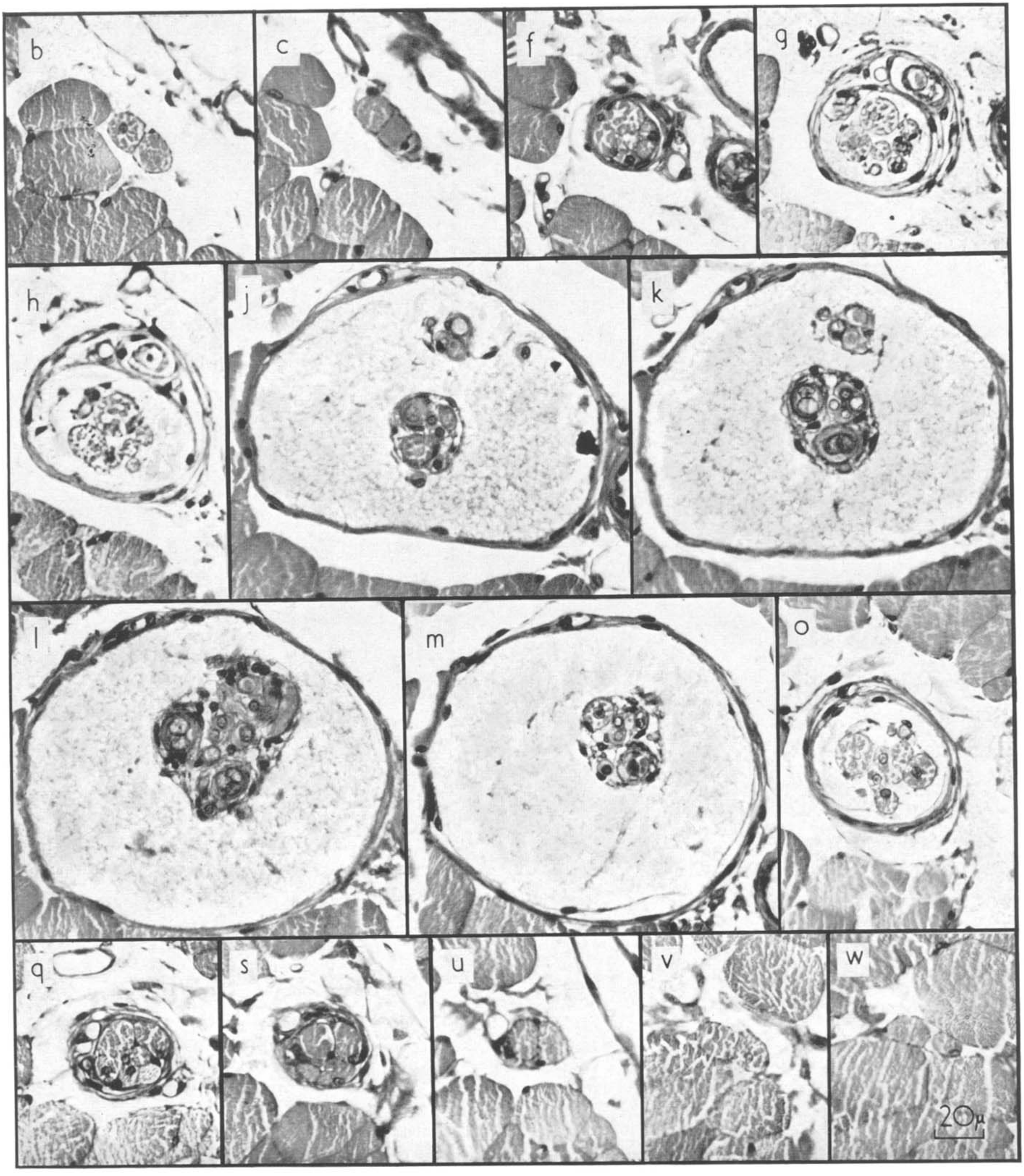
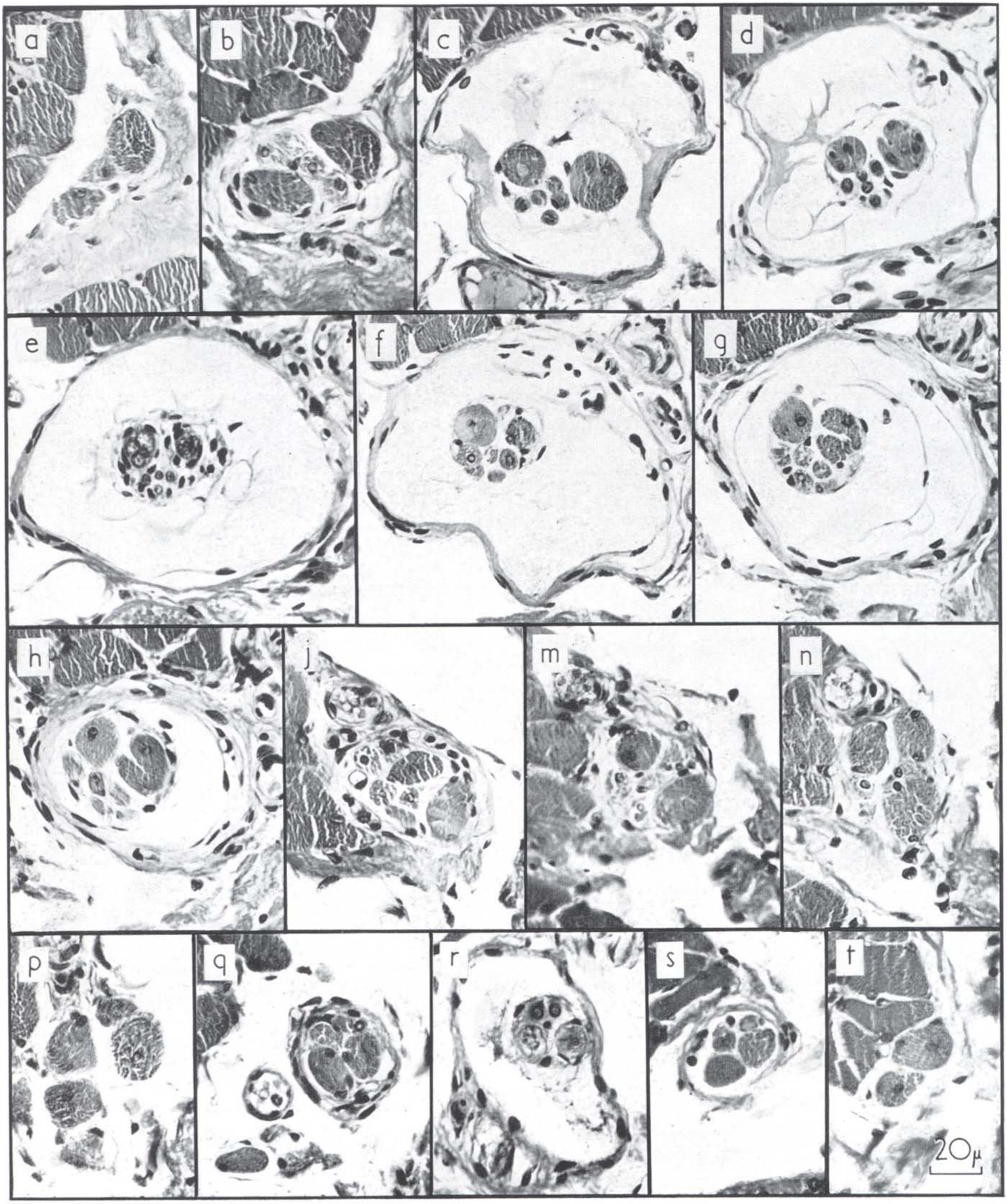


FIGURE 58. Key opposite.



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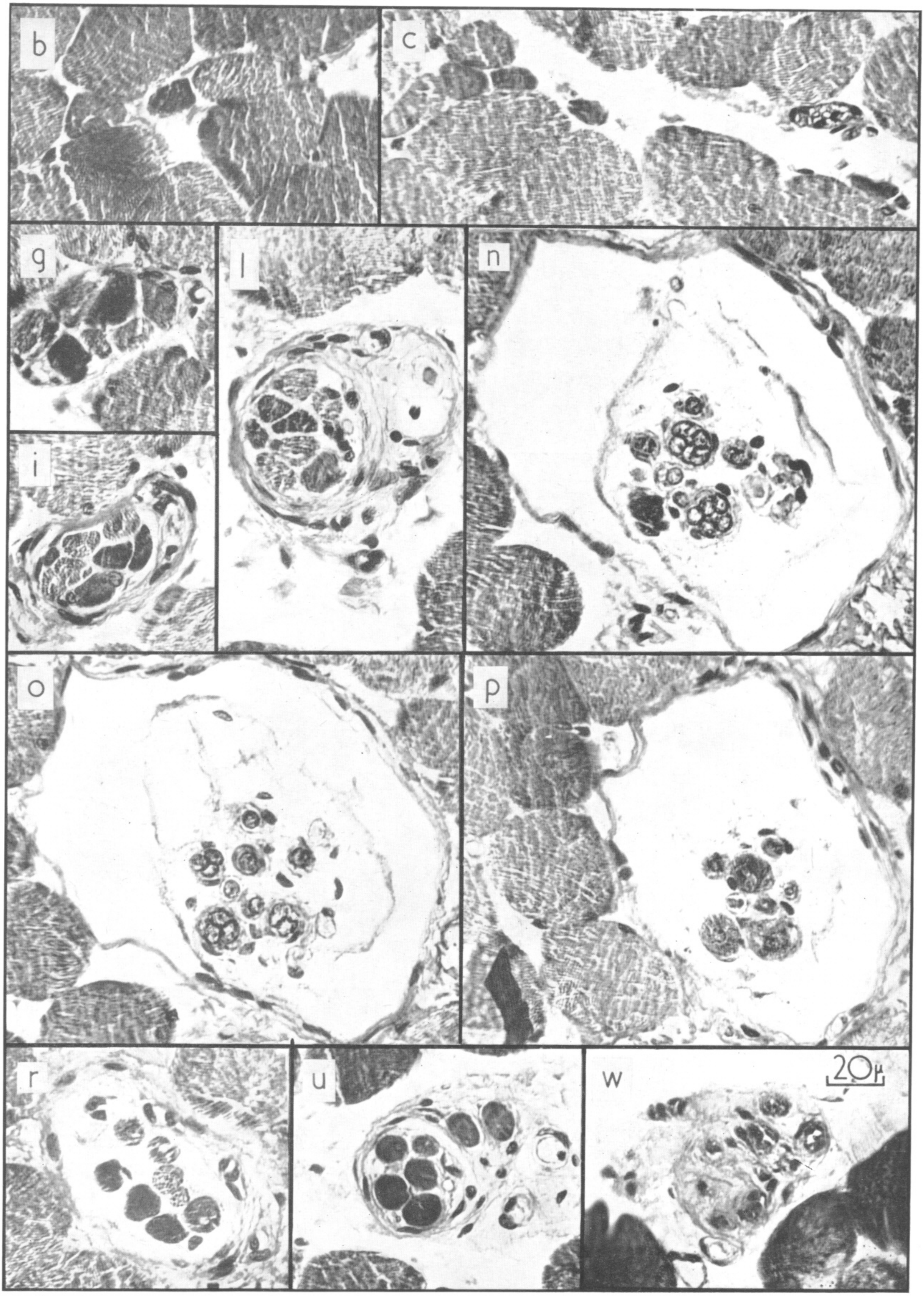

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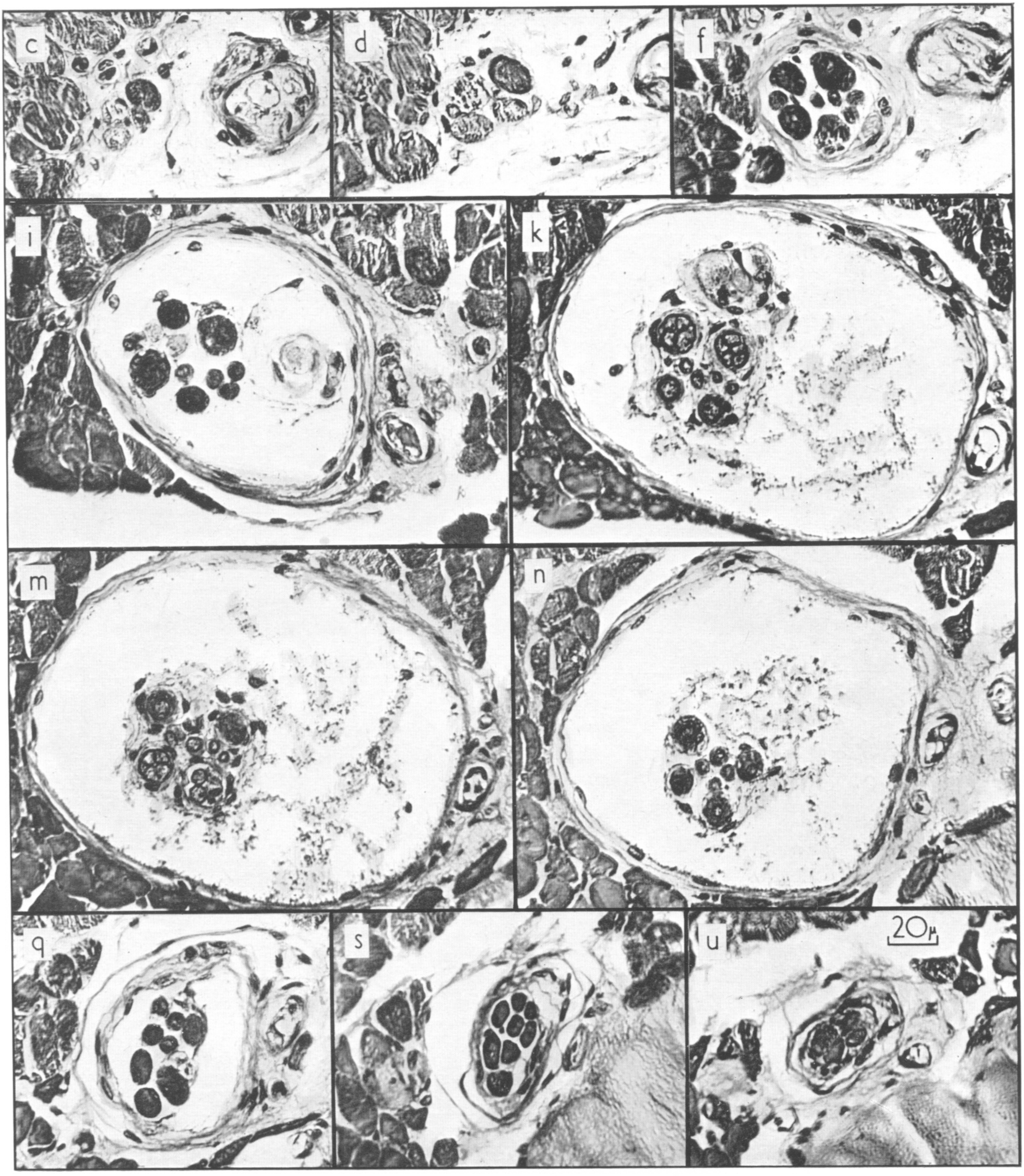

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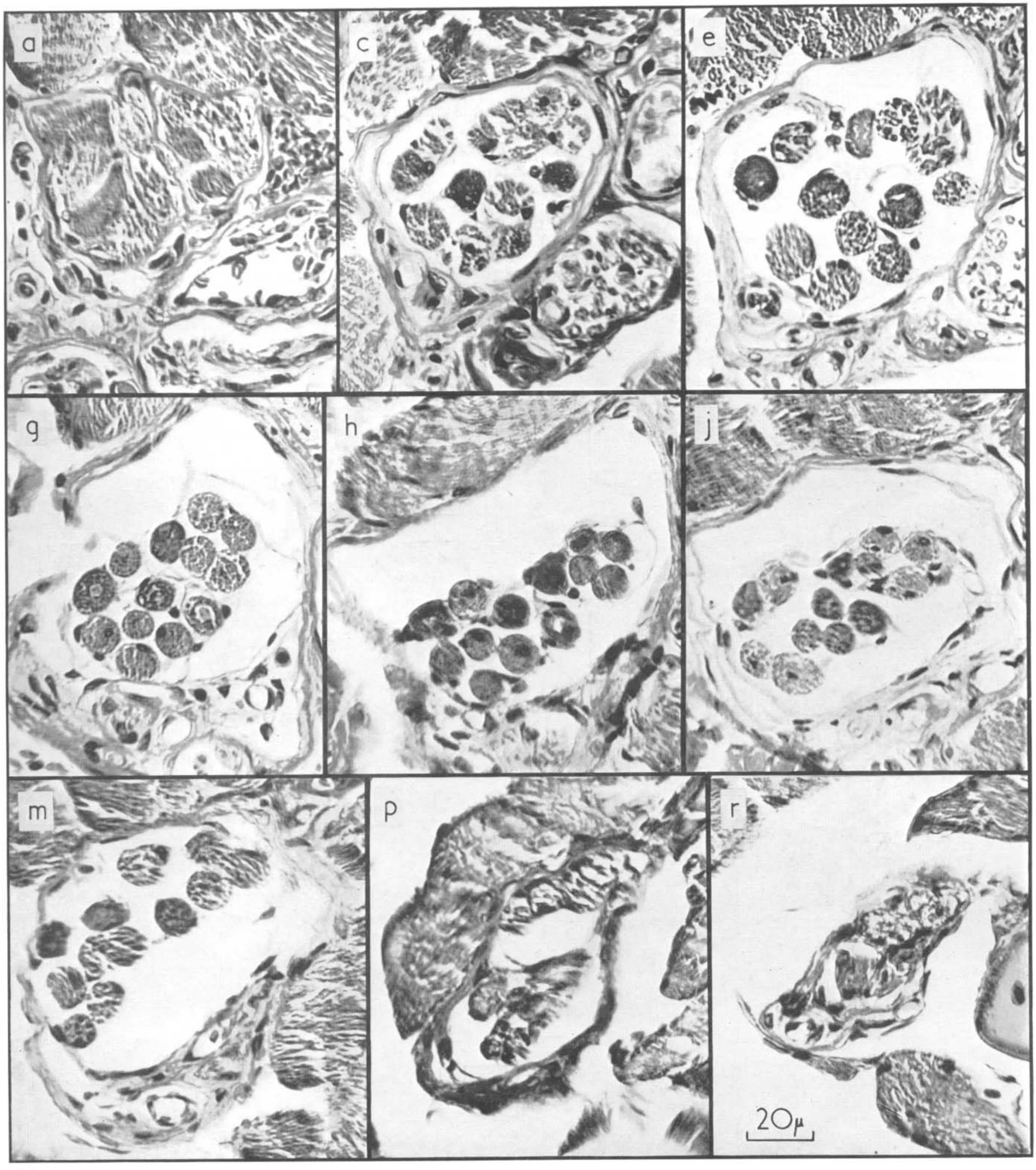

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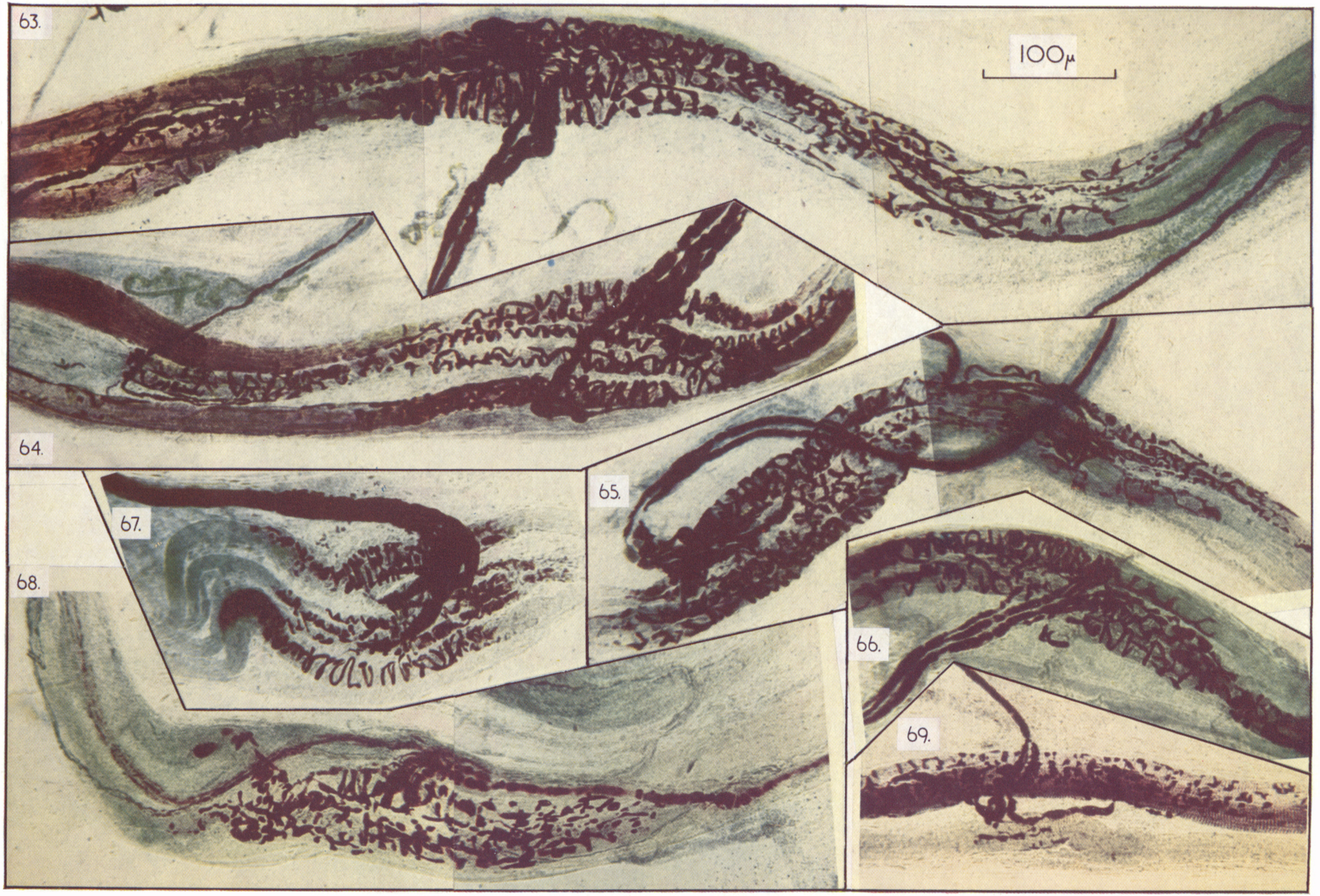
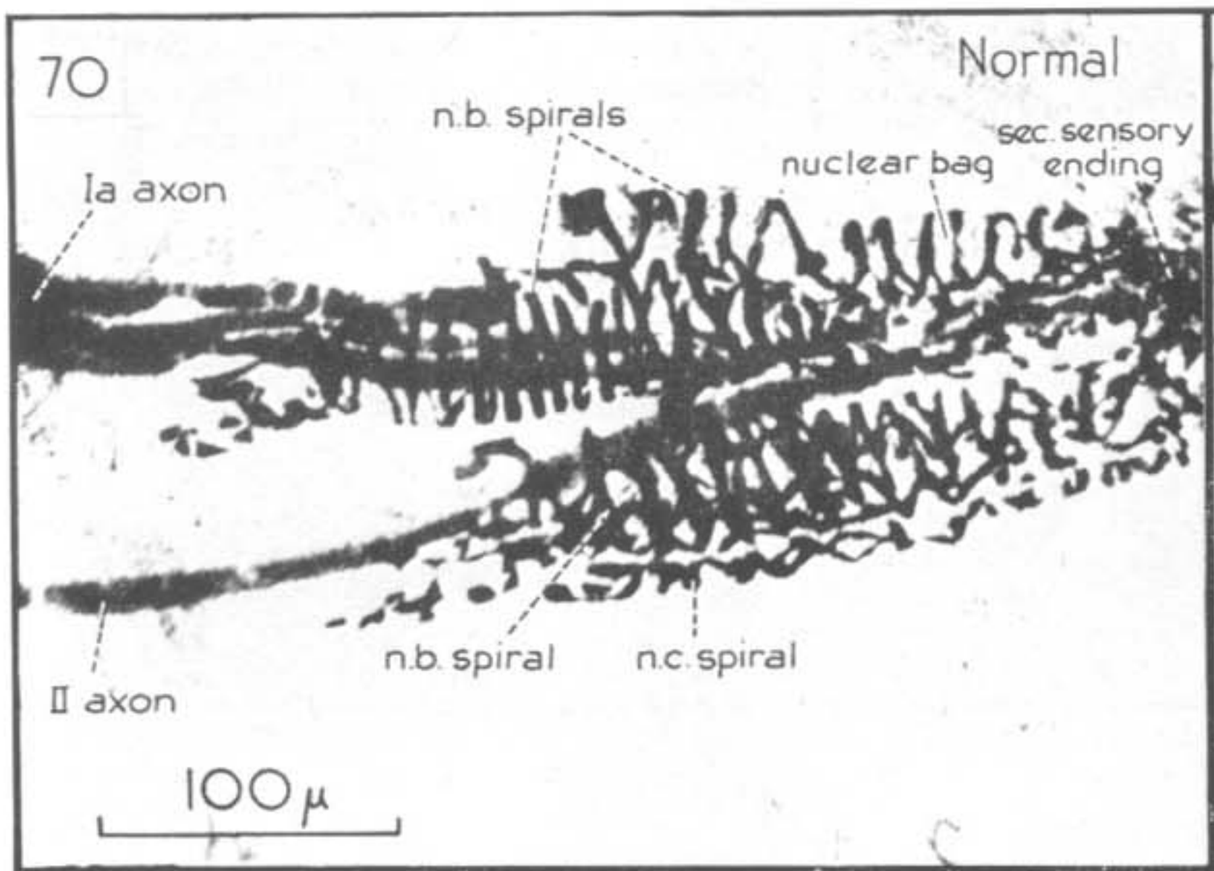
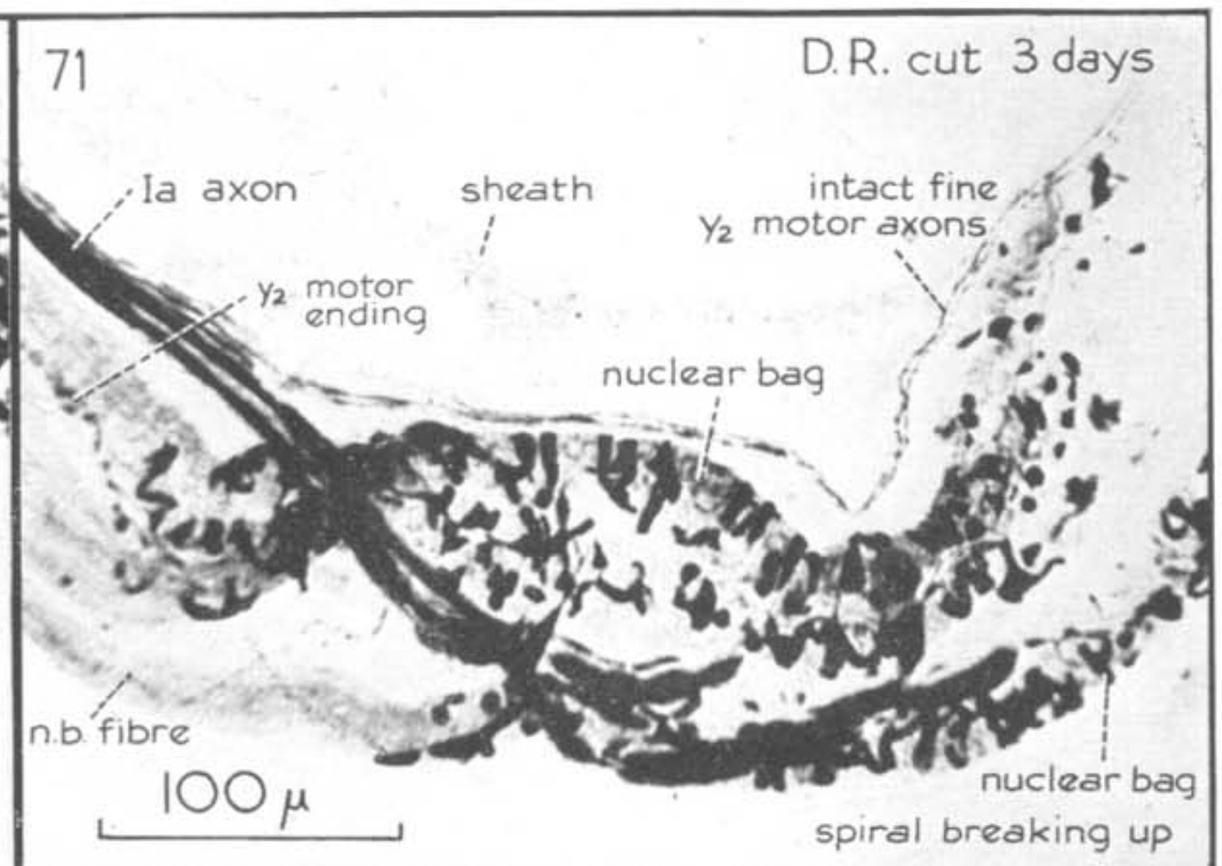
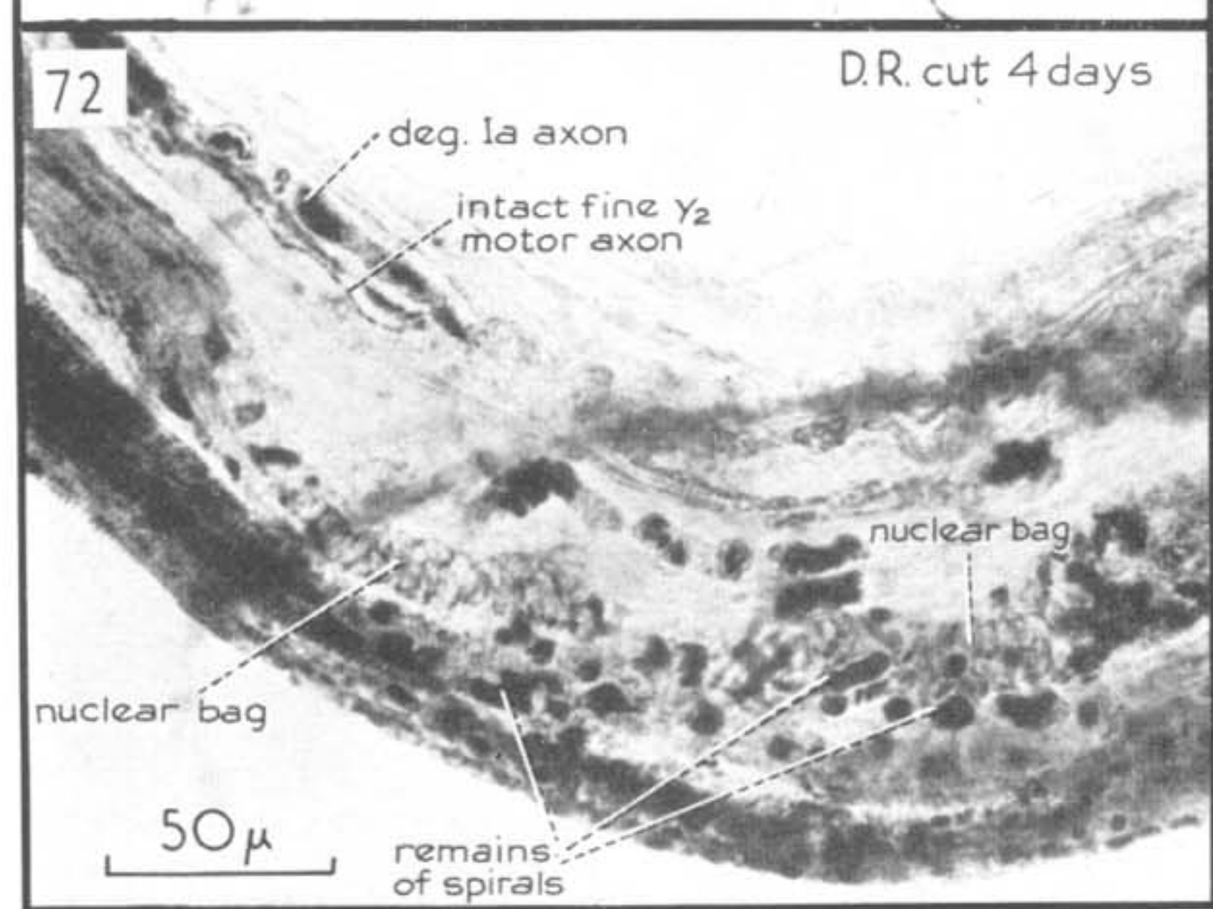
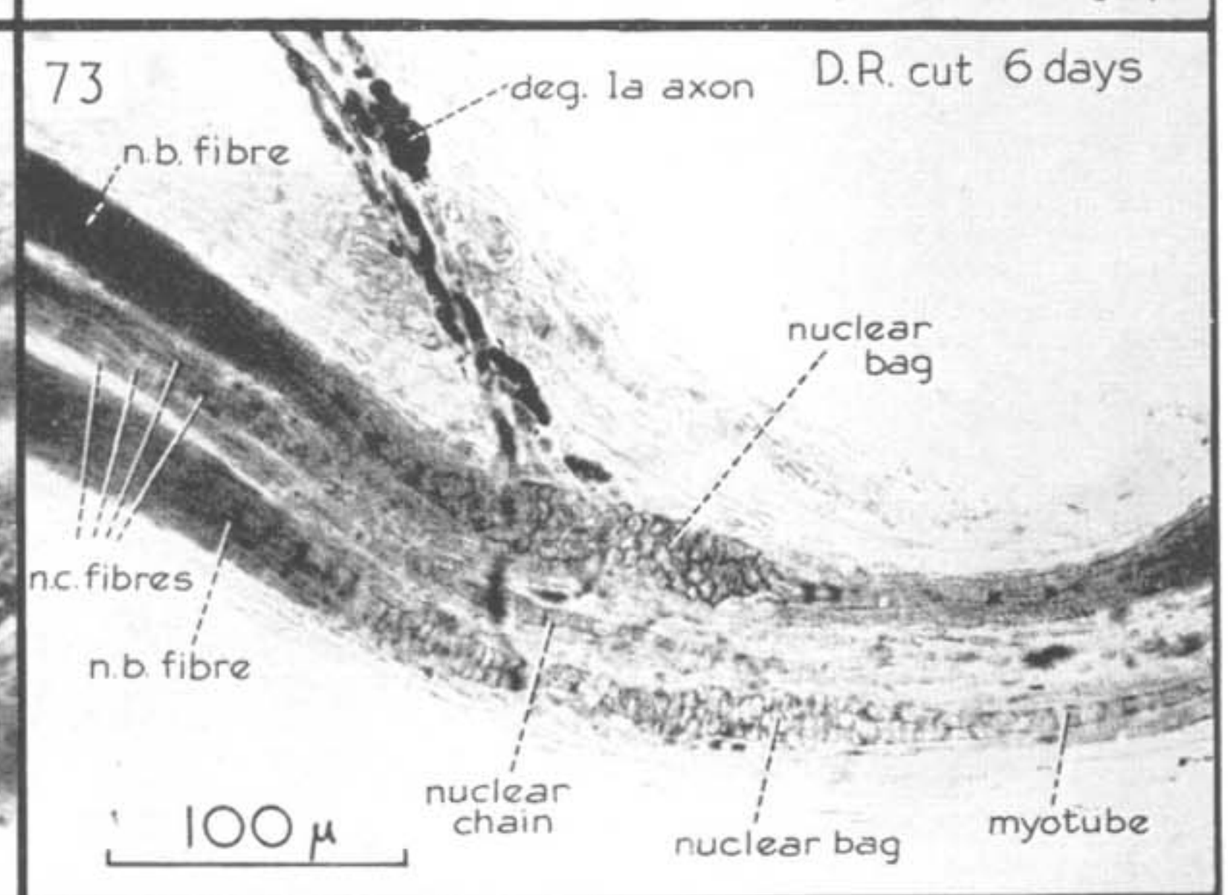


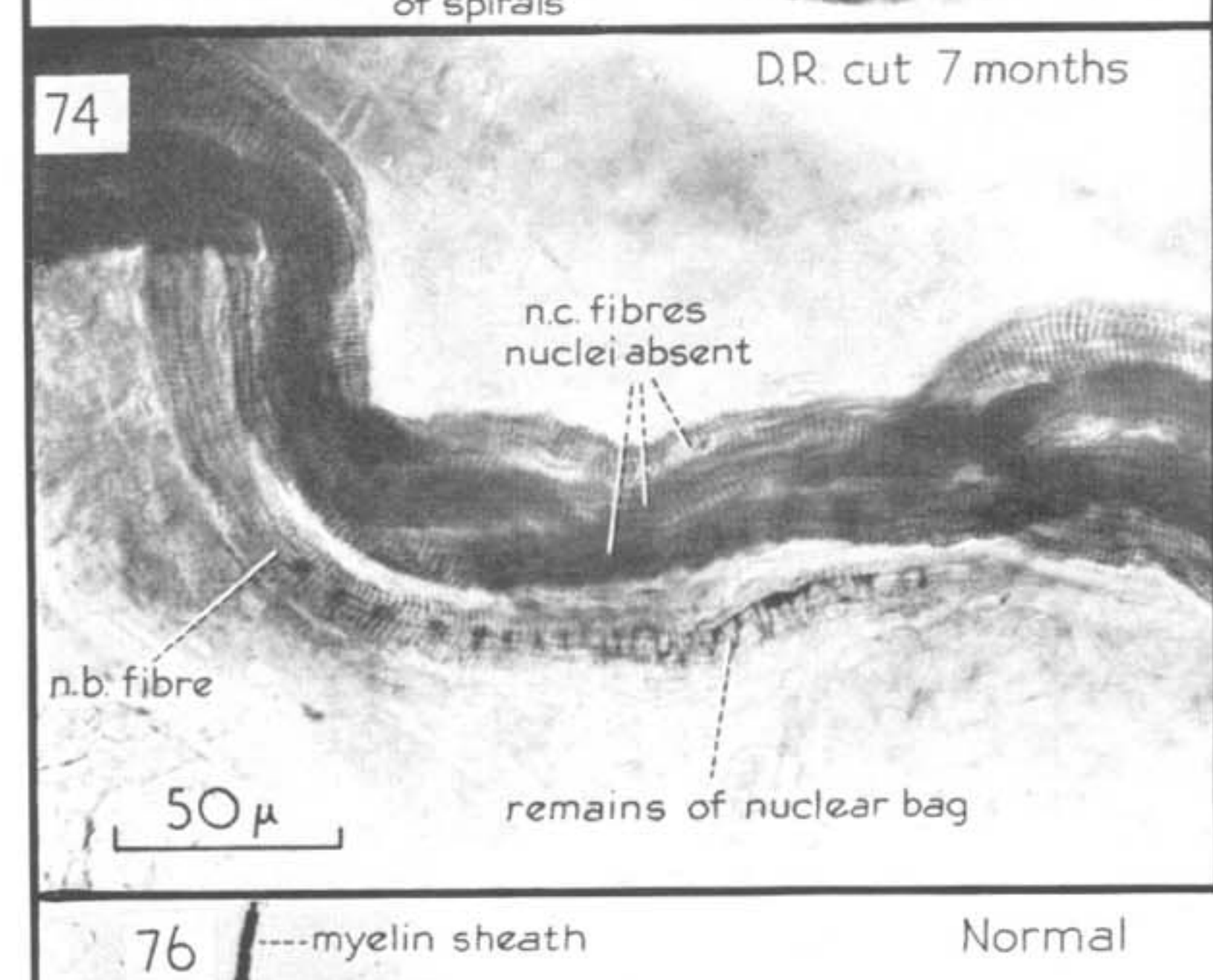
FIGURES 63 TO 69

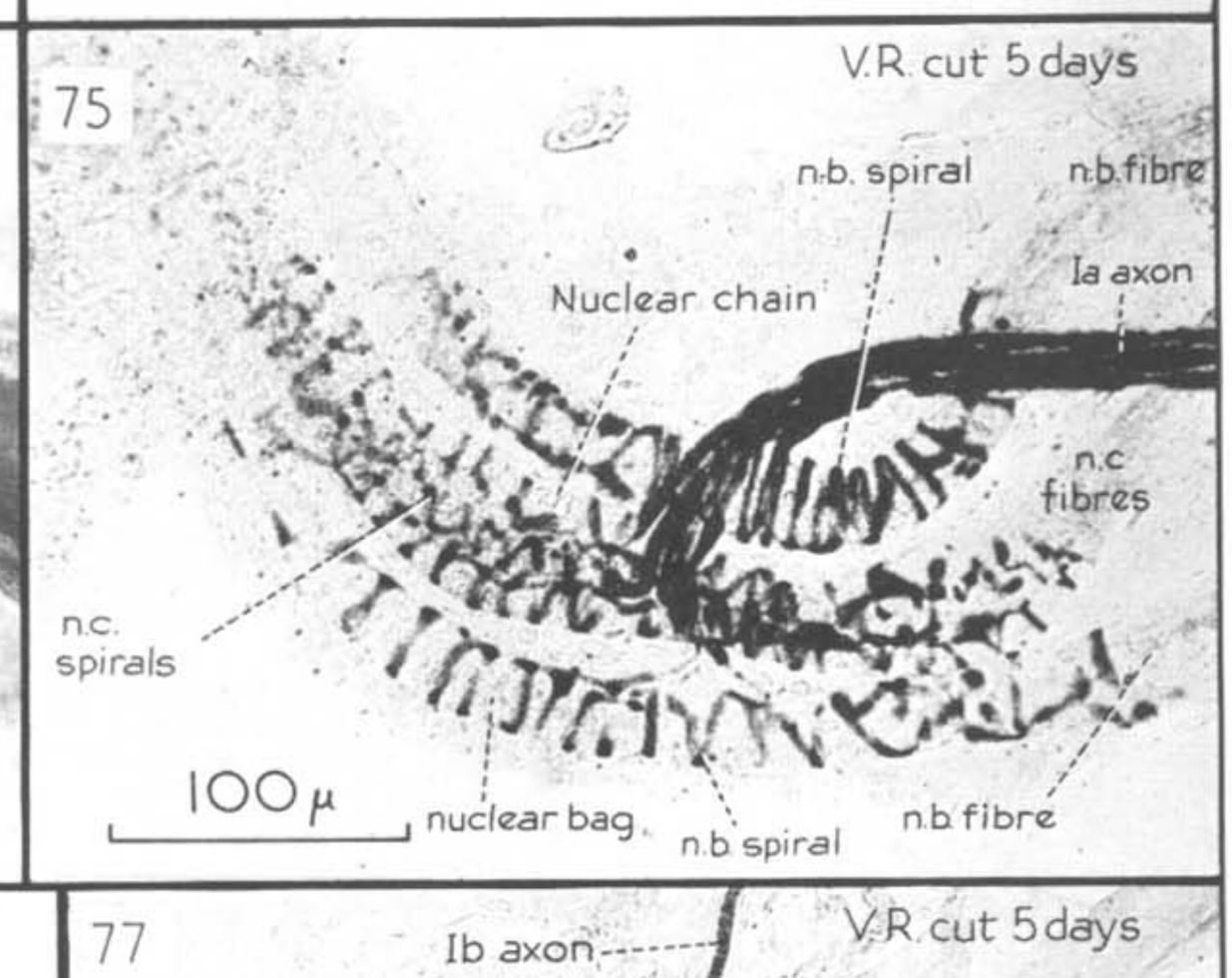


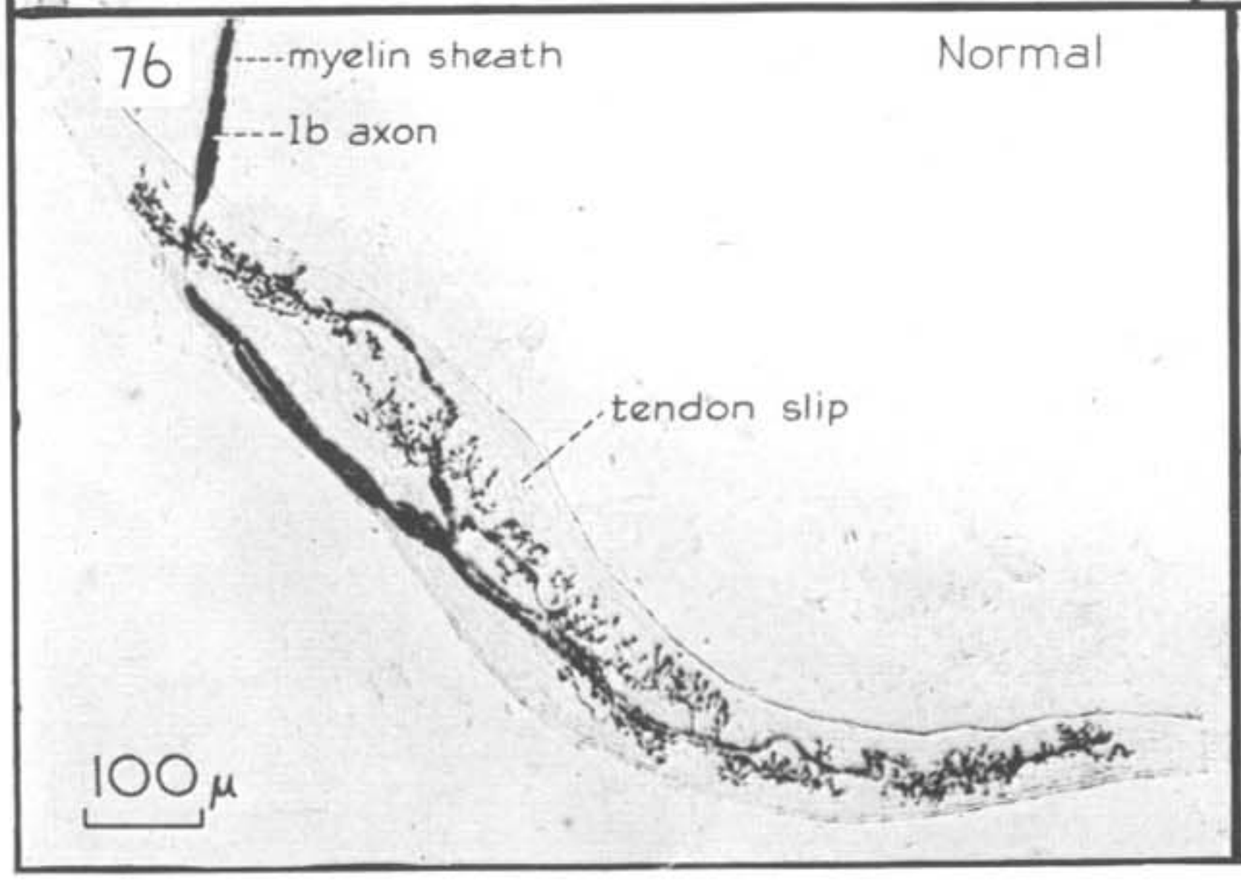


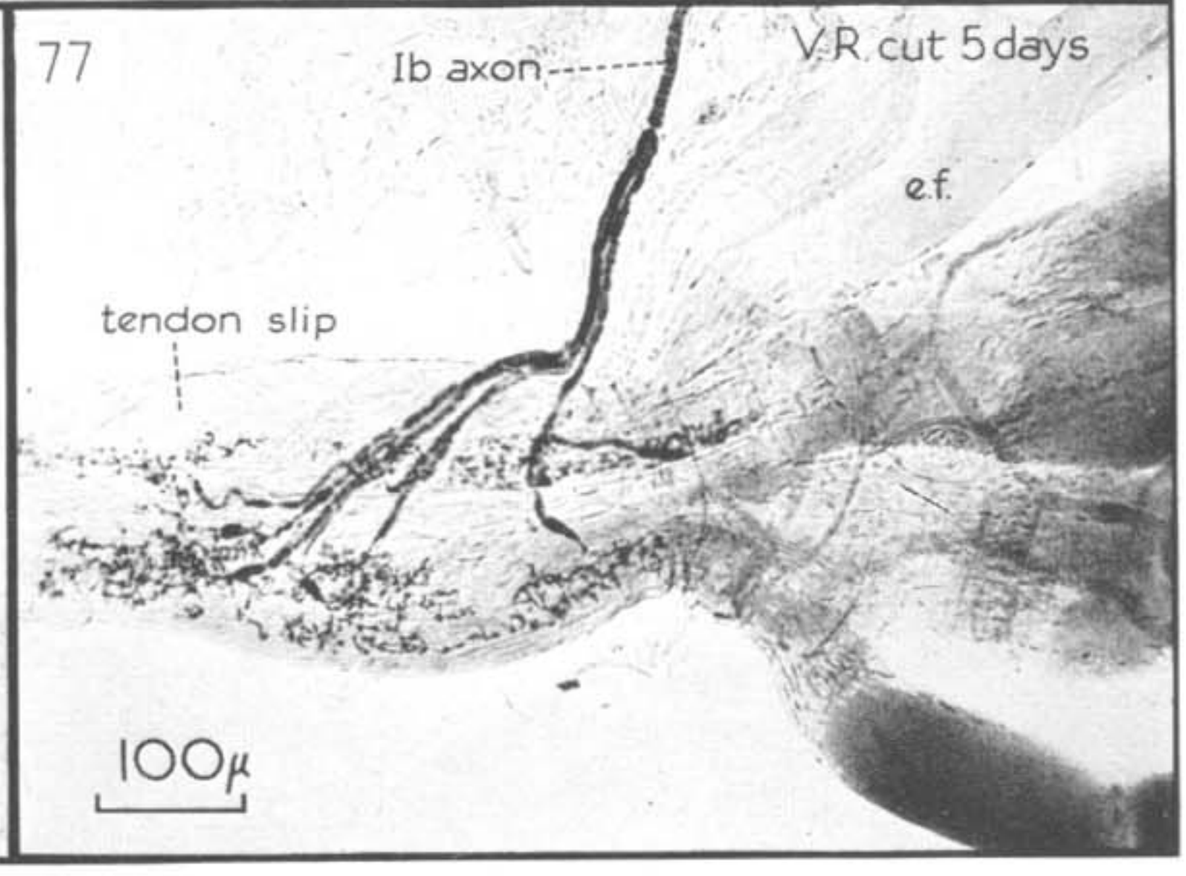




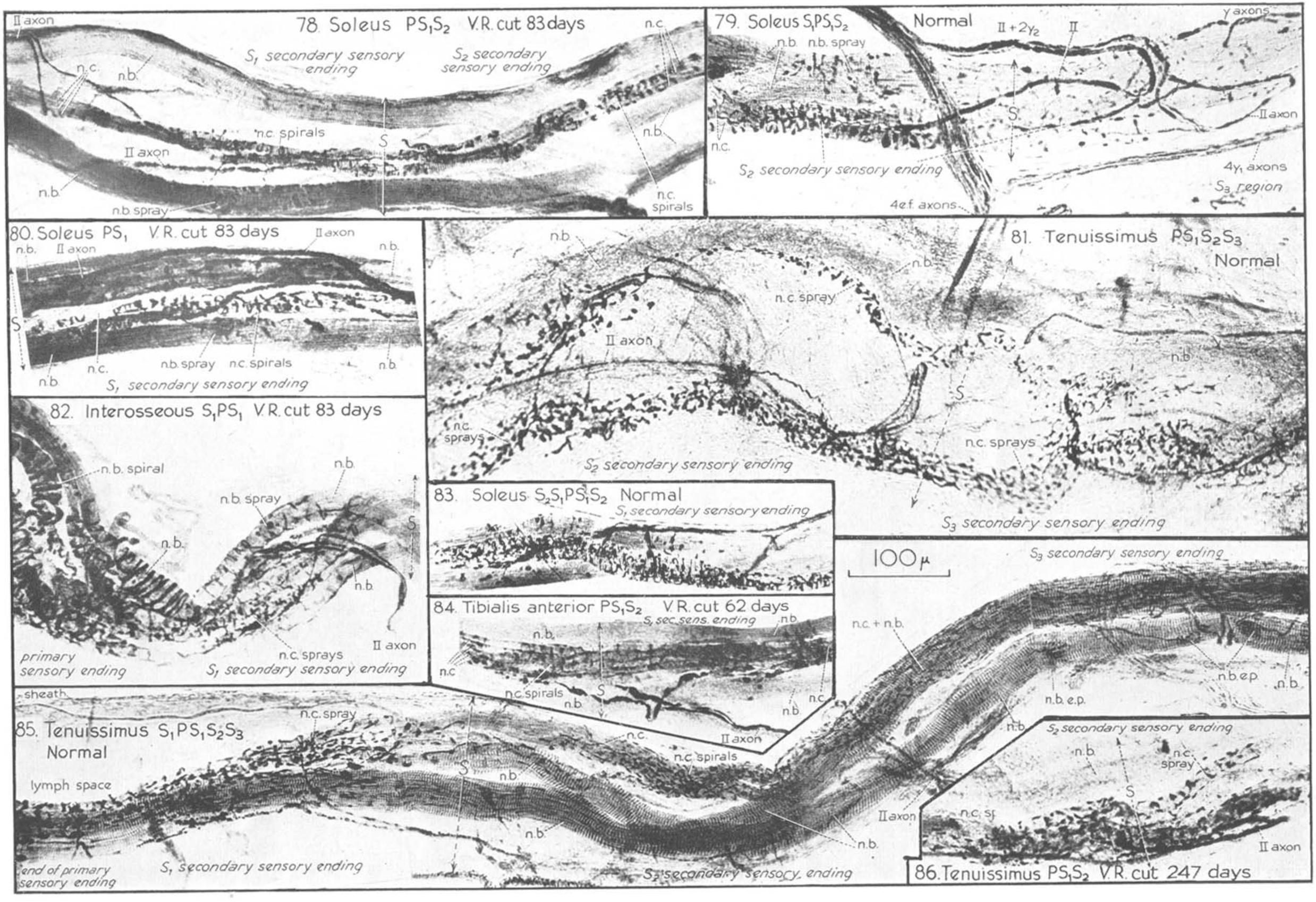




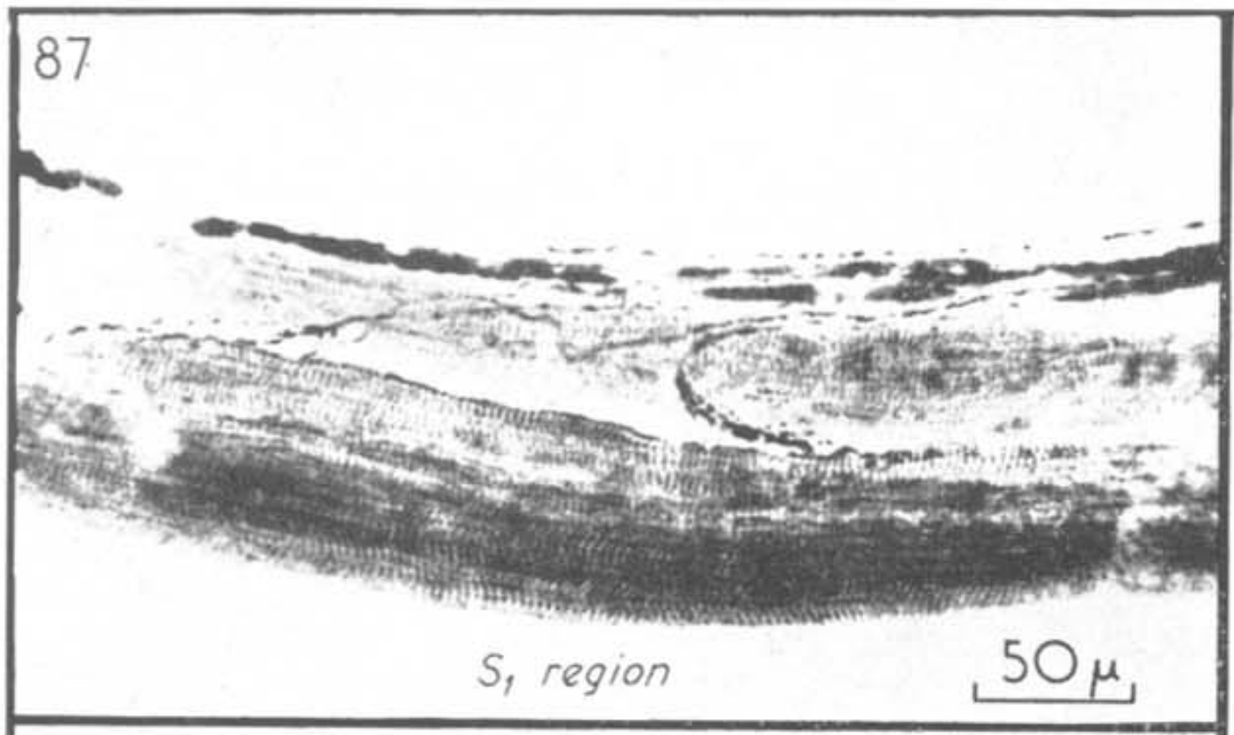


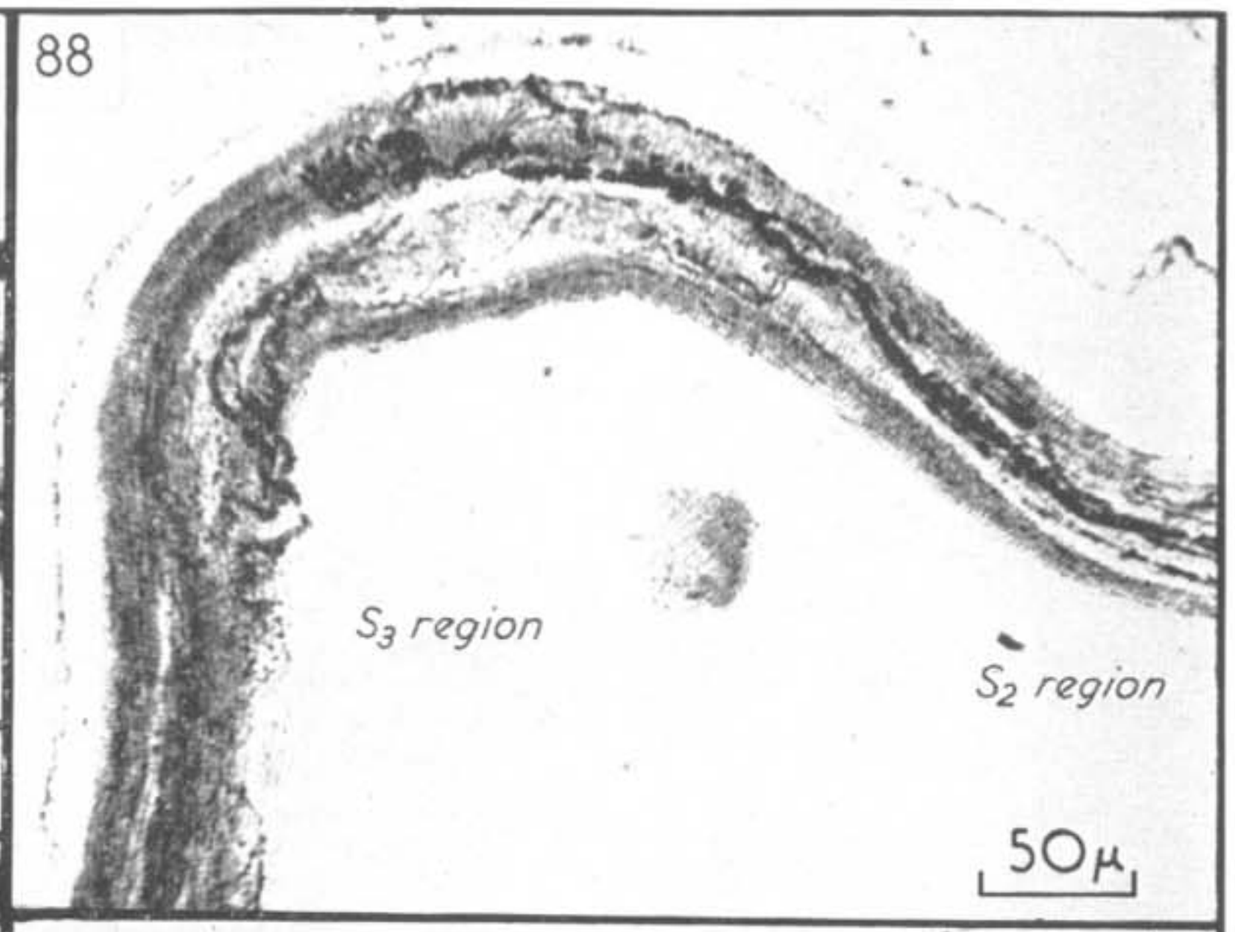


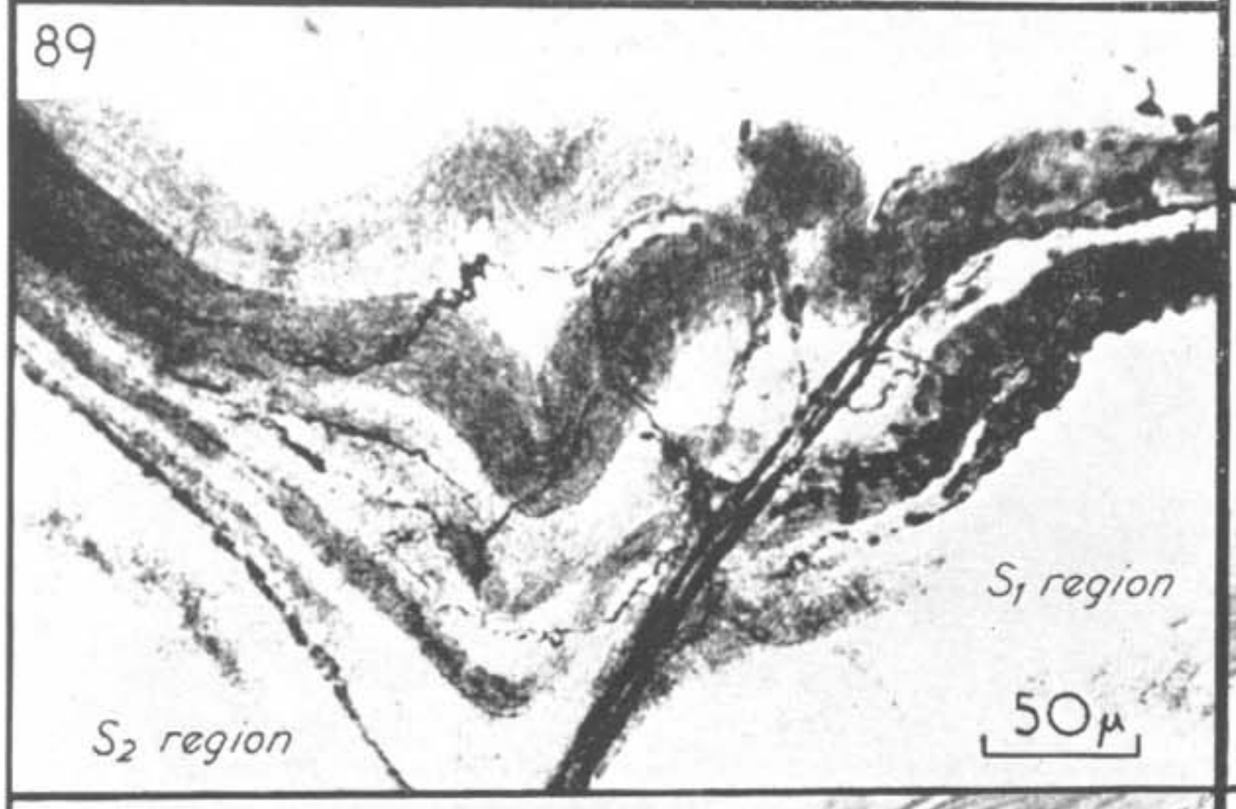
FIGURES 70 TO 77

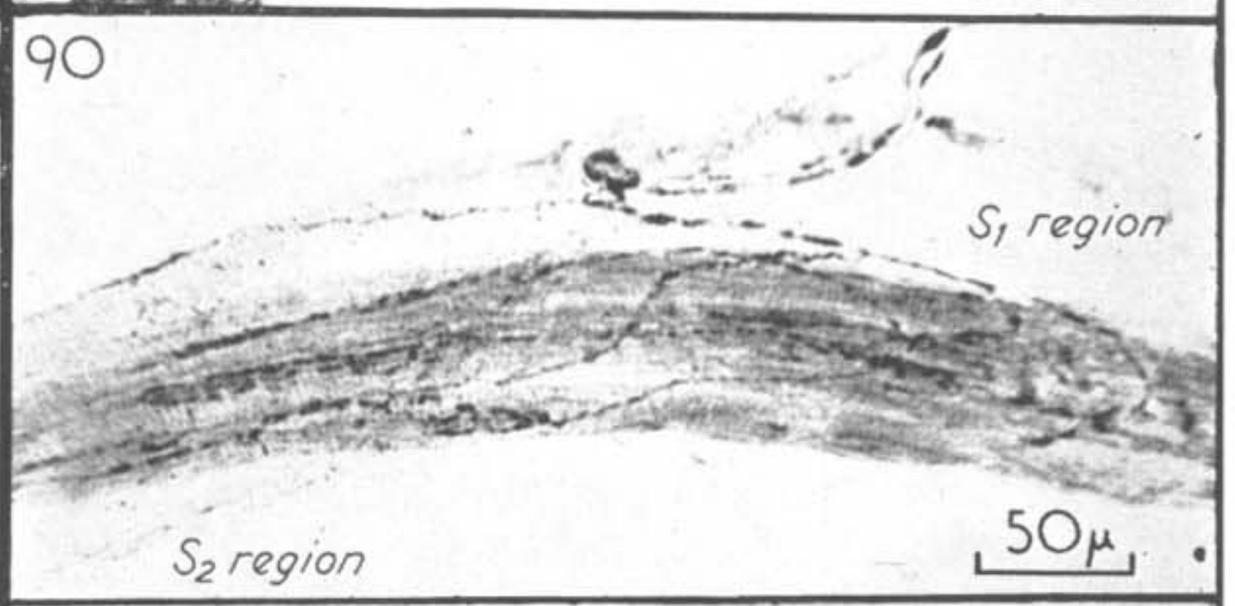


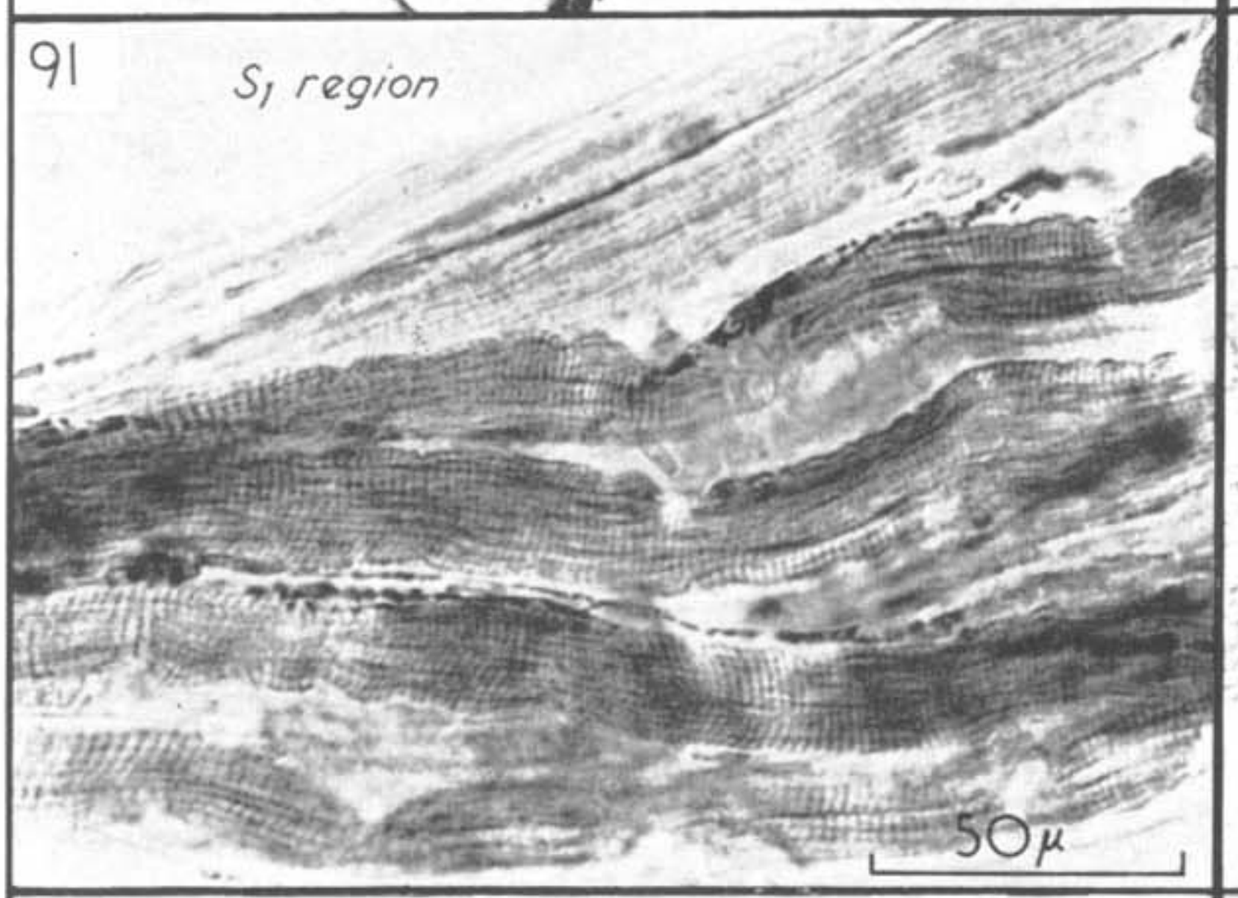
FIGURES 78 TO 86

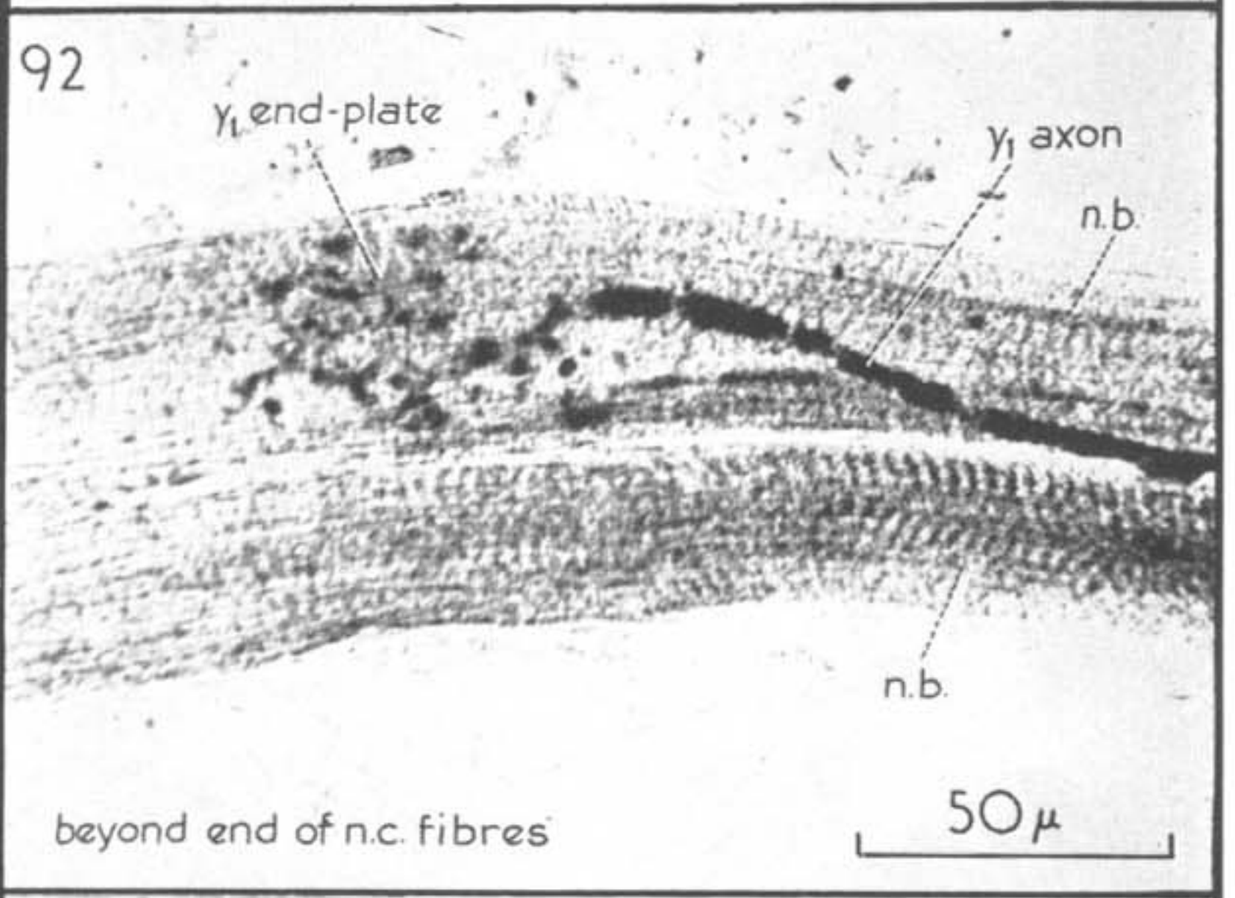


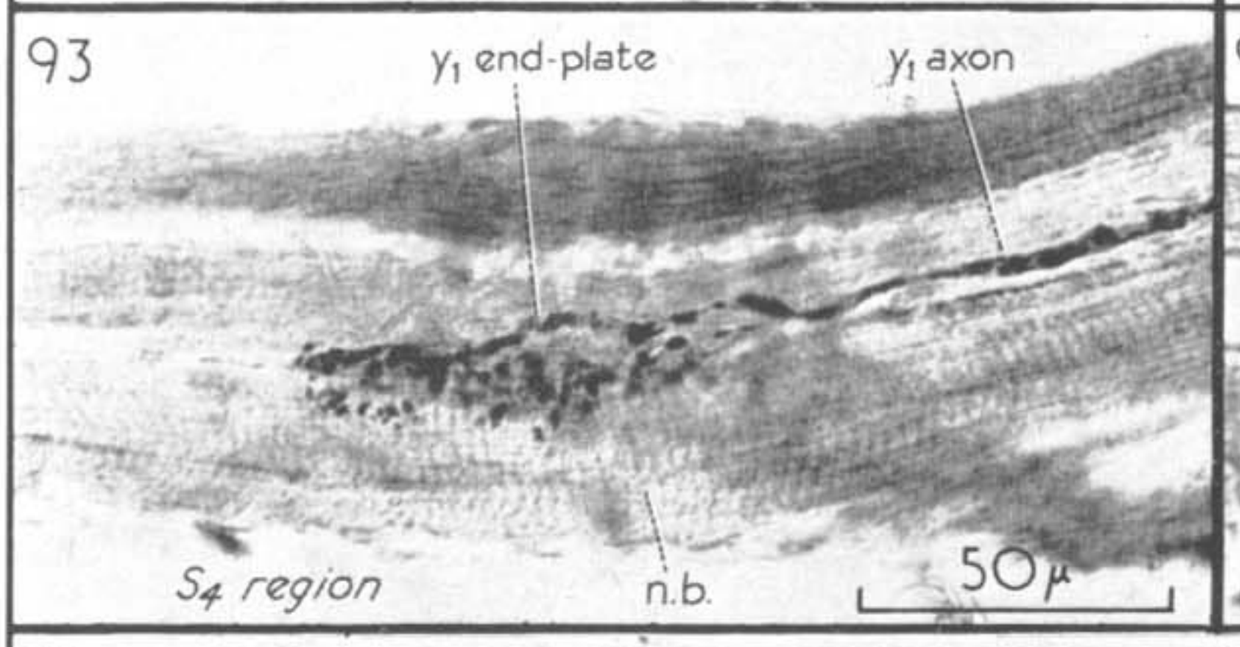


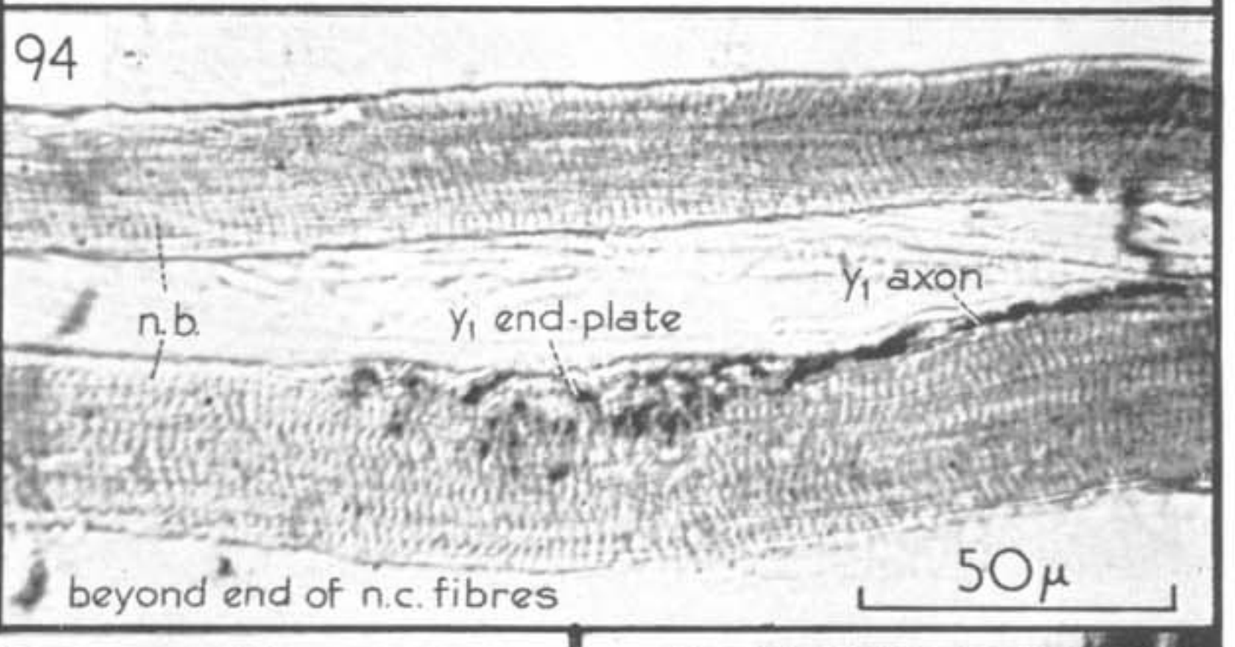


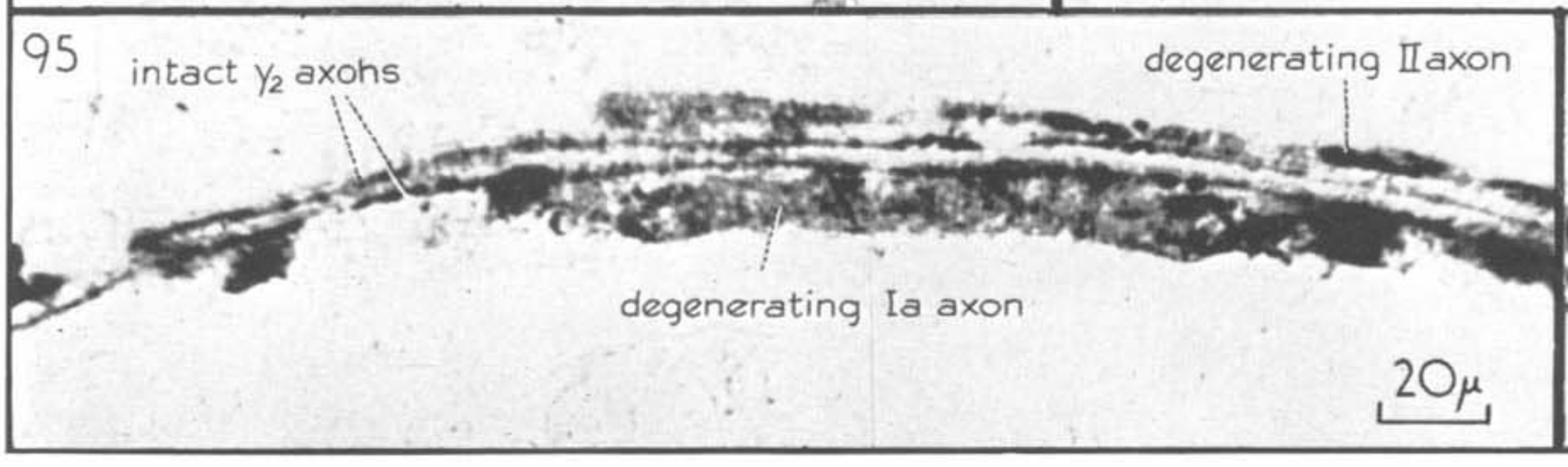


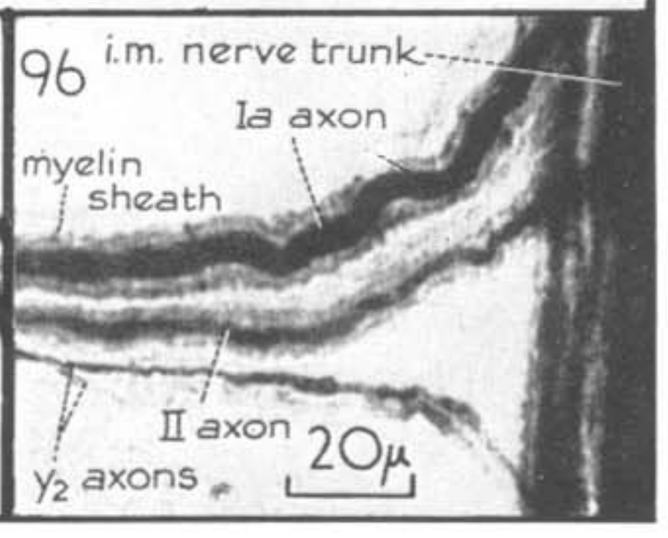




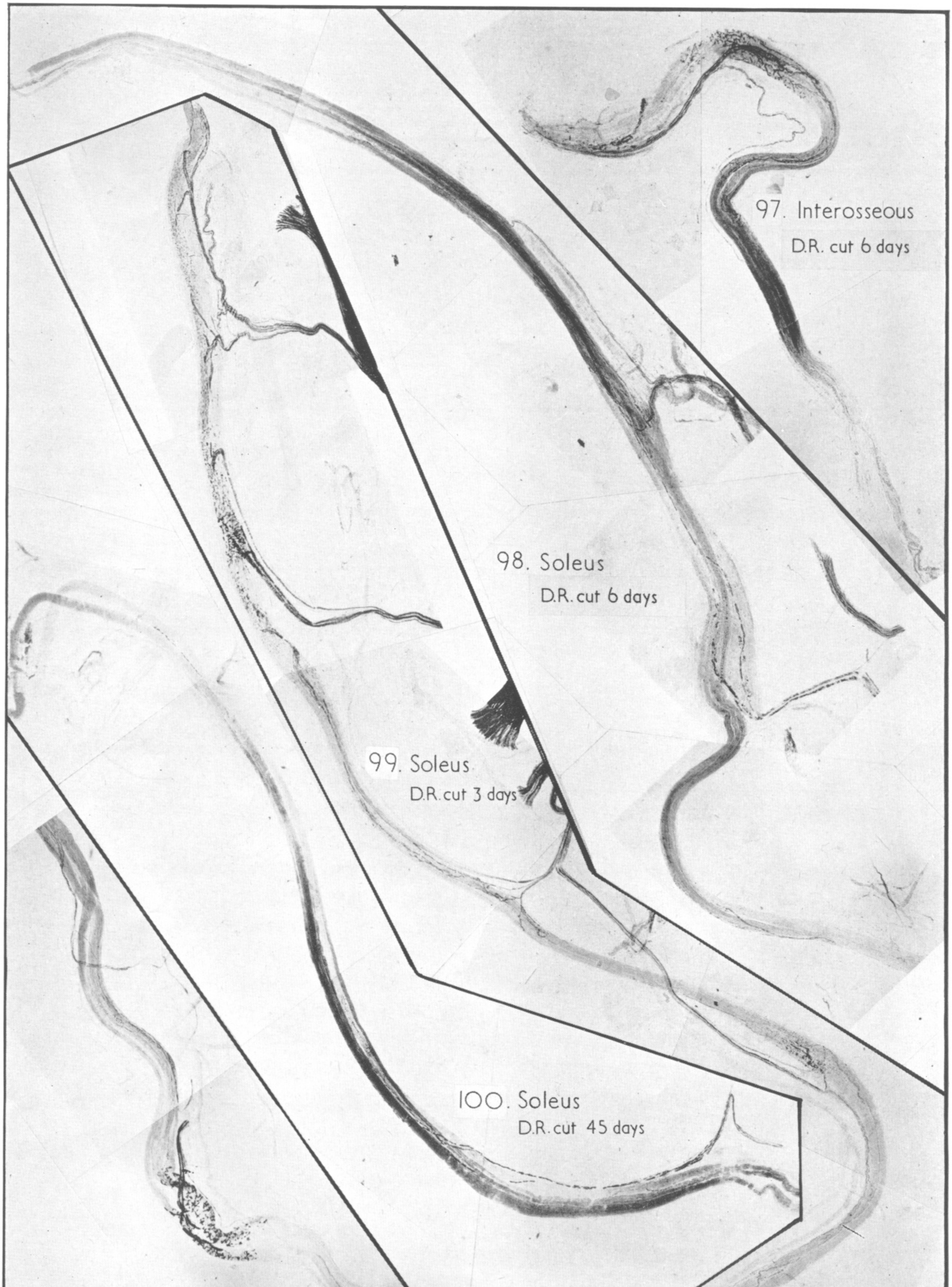




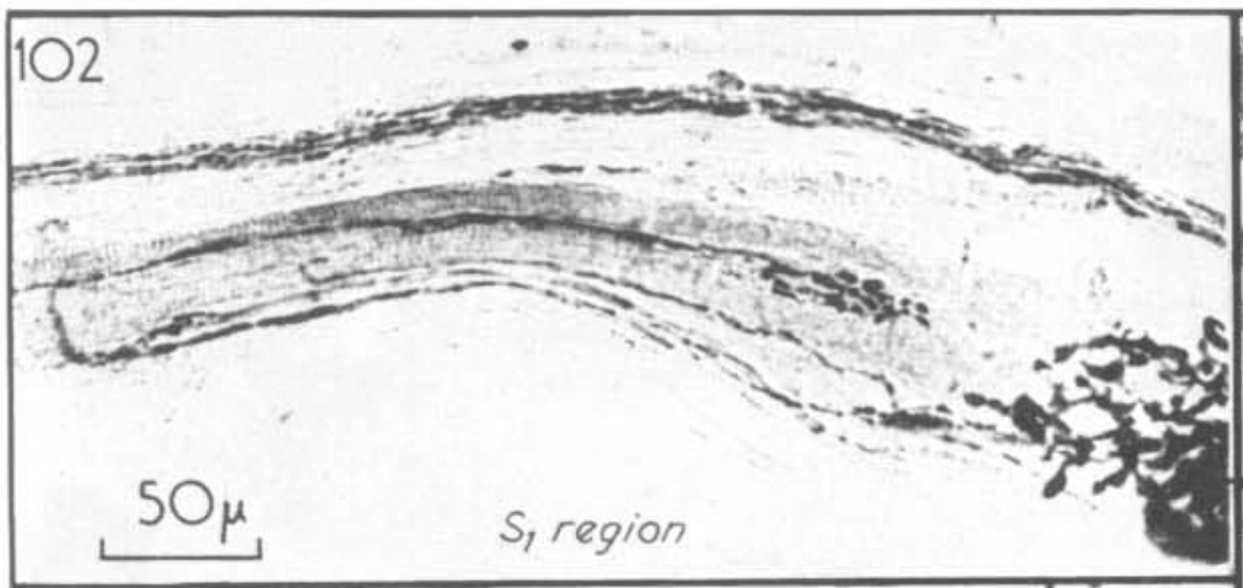


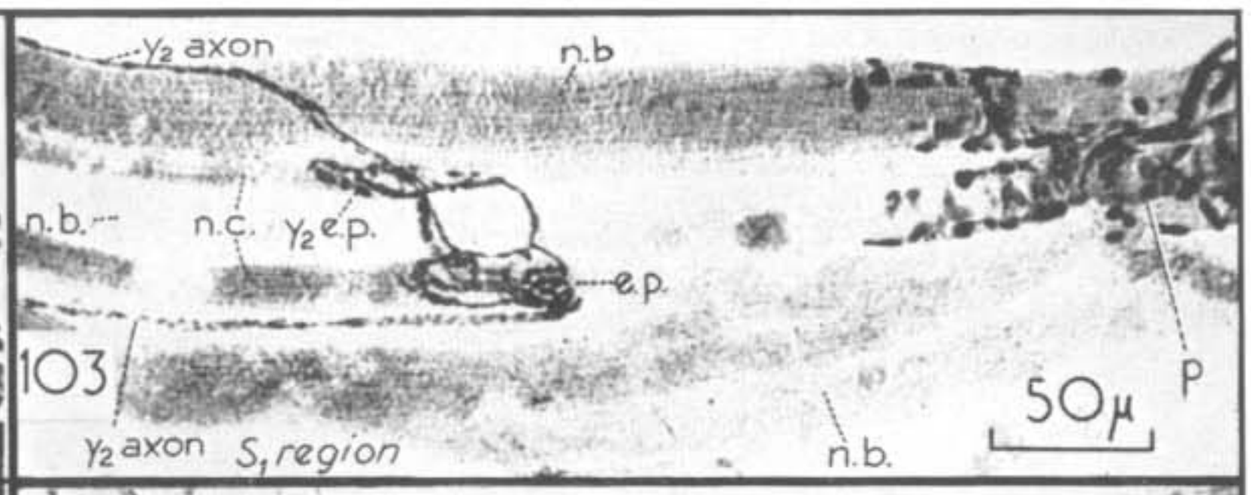


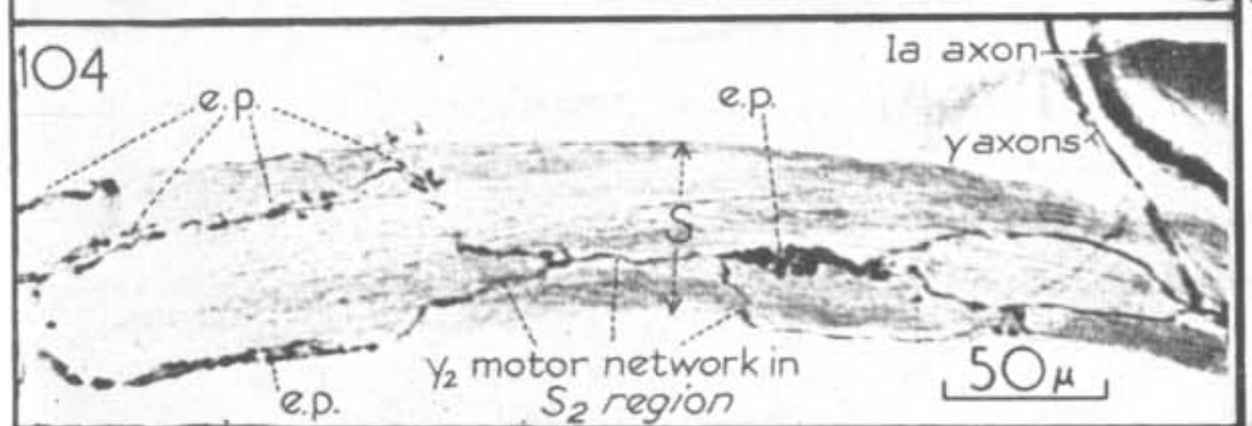
FIGURES 87 TO 96

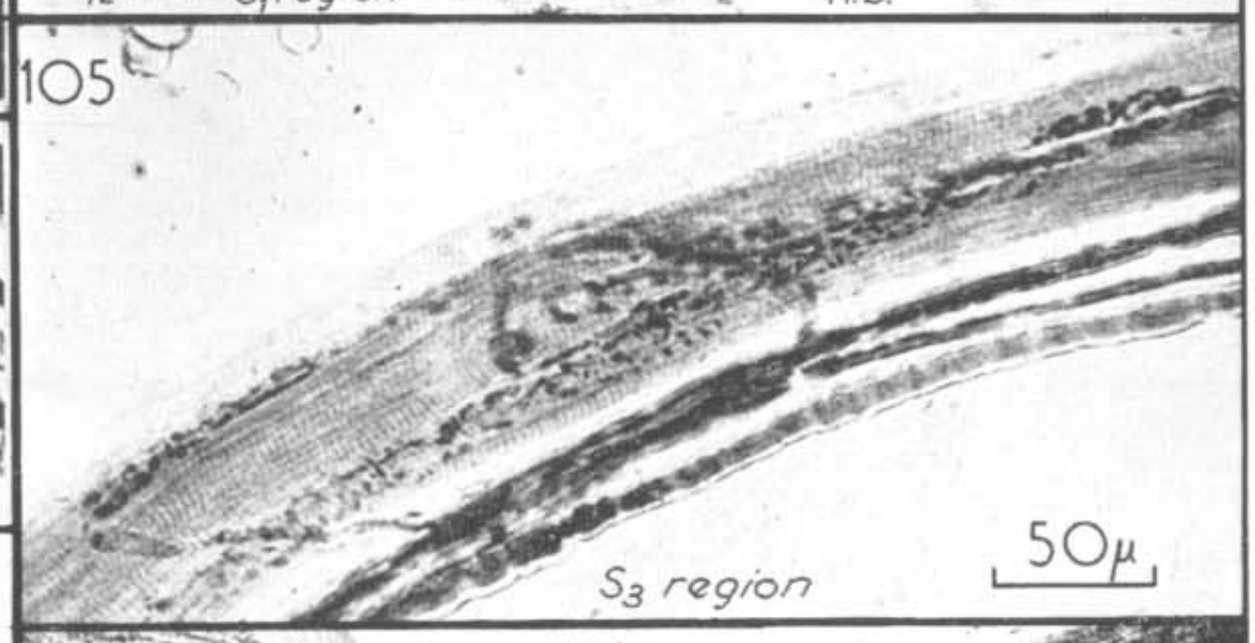


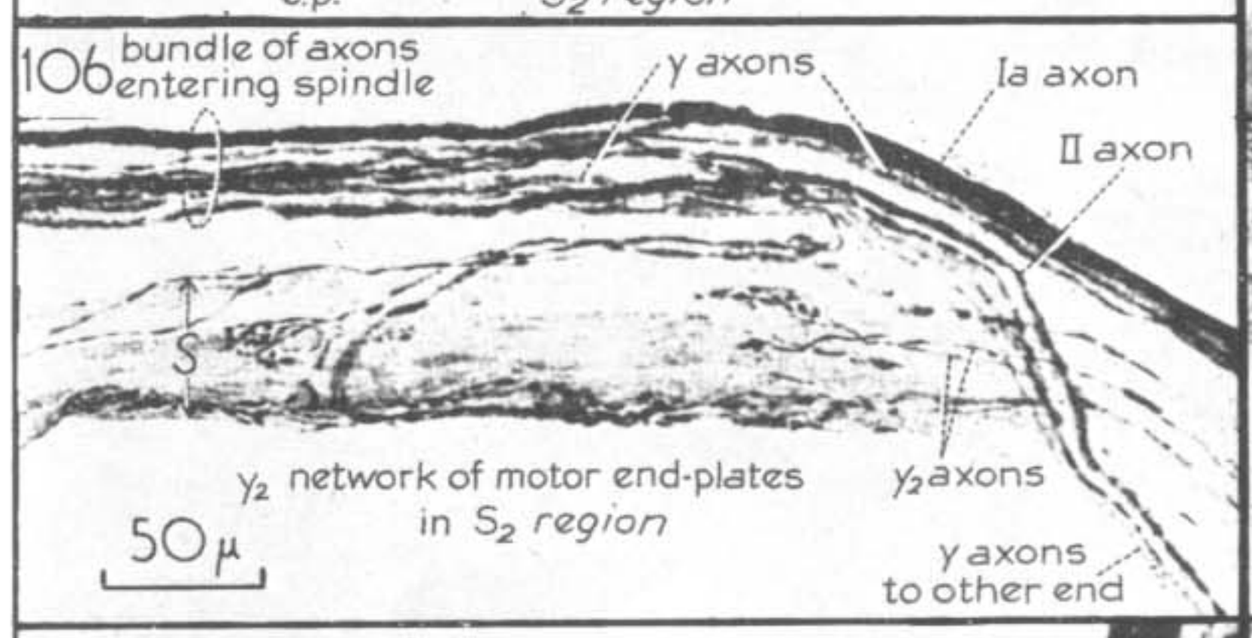
FIGURES 97 TO 101

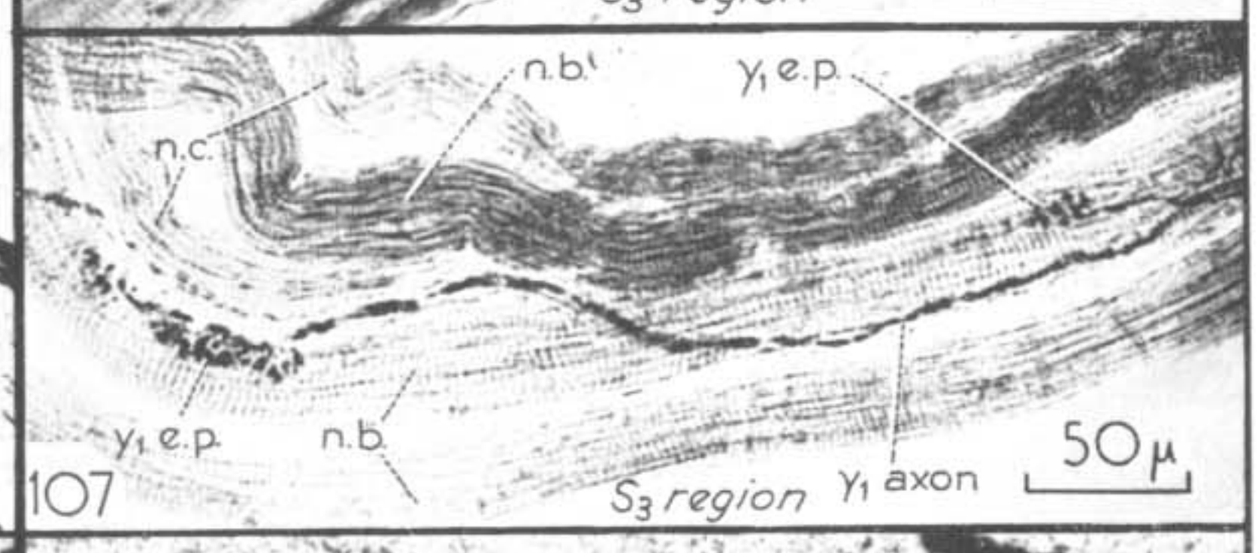


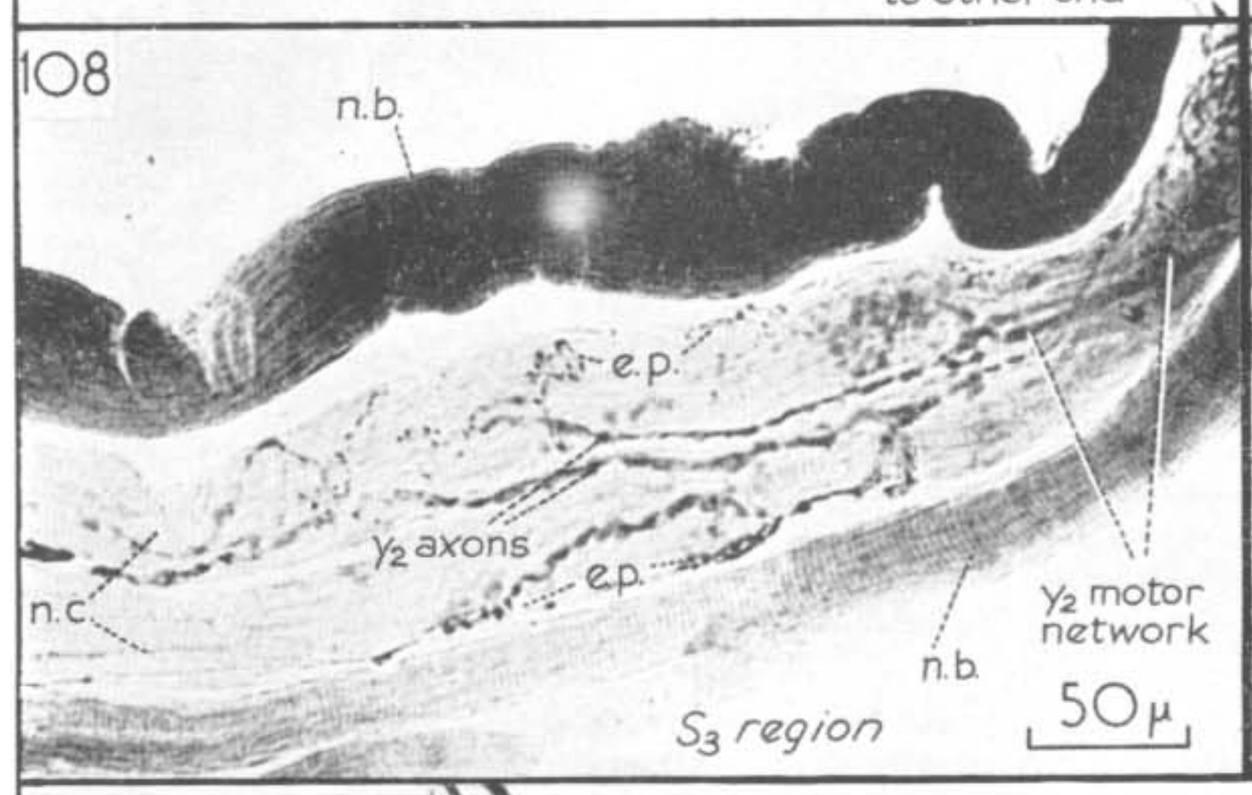


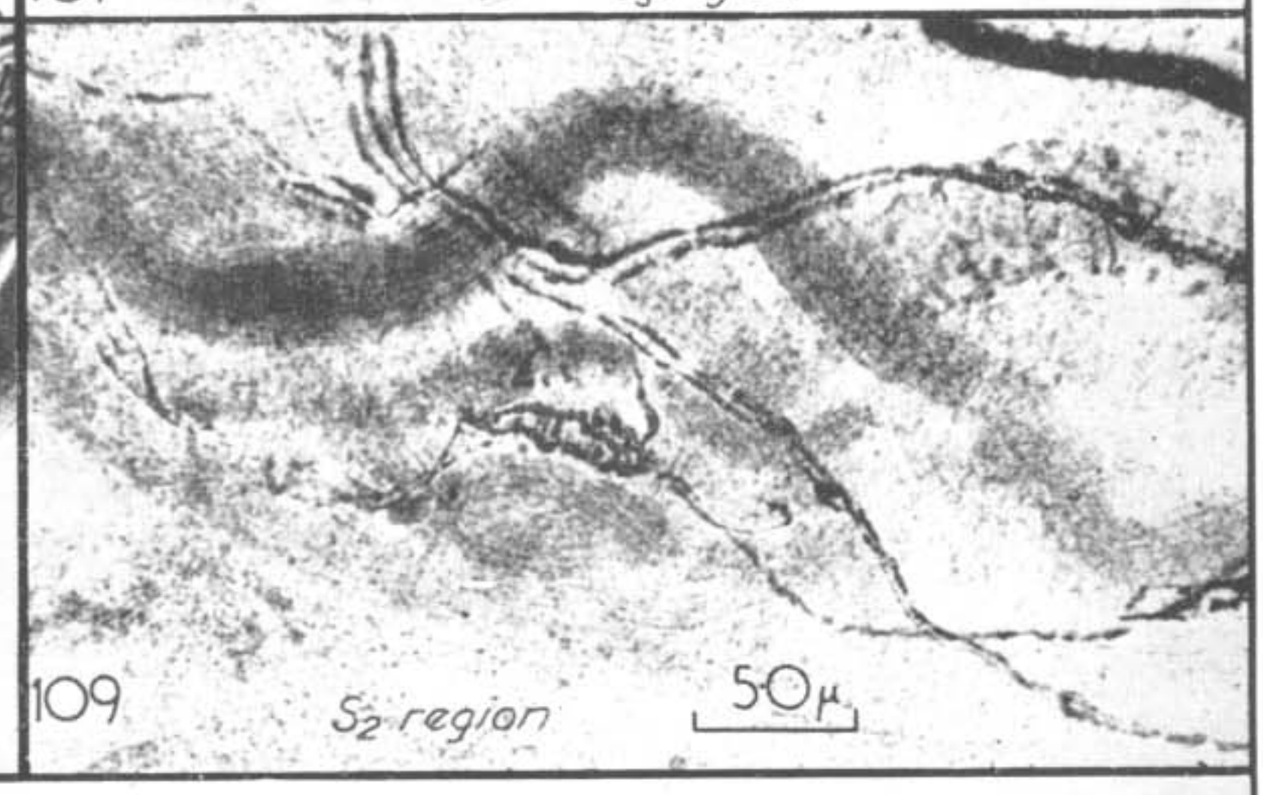


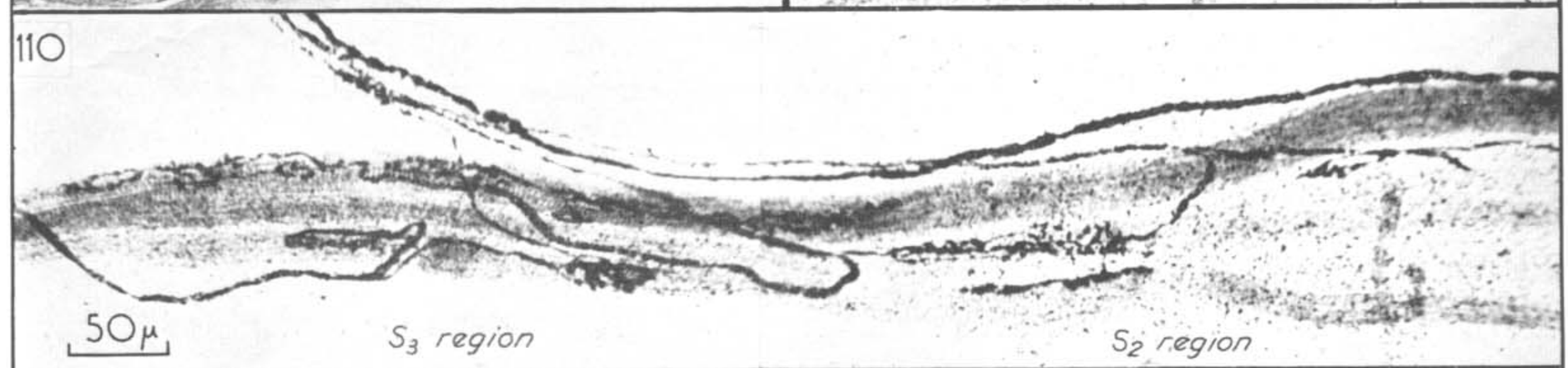


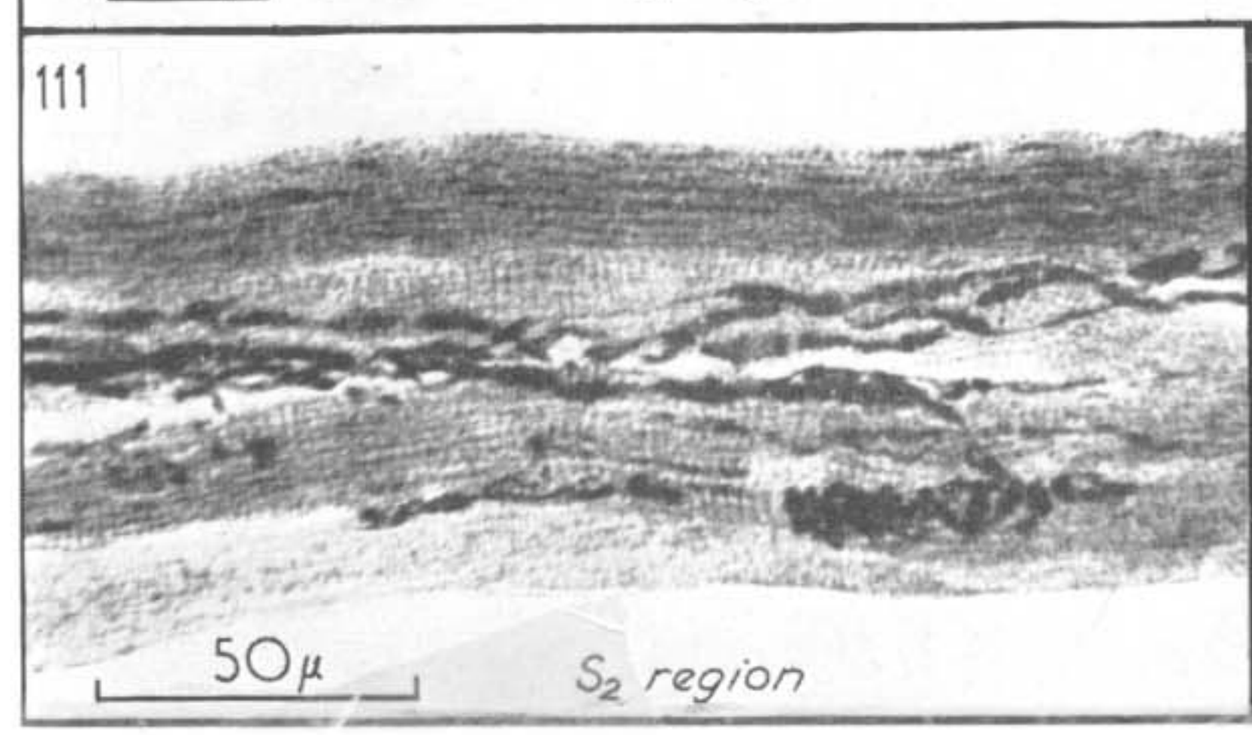


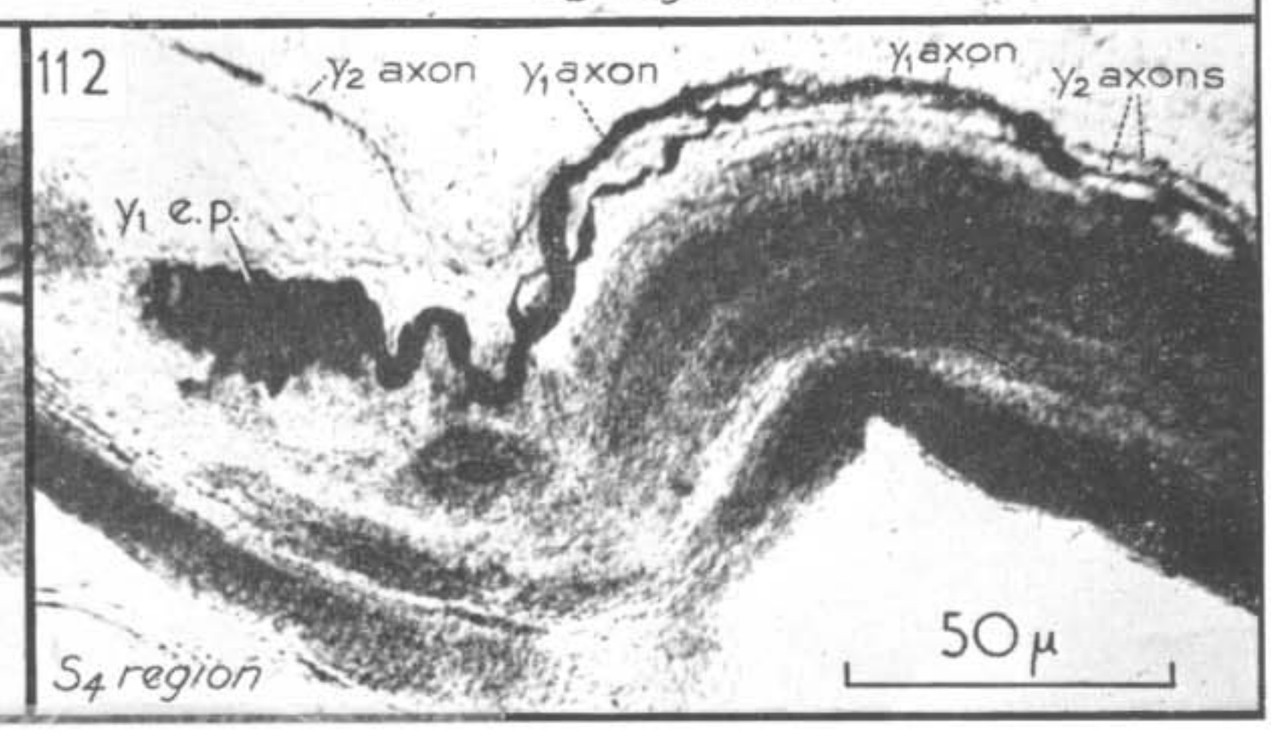




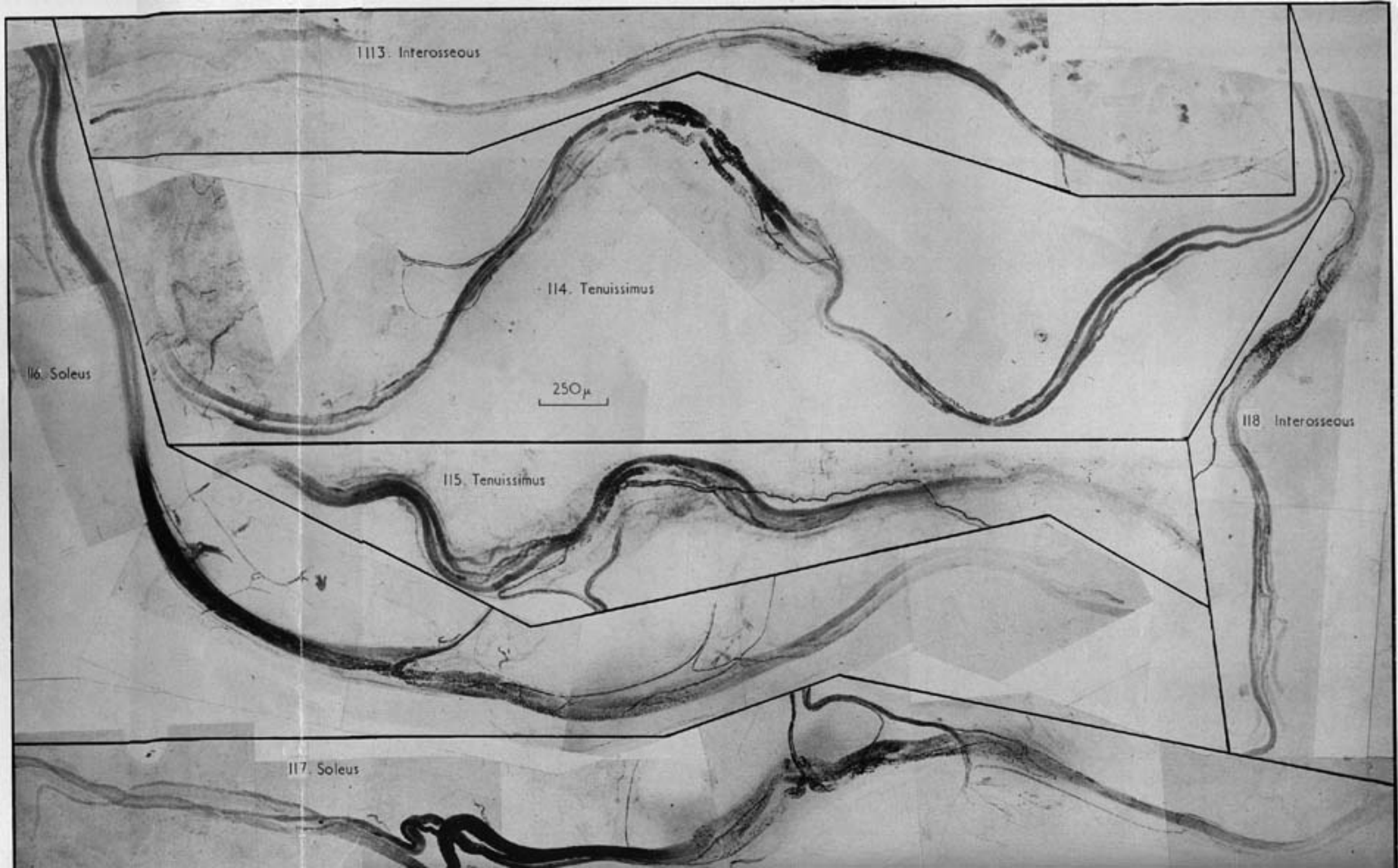








FIGURES 102 TO 112



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