THE THORACIC TRUNCUS SYMPATHICUS, RAMI COMMUNICANTES AND SPLANCHNIC NERVES IN THE CAT

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NINE FIGURES

In other papers of this series, which appear on the preceding pages, we have dealt with the cervical portion of the sympathetic trunk, the superior cervical ganglion, and the branches which it gives off. We come now to a consideration of the thoracic portion, its rami communicantes and the splanchnic nerves. Our preparations were obtained from cats because most of Langley's observations were made on these animals and we wished to compare our results with his.

The work was started with the hope of throwing some light on the origin of the various types of fibers in the splanchnic nerves. Since these fibers are known to belong for the most part to segments caudad to the fifth thoracic, we began by studying the rami from the sixth to the thirteenth thoracic nerves and the corresponding portions of the trunk. It was only after the study of this material had shown that many significant details concerning this nerve trunk had never been described that we began the study of it in the first five thoracic segments. Hence the material representing this part was taken from different cats than those in which the sixth to the thirteenth thoracic segments were studied. But in each case a sufficient number of specimens was secured to make sure that the peculiarities encountered at different levels were characteristic for those levels. In all nearly twenty cats were used, exclusive of those on which operations were performed to produce the degenerations to be reported in the following paper.

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About half of the material was fixed in osmic acid and the remainder in ammoniated absolute alcohol for the pyridine silver stain. The rami communicantes are so small and short that pyridine silver preparations were made in only a few instances, so that our observations on these are based chiefly on osmic acid preparations. For the rest of the work abundant material was available in which to compare the myelin sheath and axon content of the various parts of the sympathetic trunk and the splanchnic nerve.

When small nerves are subjected to the action of the silver and pyrogallie acid a diffuse precipitate forms throughout the specimen which renders it useless for microscopic study. In order to do away with this it is only necessary to subject large blocks of tissue to the action of the reagents. This can best be accomplished by imbedding the nerve in the spinal cord. The small nerve to be studied is dissected free and a fine silk thread is tied at either end of the stretch to be removed. With the aid of a long straight slender needle the thread attached to the end of the nerve is drawn through a piece of spinal cord and the nerve drawn in after it. The spinal cord should be prepared before the nerve is dissected out. The cervical portion of the cat's cord freed from dura and split in the median sagittal plane into two lateral halves makes satisfactory blocks. Each lateral half is then cut into segments a little longer than the pieces of nerve to be removed. During these manipulations the nerve and cord should be protected from drying by the use of normal salt solution. In drawing the nerve into the cord the needle is run longitudinally through the anterior gray column and the thread pulled through until the nerve lies imbedded in the cord. The segment of the cord is then laid with its lateral convex surface upon a glass cover-slip and the silk threads attached to either end of the nerve are tied over the cover-slip so as to put gentle traction on the nerve. After two hours in ammoniated alcohol the silk thread can be cut off near the cord, which is then removed from the cover-slip and pared down with a razor until it forms a bar, the cross-section of which is not more than 4 mm. square. This should consist chiefly of the anterior gray column in which the nerve lies imbedded.

ANATOMY

Truncus sympathicus. In the cat the thoracic portion of the sympathetic trunk presents an arrangement of its ganglia and branches somewhat different from that found in man. The chief differences are in the fusion of the upper thoracic ganglia to form the ganglion stellatum and in the mode of origin of the splanchnic nerves. The trunk lies along the sides of the bodies of the vertebrae ventral to the heads of the ribs, and consists of a series of ganglia, for the most part segmentally arranged, bound together by a continuous nerve cord. Each spinal nerve is connected with an adjacent ganglion by a gray ramus. A ganglion may send a gray ramus to two or more nerves, in which case it represents a combination of two or more segmental ganglia. Some compound ganglia are constant in their occurrence, as in the case of the stellate and the superior cervical ganglia; others may occur occasionally in any part of the trunk due to the fusion of two segmental ganglia. Thus the segmental character of the truncus is indicated by the gray rami, although in some cases adjacent segments may be fused. The white rami are much more irregular in their distribution. From all this it will be apparent that the best method of designating the ganglia is by giving them the number of the spinal nerve to which they are connected by their gray ramus. The facts concerning the connections of the fibers of the gray and white rami, which will be detailed later in this paper, also bear out this conclusion. Langley ('91 a) has made use of the same method of designating the ganglia. When we speak of the twelfth thoracic ganglion we shall have in mind the ganglion whose gray ramus runs to the twelfth thoracic nerve, although a glance at figure 1 will show that there are less than twelve separate ganglia in the thoracic region, and that this particular ganglion usually receives a white ramus from the eleventh thoracic nerve. The portion of the continuous nerve cord which joins two successive ganglia together we shall speak of as an internodal segment and shall number the successive segments to correspond to the numbers of the ganglia below which they lie.

The ganglion stellatum lies ventral to the first intercostal space and the angle of the second rib. It receives the gray and white rami from the first three thoracic nerves and sometimes from the fourth also. In addition it gives off a gray nerve, the ramus vertebralis, which follows the vertebral artery and gives off branches to the lower cervical nerves. According to Langley ('94), it can be traced in the cat as high as the third cervical nerve. The gray ramus to the eighth cervical nerve may run by itself. From its connection with the spinal nerves it is obvious that the stellate ganglion represents a fusion of elements which in man are found in the middle and inferior cervical and the first three (and sometimes four) thoracic ganglia. Beginning with the fourth or fifth thoracic segment, the ganglia are more regularly arranged. But sometimes a ganglion from which a gray ramus arises may be very small, and occasionally scattered ganglion cells or even fairly large ganglionic masses are found in the internodal segments.

Rami communicantes. While there is a gray ramus for each spinal nerve the white rami have a more limited distribution. Gaskell ('86) thought that in the dog they were associated with the second thoracic to the second lumbar nerves only. But Langley ('92 a) has shown that in the dog, cat, and rabbit, white rami run from the first thoracic to the fourth lumbar nerves inclusive. Miller ('09) has shown that in man, contrary to the usual statement, the third and fourth lumbar nerves possess white rami. The rami communicantes of the first two thoracic nerves in the cat run directly to the stellate ganglion, those of the third usually join the trunk a short distance below and ascend in a common sheath with the trunk to reach this ganglion. The gray and white rami of the upper two or three thoracic nerves are commonly fused together, forming one mixed ramus for each of these nerves. From the fourth to the eighth spinal nerve the

Fig. 1 Diagram of the thoracic portion of the sympathetic trunk in the cat. Any branches which may run to the pulmonary or aortic plexuses are usually so fine as to escape notice in a careful dissection carried out with the aid of binocular lenses of $\times 2$ magnification. In one case we found a branch from the sixth thoracic ganglion to the pulmonary plexus and one from the tenth to the aorta.

gray and white rami run close together and join the trunk at the level of the corresponding ganglion. From the level of the ninth or tenth thoracic nerve to the fourth lumbar the white rami are directed caudad and reach the truncus below the level of the ganglion to which the corresponding gray rami run, often at the level of the next ganglion below. In some cases a nerve may give off, in addition to this descending white ramus, a direct one which accompanies the gray ramus to the segmental ganglion.

A nerve may be connected with the corresponding ganglion by more than one gray ramus or a nerve may receive gray rami from two successive ganglia. This is particularly likely to be the case in the lower thoracic and lumbar regions where, in addition to the gray ramus from its own segmental ganglion, a nerve may receive a bundle of unmyelinated fibers from the next more caudal ganglion, which bundle accompanies the descending white ramus of the nerve. Langley ('94) has shown that "when the white ramus runs downward to a ganglion, as occurs from the ninth or tenth thoracic to the fourth or fifth lumbar nerves, the ganglion may supply pilomotor fibers to the two nerve areas, thus the fourth lumbar ganglion sends fibers to the fourth lumbar nerve by its gray ramus, and may also send fibers to the third lumbar nerve by the white ramus of this nerve."

Gaskell ('86) has shown that when a gray ramus is followed toward its corresponding spinal nerve it can usually be seen to give off branches which ramify in the connective tissue overlying the vertebrae. On these branches accessory ganglia may sometimes be found. In some cases the gray ramus could be seen to divide on reaching the spinal nerve, part of the fibers passing centrally, the rest peripherally.

The splanchnic nerves. In the cat the splanchnic fibers leave the sympathetic trunk in a series of six to ten small nerves. The first of this series is the largest and corresponds to the greater splanchnic nerve in man. The level of the trunk at which this nerve is given off varies. In a total of seventeen dissections it took origin from the thirteenth thoracic ganglion in six cases, from the thirteenth internodal segment in three, from the first lumbar ganglion in four, from the first lumbar internodal

segment in three and from the second lumbar ganglion in one. Since it is well known that fibers of the splanchnic nerve come from segments as high as the fifth and sixth thoracic, it is obvious that these fibers must have descended in the sympathetic trunk to the point of origin of the splanchnic nerve. In man these same fibers leave the trunk in small bundles from the level of the fifth or sixth thoracic ganglia downward to the ninth, and these bundles are then gathered together to form the greater splanchnic nerve. In the cat other splanchnic nerves are given off somewhat irregularly from the upper five lumbar ganglia and internodal segments.

The thoracic rami communicantes. It is not necessary to review the early literature dealing with the rami communicantes, since the work of Gaskell ('86) may be regarded as the starting point of modern investigations on this subject. He made a careful histological examination of the spinal nerves and rami communicantes. The gray rami were found to be composed chiefly of unmyelinated and the white rami chiefly of myelinated fibers. In the roots of the spinal nerves only myelinated fibers were found. He argued that, since he found only myelinated fibers in the roots of the spinal nerves as they left the spinal cord, the only connection between the spinal cord and sympathetic trunk must be by way of the myelinated white rami, and that through them occurred the only possible outflow of visceral efferent fibers from the spinal cord. The ventral roots of those spinal nerves which he found associated with white rami, the second thoracic to the second lumbar inclusive, were seen to contain large numbers of fine myelinated fibers like those in the white rami, while the ventral roots of the other spinal nerves contained very few such fibers. These he regarded as visceral efferent fibers. A gray ramus was found associated with each spinal nerve. On reaching the nerve such a ramus was seen to divide, one part passing centrally, the other peripherally. Most of the unmyelinated fibers which ran centrally were seen to pass into the sheath of the nerve and become lost in the dense layers of connective tissue within the intervertebral foramen. Since no unmyelinated fibers could be found in the ventral roots nor in the dorsal

roots proximal to the spinal ganglion, Gaskell asserted "that no non-medullated nerves leave the central nervous system either in the posterior or in the anterior roots, any such nerves being in reality peripheral nerves for the supply of the spinal membranes."

This was the status of the question when Langley began his work. In 1892 he said:

It may be regarded as shown that only medullated fibers run from the spinal cord to the sympathetic chain, and that the white rami contain very many medullated fibers whilst the gray rami contain very few. The asserted sharp distinction between white and gray rami stands, however, on a different footing. So far as concerns their histological characters the difference between them is rather one of degree than of kind, they both contain medullated fibers of various sizes, and non-medullated fibers.

On such evidence alone it could not be confidently asserted that no preganglionic fibers left the cerebrospinal nervous system by way of the gray rami. This question could best be attacked by physiological methods, i.e., by stimulating the spinal nerves within the spinal canal. Langley ('92 a) showed that, while stimulation of the nerves which were associated with white rami gave rise to responses in smooth muscles and glands, stimulation of those which possessed only gray rami produced no noticeable effect on these structures. He concluded that the myelinated fibers in the gray rami were either not preganglionic efferent fibers or were too few to produce any perceptible effect.

Most of Langley's histological observations were made on teased nerves, and it has seemed worth while in connection with the general review of the entire sympathetic nervous system which is being made in this laboratory to check up his histological observations by a careful examination of the rami communicantes of all the spinal nerves in sections stained with osmic acid. In this paper the rami of only the cervical and thoracic nerves are considered.

White rami communicantes. The course of the white rami within the sympathetic trunk will be taken up in connection with that nerve cord. Our present concern is with the character of the fibers. The white rami are not always pure, but are often accompanied by one or more fascicles of unmyelinated fibers

having all the characteristics of small gray rami. Such fascicles are, however, always sharply defined and do not form a part of the white ramus proper. These composite rami are especially frequent in the upper thoracic region where the gray and white rami are regularly fused. The first two or three thoracic nerves usually have each a single mixed ramus. Mixed rami are also not uncommon in the lower thoracic and upper lumbar regions where the white ramus runs downward.

Osmic acid preparations of the white rami of the cat show that these contain great numbers of small myelinated fibers with which are mingled some larger fibers varying in number in the different rami. In the dog Gaskell found that the small fibers measured 1.8 to 3.6μ . He believed that all visceral efferent fibers were of this size. Langley ('96 a) states that:

In the cat, the medullated fibers of the sympathetic appear to be somewhat smaller than in the dog. In the dog, I found that most of the nerve fibers could be classed as belonging to one of three types, viz., large fibers about 8μ in diameter, medium fibers about 5μ in diameter, and small fibers about 3μ in diameter, though all sizes from 2 to 12μ were present. In the cat the corresponding fibers are about 7μ , 4.5μ and 2.5μ ; fibers from 2 to 10μ and occasionally of greater diameter than 10μ being present.

Our measurements of the medullated fibers in the white rami of the cat show that the small fibers vary in diameter from 1.5 to 3.5μ . Between these two extremes there are fibers of all sizes and in about equal proportion. There are also fibers of larger size, but in much smaller proportion. The second thoracic white ramus contains, however, a great many fibers measuring 4.5μ or 5μ , as will be seen in figure 2. The larger fibers, which vary in size from 5 to 13μ are not evenly distributed in the white rami and will be considered more in detail when some of the individual rami are taken up.

There does not seem to be any reason for grouping the fibers into three classes as Langley has done. There would be more reason for making two groups: one less than 4.5μ , the other larger. It is probable that nearly all of the preganglionic efferent fibers would fall in the first group, but this group would also contain, as we shall see, some of the smaller sensory fibers. The

second group would include the large and medium-sized sensory fibers.

Are there unmyelinated axons scattered among the myelinated fibers of the white rami? We must exclude from consideration

Fig. 2 Second thoracic ramus communicans in the cat consisting of two fascicles, the larger representing the white and the smaller the gray ramus. Osmic acid. $\times 425$.

here the bundles of unmyelinated fibers which run as definite fascicles and represent small gray rami included in the white. Gaskell ('86) found unmyelinated fibers in the white rami and said that "there is strong evidence that they arise from the

posterior root ganglia." It is clear from the context that he believed the spinal ganglia contained autonomic cells and that the unmyelinated fibers running from these ganglia by way of the white rami were of the same nature as the unmyelinated fibers arising from sympathetic ganglia.

We have pyridine silver preparations of the tenth, eleventh, and twelfth white rami from one cat. While these are not altogether satisfactory, it is possible to see that they contain a considerable number of unmyelinated fibers. In the paper which follows we shall present evidence to show that these fibers arise in the spinal ganglia, but we believe that they are to be interpreted as afferent, not as postganglionic efferent fibers. If they belonged to the latter category it would be hard to account for the negative results of stimulating the splanchnic nerves after injection of nicotin (p. 436).

There has been some difference of opinion concerning the rami of the first thoracic nerve. Gaskell ('86) found only a gray ramus connected with this nerve in the dog. Edgeworth ('92) found that this ramus in the dog contained unmyelinated, large myelinated, and a few fine myelinated fibers. From this account we would conclude that there was no clear separation of the fibers into fascicles representing gray and white rami. Langley ('92 a) studied the rami of the first thoracic nerve in the cat, dog, and rabbit, and in every case found the highest white ramus coming from the first thoracic nerve. In the cat we find the gray and white rami of the first thoracic nerve united in a mixed ramus in which they appear as separate fascicles. The white fascicle contains a rather large number of fibers over 6μ . It is particularly in the number of these large fibers that the white rami differ from one another. In individual white rami the content of large fibers was found as follows:

First thoracic white ramus, 40 fibers over 6μ in diameter, one of which was much larger than the others and measured 13μ .

Second thoracic white ramus, 17 fibers 6μ in diameter or larger. Of these 5 measured 13μ . There were also a rather large number of fibers from 4 to 6μ in diameter.

Third thoracic white ramus, 23 fibers 6μ in diameter or larger. There were no very large fibers like those in the two preceding rami.

Fourth thoracic white ramus, 10 fibers 6μ in diameter or greater. No very large fibers.

Fifth thoracic white ramus, 24 fibers 6μ in diameter or greater, of these 2 measured 13μ .

Sixth thoracic white ramus, 73 fibers 6μ in diameter or greater, the largest of which measured 10μ .

Seventh thoracic white ramus, 109 fibers 6μ in diameter or larger. There were no fibers of 10 to 13μ diameter.

Eighth thoracic white ramus, 101 fibers 6μ in diameter or greater. None of them very large fibers.

Ninth white ramus, contained 174 large fibers, but many of them were a little under 6μ in diameter.

Tenth white ramus. In this specimen we found a direct ramus to the tenth thoracic ganglion and a descending ramus to the eleventh. The direct white ramus contained 130 large fibers, one of which measured 10μ ; the descending white ramus in this case consisted very largely of fibers 6 to 8μ in diameter, 106 in number. The total number of large fibers coming from the tenth thoracic nerve was thus 236.

Eleventh thoracic white ramus. Here again we found a direct and a descending white ramus and in both together there were 59 large fibers.

Twelfth thoracic white ramus, 11 large myelinated fibers, of which the largest was 8μ .

Thirteenth thoracic white ramus, 56 large myelinated fibers.

While these white rami did not all come from a single animal—the first was from one cat, the second to the fifth from another, and the sixth to the thirteenth from a third cat—the results have been checked on a sufficient number of other cats to show that the larger differences between the rami of the several levels are significant. The greatest outflow of large fibers occurs through the seventh to the tenth or eleventh white rami, inclusive. Figure 3 shows the relatively large number of them in the tenth.

There seems also to be a rather large number in the first thoracic ramus. The upper two thoracic rami are also characterized by the presence of fibers as large as 13μ , which are usually absent from the others.

Fig. 3 Tenth thoracic white ramus of the cat with associated gray fascicles. There was a large separate gray ramus not shown in the figure. Osmic acid. $\times 425$.

Bidder and Volkman ('42) were the first to consider these larger fibers as sensory. Langley ('92 a) found difficulty in correlating the degree of sensitiveness of different parts of the sympathetic system, as evidenced by the ease with which their stimulation would produce general reflexes, with the number of

large myelinated fibers they contained. He suggested the possibility that many of the larger fibers mediate some special sense or subserve special visceral reflexes. Many of them can be traced to the Pacinian corpuscles (Langley, '00). Edgeworth ('92) devoted special attention to the "large-fibered sensory supply of the thoracic and abdominal viscera" in the dog. According to him,

It was found that the large medullated sympathetic fibers exist in the rami communicantes of the nerves from the first dorsal to the third lumbar inclusive; none were found in the rami aboral to this. The large sympathetic fibers are found scattered among the other fibers in the nerve bundles forming the ramus, and not grouped together or isolated by any septa from the other fibers. In the uppermost dorsal rami the large sympathetic fibers are fairly plentiful, in the upper and middorsal rami they are somewhat fewer in number, whilst in the lower dorsal rami a sudden large increase takes place, which continues as far as the second lumbar ramus where the outflow practically ceases. A few however are constantly to be found in the third lumbar ramus—whilst below this as stated above none are seen.

Edgeworth included among the large fibers those measuring 7.2 to 9μ and ignored the even larger number of fibers measuring less than 7μ but still distinctly larger than preganglionic fibers, so that his results are only in a general way comparable to ours. He states that the large fibers are as numerous in the gray as in the white rami. In the cat, as we shall see, they are usually not present in the gray rami of the cervical and thoracic regions. Langley ('92), working with the cat, found some large fibers, 7.2μ or upwards, in the gray rami of the lower cervical nerves; in the white and in the gray ramus of the fourth lumbar nerve, and in the gray rami of the fifth, sixth, and seventh lumbar nerves. These were not numerous, but with them were a considerable number of fibers about 5μ in diameter.

It has been assumed that all the large myelinated fibers are afferent, but are all the visceral afferent fibers large? Added precision could be given to this question of the myelinated visceral afferent fibers by the study of the white rami after degeneration of the preganglionic fibers resulting from section of the corresponding spinal nerve roots proximal to the spinal ganglia. We have examined the white rami of the ninth, tenth, and elev-

enth thoracic nerves after all the preganglionic fibers had been eliminated. As is shown in the figure on page 444 of the eleventh thoracic white ramus, the majority of the fine myelinated fibers have degenerated, but a considerable number of all sizes remain. In this particular case the small and medium-sized fibers are more numerous than the large ones. In some other degenerated white rami the large ones are relatively more numerous. On the whole, the sensory fibers of the white rami may be said to be of all sizes from 1.5 to 8 or 10 μ , no one size greatly predominating over the others. In some rami as in the upper thoracic larger fibers up to 13 μ may be present.

These sensory myelinated fibers which are found in the white rami after section of the corresponding nerve roots proximal to the spinal ganglia take their origin from nerve cells in these ganglia. In the second paper of this series we have shown that there was no reason for assuming that there were sensory cells in the sympathetic ganglia which sent their axons into the dorsal roots or spinal ganglia (p. 333). Langley has shown that

Section of the inferior splanchnics, the lower lumbar sympathetic chain, or of a white ramus does not as a rule cause degeneration of any medullated fibers in the central ends of the nerves. Sometimes a few degenerated fibers may be followed for a short distance, but these appear to belong to small gray bundles and to pass off to peripheral tissues.

When we come to the study of the sympathetic trunk we shall find that while some of the fibers of a white ramus end in the nearest ganglion, a larger proportion of the fibers run up or down in the trunk for longer or shorter distances. That is to say, a white ramus is in no special sense associated with its own segmental ganglion. The gray rami, on the other hand, are in a very special sense the branches of the corresponding ganglia.

Gray rami communicantes. The physiological experiments of Langley ('91 a, '94) on pilomotor, vasomotor, and secretory fibers show that the majority of these postganglionic fibers take origin from the cells of that ganglion to which the gray ramus is attached, but in some cases a minority of the fibers are connected with cells in an immediately adjoining ganglion. On the histological side this arrangement is indicated by the fact

that a gray ramus plunges directly into a ganglion, its fibers being lost in the fiber complex; while in the case of the white rami it is easy to see that a large part of the fibers do not enter the ganglion, but pass along its surface to join the trunk above or below.

While the gray rami are composed in by far the greater part of unmyelinated fibers, each contains at least a few myelinated fibers and some contain a very considerable number. Langley ('96 a) has shown that the number of such fibers has been greatly underestimated. The seventh lumbar gray ramus of the cat may contain more than 300. According to Edgeworth ('92), the branches from the stellate ganglion to the cervical nerves in the dog contain a few small myelinated fibers, but no large ones. In commenting on Edgeworth's paper Langley ('92) states that he has always found some large myelinated fibers in the gray rami of the lower cervical and fourth, fifth, sixth, and seventh lumbar nerves. The number of small myelinated fibers is in general proportional to the size of the gray ramus, i.e., to the number of unmyelinated fibers it contains (Langley, '96 a). He states that the myelinated fibers range in size from 1.8 to 10μ and the variation in number affects almost entirely the small ones, the most constant form being the fiber of medium caliber. The number of myelinated fibers varies considerably in different mammals, there being many more in the cat than in the rabbit (Langley, '00). Müller ('09) demonstrated the presence of myelinated fibers in the gray rami of man.

In the rami to the first three cervical nerves from the superior cervical ganglion we found that the number of myelinated fibers varied greatly in different specimens. Most of these fibers were less than 3.3μ in diameter, although occasionally larger fibers up to 6 or 7μ were found, also in one case a single fiber measuring 10μ . We have examined sections of the ramus vertebralis of the stellate ganglion in one cat and found that it contained about the same proportion of myelinated fibers as the other gray rami. There were no fibers as large as 6μ . All of the thoracic gray rami contain a few myelinated fibers. These are for the most part small, but a few large fibers were found in the upper thoracic gray rami. We cite some enumerations which may be regarded

as typical. In one cat the sixth thoracic gray ramus contained one myelinated fiber 6.6μ in diameter and three others much smaller. The seventh was fused with the white ramus, and it was difficult to be sure which myelinated fibers belong to it. The eighth contained 3, the ninth 20, the tenth 27, the eleventh 14, the twelfth 6, and the thirteenth 16, all under 4μ in diameter.

What is the function of these myelinated fibers and from what cells do they arise? Many are postganglionic fibers arising from the cells of the ganglia of the sympathetic trunk. The observations to be found in the literature showing that postganglionic fibers in some instances acquire myelin sheaths have been given on page 323. As already mentioned, Gaskell showed that as a gray ramus reaches its spinal nerve it divides into two fascicles, one of which is directed peripherally. This peripheral branch receives its share of the myelinated fibers. These being directed toward the periphery can scarcely be other than postganglionic fibers. It is reasonable to suppose that many of those which turn centrally are of the same nature (Langley, '92 a).

In 1896 Langley made a careful study of this problem. After a variety of experimental lesions involving degeneration of fibers of various origin in different experiments, he counted and measured the normal and degenerated fibers in the gray rami of the lumbar and cervical nerves. We quote his conclusions:

The great majority of these (myelinated) fibers arise from sympathetic nerve cells in the corresponding sympathetic ganglion. In some cases, but not always, a few arise from sympathetic cells in an adjoining ganglion. No efferent fibers run from the spinal cord to the sympathetic by way of the gray rami. In some cases, but not commonly, a few efferent medullated fibers, passing to the sympathetic by the white rami, leave the sympathetic by the gray rami. These are to be considered as fibers on their way to aberrant sympathetic nerve cells lying in the gray rami before they reach the spinal nerves. The afferent medullated fibers of the gray rami are of various sizes, 2μ , 4μ , 6μ , and in some cases 8 to 12μ . These are few in number and rapidly diminish (especially those of more than 4μ in diameter) in passing from the lower lumbar to the coccygeal rami. Most of (these) afferent fibers join the sympathetic by white rami (only to leave again by the gray), but there is some evidence that a few, especially the larger ones may run to the sympathetic by the gray rami.

In spite of the presence of a few myelinated sensory fibers in the gray rami "no reflex of any kind has been obtained by stimulating them" (Langley, '00). This may be due to their small number, or it may be as Langley ('92 a) has intimated, to the fact that these large afferent fibers are not fibers of general sensibility.

STRUCTURE OF THE THORACIC PORTION OF THE TRUNCUS SYMPATHICUS

In order to understand the structure of the sympathetic trunk it is necessary to think of it as a ganglionated nerve which receives preganglionic myelinated fibers from the various white rami and through which these fibers are distributed to ganglia more or less remote from the point where the fibers enter the trunk (fig. 4). Above the sixth thoracic ganglion the trunks consist chiefly of ascending preganglionic fibers from the upper white rami destined to end in the upper thoracic, stellate, and cervical ganglia. Below the tenth thoracic ganglion it consists chiefly of descending preganglionic fibers from the lower thoracic and lumbar white rami to the more caudal ganglia of the trunk and to the splanchnic nerves. From the sixth to the ninth ganglia it contains both ascending and descending preganglionic fibers. The lowest known origin of ascending fibers to the superior cervical ganglion is from the seventh thoracic white rami and consists of pilomotor fibers for the face and neck. Fibers ascend to the stellate ganglion from white rami as low as the ninth. The highest fibers running to the splanchnic nerve come from the fifth or possibly the fourth. Fibers from a given white ramus may be distributed to from five to ten successive ganglia of the sympathetic trunk, though the branches of an individual preganglionic nerve fiber would be distributed to a smaller number. These statements are based on Langley's ('92 a, '00, '03 a) work on the cat. In more general terms this distribution of the fibers of the white rami has been known for many years and was well stated by Gaskell ('86). According to him, the white rami from the second to the fifth thoracic nerves, inclusive, in the dog are directed upward, below the fifth they are directed mainly

Fig. 4 Diagram illustrating the course of the fibers from the thoracic white rami through the sympathetic trunk in the cat. A. The course of the afferent fibers. B. The course of some of the more important groups of preganglionic fibers, those terminating in the thoracic ganglia below the stellate are not indicated.

TABLE 1

Connections of the spinal nerves with the vertebral ganglia, so far as these supply the skin, except that of the head and the anogenital region in the cat with an anterior arrangement of the spinal nerves—after Langley-Schafer's Physiology, vol. 2, p. 634

SPINAL NERVE	SYMPATHETIC GANGLIA	SPINAL NERVE
IV	G St.....	IV
V	G St.....	V
VI	G St.....	VI
VII	G St 4, 5, 6, 7, 8, 9.....	VII
VIII	G St 4, 5, 6, 7, 8, 9, 10.....	VIII
IX	(G St) 4, 5, 6, 7, 8, 9, 10, 11.....	IX
X	8, 9, 10, 11, 12, 13.....	X
XI	12, 13, 1, 2, 3.....	XI
XII	13, 1, 2, 3, 4 (5) (6) (7).....	XII
XIII	1, 2, 3, 4 (5) (6) 7 (1).....	IXII
I	2, 3, 4 (5) (6) 7, 1, 2.....	I
II	3, 4 (5) (6) 7, 1, 2, 3.....	II
III	4 (5) (6) 7, 1, 2, 3 Coc..	III

downward. This is associated with the course of the fibers of which they are composed which pass not only into their segmental ganglia, but also upward into the cervical ganglia, downward into the lumbar and sacral ganglia and outwards into the collateral ganglia. Müller ('09) has shown that the preganglionic fibers in man have a similar distribution. The connections of the spinal nerves with the ganglia of the sympathetic trunk so far as these supply vasomotor, pilomotor, and secretory fibers to the skin has been worked out in detail by physiological methods and is expressed in table 1. This shows that these preganglionic fibers from the nerves above the seventh thoracic are directed upward from the nerves below the tenth downward and from the seventh to the tenth, inclusive, both up and down.

With the exception of the cervical and stellate ganglia, which contain other elements also, the ganglia of the sympathetic trunk may be regarded as aggregations of postganglionic pilomotor, vasomotor, and secretory neurones whose axons are distributed through the corresponding gray rami and spinal nerves. As we have stated before, the fibers of a gray ramus arise from the associated sympathetic ganglion, though a few fibers may

come from the next higher or next lower ganglion. The ganglia and gray rami are therefore more nearly segmental than the white rami. As we shall see, few if any postganglionic fibers, arising in the ganglia of the sympathetic trunk, pass by way of the splanchnic nerves to the abdominal viscera.

With these facts in mind we are prepared to understand the observations which follow and which show that the sympathetic trunk is a well myelinated nerve.

The sympathetic trunk caudad to the sixth thoracic ganglion has the structure shown in figure 5. It consists like other portions of the thoracic trunk of two fascicles which, though not sharply separated from each other by connective-tissue septa, maintain their identity throughout, and in cross-sections of the stained nerve are easily distinguished from each other because of their markedly different fiber content. The larger fascicle, well myelinated, presents in cross-section a round outline and occupies the greater part of the area of the cross-section. The other, which makes up but a small part of the area, is composed almost exclusively of unmyelinated fibers, and is flattened out like a crescent upon the surface of the larger bundle. For convenience of reference and until its nature is better known we will speak of this bundle as the crescent. The larger, more rounded, area will be referred to as the oval.

When followed in serial sections the crescent of unmyelinated fibers is seen to enter the ganglion at either end of the internodal segment and become lost in the ganglion. The crescent contains a very few fine myelinated fibers, and has in fact the structure of a gray ramus. The fibers of the larger well myelinated bundle, the oval, run in part into the ganglion at either end of the internodal segment, but in even larger part pass by along the side of the ganglion. Every internodal segment of the thoracic sympathetic trunk presents this separation into two fascicles—and in every case where serial sections of an internodal segment, including the ganglia at both ends, were examined the crescent was found to be continuous from ganglion to ganglion.

The same structure was described as a peripheral fascicle of unmyelinated fibers in the cervical sympathetic trunk. As

the fascicle was followed caudad from the superior cervical ganglion it was seen to give off very small bundles of fibers which left the trunk as gray branches, bringing about a gradual reduction in the size of the fascicle. One set of serial sections of the entire cervical portion of the sympathetic trunk was prepared,

Fig. 5 The sixth thoracic internodal segment of the sympathetic trunk in the cat. Two fascicles may be recognized, one appearing in the cross-section as a large oval well myelinated field, the other as a crescentic field with few myelinated fibers. Osmic acid. $\times 425$.

and in this preparation it was found that in tracing the crescent downward it decreased in size and finally disappeared. It is obvious, therefore, that in the upper cervical region a fascicle similar to the crescent consists of postganglionic fibers which accompany the trunk for a certain distance before being given off

in gray branches. In the thoracic region one cannot often see this fascicle of the trunk give off branches. It appears rather to serve as a commissural cord joining two successive ganglia together.

There are three possibilities concerning the nature of the fibers of this fascicle: 1. It may consist of commissural fibers arising from the cells of one ganglion and running to another. Against this assumption is all the evidence presented by Langley to show that such commissural neurones do not exist. The most important evidence in this connection is that based on degeneration experiments. Langley has shown ('03 b) that after degeneration of the lower thoracic and lumbar spinal roots, the lower part of the sympathetic trunk is in the same condition as after injection of nicotine. Stimulation between the ganglia has either no effect or only such effect as could be interpreted as due to post-ganglionic fibers. The literature on this question was considered at some length in the second paper of this series on page 320. In the paper by Dr. Johnson this question is again considered, and what seems to be conclusive evidence is presented that no commissural fibers exist in the sympathetic trunk of the frog. In view of these facts, it does not seem probable that the crescent is composed of commissural fibers.

2. The crescent may consist of fibers belonging to gray rami which ascend or descend in the trunk for a short distance. From what has been said about the crescent in the cervical region and from the fact that, as we have already stated, the fibers of a given gray ramus may come in part from the ganglion next above or next below, it seems obvious that some at least of the fibers of the crescent must be of this nature. Since, however, gray ramus fibers do not ascend or descend in the trunk for more than one segment and since such fibers are not numerous nor constantly present, it seems doubtful if they can account for the large number of fibers constantly present in the crescent.

3. A third possibility is that the crescent is formed by unmyelinated terminal branches of preganglionic fibers. There is some evidence that these fibers may lose their sheaths before terminating. This evidence has been summarized by Langley ('00) as follows:

By the degeneration and by the nicotine method, it can be shown that in the cat fibers run from the upper lumbar white rami to the sacral and coccygeal ganglia without passing through nerve cells. In the rabbit the nicotine method only has been tried; it gives the same results. We may then conclude that in the rabbit there are preganglionic fibers, stretching from the upper lumbar white rami to the sacral coccygeal ganglia. But since the sympathetic in the sacral and coccygeal region of the rabbit contains very few medullated fibers, it follows that the preganglionic fibers in this region must be non-medullated, and as they are medullated in the white rami they must become non-medullated in passing down the sympathetic chain. In other words, preganglionic fibers may become non-medullated some distance from their termination in the vertebral ganglia.

But after all has been said it must be admitted that we are not in possession of a satisfactory explanation of the bundle of unmyelinated fibers which we have provisionally called the crescent and we do not know what the source of its fibers may be.

As seen in figure 5, the myelinated fibers which constitute the larger oval field are of various sizes. The small fibers 1.5 to 3.5μ in diameter are by far the most numerous. They have the size and appearance of white rami fibers with somewhat thicker sheaths than is usual on postganglionic fibers of the same caliber. The larger fibers are rather conspicuous but are not present in great numbers. They will be recognized as the large fibers of the white rami which, as we have seen, take their origin from the dorsal root ganglia.

Sections stained with osmic acid through successive internodal segments from the sixth thoracic downward to the origin of the first splanchnic nerve show no great change in structure. There is obvious a rather considerable increase in area of the oval myelinated fascicle without any regular increase in the area of the crescent. The most noticeable feature is, however, the absolute and relative increase in the number of large myelinated fibers. A comparison of figures 5 and 6 will show that they are relatively much more numerous in the eleventh thoracic internodal segment than in the sixth. And the area of the cross-section at the eleventh is much greater than at the sixth. This increase in area is caused by the large number of fibers descending in the trunk to enter the splanchnic nerves. All of the large fibers of

the lower eight thoracic white rami turn downward toward the splanchnic nerves, and accumulate in the trunk. It is probable that many of them branch on their way down. Langley ('00) states that the large fibers of the sympathetic system occasionally divide. In this case the branches are of somewhat less diameter than the parent fibers. He does not state how these observations were made, but most of his histological observations were made on teased preparations. As evidence that division of the large

Fig. 6 A small part of a section of the eleventh thoracic internodal segment in the cat. Osmic acid. $\times 425$.

fibers occurs in the sympathetic trunk we may mention the results of the enumeration of the large fibers in the lower thoracic white rami and in the trunk just above the origin of the first splanchnic nerve. Only fibers 6μ or greater were counted. The total number of large fibers in the lower eight thoracic white rami was 864. In the trunk just above the origin of the first splanchnic nerve there were 464, i.e., a little more than half as many as in the rami. Since, as we shall see, all or practically all of the large fibers from these rami turn downward in the trunk, and since none or almost none are given off in any of the other

branches of the truncus, and since being sensory fibers, it is not likely that they terminate in the ganglia, the simplest explanation of these numerical results would be that through branching about half of them became reduced in size below a diameter of 6μ .

In serial sections of the sympathetic trunk with the white rami attached it is easy to trace the course of the myelinated fibers from the latter. In one cat longitudinal serial sections of the trunk at the level of the entrance of the sixth white ramus were prepared from osmic acid material, also similar sections of the trunk at the level of the seventh white ramus. These rami joined the trunk at the level of the lower end of the corresponding ganglia and could be seen to divide into two bundles, a smaller ascending and a larger descending bundle. The majority of the fibers do not plunge directly into the ganglion, but seem to run by on its surface. This is especially evident in case of the descending bundle which can be followed into the trunk below the ganglion. It is very easy to follow the large medullated fibers and to see that practically all of these in the sixth and seventh white rami turn downward past the ganglion into the internodal segment.

An instructive set of preparations was obtained from another cat in which the seventh thoracic ganglion and the associated rami were cut into transverse serial sections. The white ramus on reaching the ganglion divided into two parts: the smaller of the two joined the myelinated portion of the truncus on the surface of the ganglion; the other part turned downward in a well-defined fascicle separated from the ganglion by a connective-tissue septum and could be traced downward for a considerable distance along the side of the seventh thoracic internodal segment before it joined with the trunk. So far as could be determined all the large fibers of this white ramus turned downward in this fascicle. Such a separate descending fascicle is of course atypical, but this ramus serves to indicate in a diagrammatic way the course taken by the fibers of the white rami on entering the trunk. Of course the corresponding fibers of the upper thoracic white rami turn upward instead of downward.

At the point where the first and largest splanchnic nerve is given off, which is usually near the thirteenth thoracic ganglion, the size of the trunk becomes abruptly reduced, and it is obvious, when serial sections are studied, that a large part of its myelinated fibers run into this nerve.

The sympathetic trunk cephalad to the sixth thoracic ganglion is characterized by the small number of large myelinated fibers which it contains. The peripheral crescent-like bundle of unmyelinated fibers is seen here as well as in lower segments and can be traced continuously from one ganglion into another. Above the fourth thoracic ganglion the trunk sometimes breaks up into two or three fascicles which run parallel to one another to

Fig. 7 One of three fascicles composing the sympathetic trunk above the level of the fourth thoracic ganglion in the cat. Osmic acid. $\times 425$.

reach the stellate ganglion. A cross-section of such a fascicle just above the level of the fourth thoracic ganglion is seen in figure 7. The crescent of unmyelinated fibers was joined with one of the other two fascicles of which the trunk was composed. The fascicle which is seen in cross-section in figure 7 contained no bundle of unmyelinated fibers large enough to be recognized in osmic acid preparations. With the exception of two larger fibers, it was composed of myelinated fibers of uniformly small size. The other fascicles of the trunk were also characterized by the paucity of large and medium-sized myelinated fibers.

In studying the white rami we have found reason for believing that the large and medium-sized fibers of the sympathetic system are afferent. There are also small myelinated afferent fibers, but these are not readily distinguished from the preganglionic efferent fibers. It will be evident from what has been said that the large and medium-sized myelinated afferent fibers are present in varying numbers in different parts of the thoracic sympathetic trunk. Between the stellate ganglion and the sixth thoracic ganglion they are few in number. Caudal to the sixth ganglion there is a steady increase in these fibers with the accession of each successive white ramus until the point of origin of the greater splanchnic nerve is reached through which nerve a large part of these fibers run toward the viscera (fig. 4 B). We shall now see that unmyelinated afferent fibers from the white rami are distributed in the same way as these myelinated sensory fibers which we have been studying.

Above the level of the fourth thoracic ganglion there are very few unmyelinated fibers in the trunk except for the well-defined bundle which we have referred to as the crescent. The fine myelinated fibers of which the rest of the cross-section is composed are almost free from an admixture of unmyelinated fibers. These are also not very numerous in the oval of the seventh internodal segment. In the lower thoracic segments the oval well myelinated portion of the section does not consist entirely of myelinated fibers, but, as is shown in figure 8, it contains also very large numbers of unmyelinated axons. These are grouped in small bundles which lie among the myelinated fibers. The distribution of the three kinds of fibers, large myelinated, small myelinated, and unmyelinated, is not uniform throughout the cross-section. The large myelinated fibers are much more numerous in some parts of the field than in others (fig. 5). They also show a tendency to be arranged in bundles which are separated from each other by the small myelinated fibers. Now it is in and about these bundles of large myelinated fibers that the greatest number of the unmyelinated axons are found. The grouping of these with the large myelinated sensory fibers suggests that they also may be afferent in function. The data thus

far presented would not exclude the possibility that these unmyelinated fibers might be preganglionic fibers that had lost their myelin sheaths, but in the paper which follows we will present evidence to show that they are afferent fibers and arise from the cells in the spinal ganglia.

Since there are few large myelinated and unmyelinated fibers

Fig. 8 A part of a section through the tenth thoracic internodal segment in the cat. Pyridine silver. $\times 425$.

in the sympathetic trunk below the stellate ganglion and practically none in the cervical part of the trunk, we must conclude that the sensory fibers which reach the stellate ganglion by way of the first three white rami run out again through the branches of the stellate or the inferior cervical ganglion. These branches have been studied in only one cat. The cardiac branch of the stellate ganglion, while consisting chiefly of unmyelinated fibers, contained a somewhat larger number of myelinated fibers than

the internal carotid nerve. These were all under 4.5μ except two, which measured 6μ . Large myelinated fibers were found in both limbs of the subclavian ansa which joined to form a single trunk just below the middle cervical ganglion. A cardiac branch given off by the trunk in this position contained a considerable number of fibers between 4.5 and 7μ . We counted forty-eight that measured approximately 6μ . Aside from the presence of these larger fibers, this nerve had the same structure as the cardiac branch of the stellate ganglion. These observations indicate that the large myelinated fibers pass through the stellate ganglion, run in both limbs of the ansa, and leave through the cardiac branch coming from the middle cervical ganglion or from the ansa subclavia. This is in keeping with the work of Edgeworth ('92), who found that the large myelinated fibers in the dog could be followed in the stellate ganglion through the ansa subclavia and middle cervical ganglion, whence they were distributed to the heart and lungs. This question deserves thorough study. As is indicated in figure 4 B, the sensory fibers from the lower eight thoracic rami run downward in the trunk and out through the splanchnic nerve. In the segments just below the stellate ganglion there are few large myelinated and unmyelinated sensory fibers, as is indicated in the diagram by the dotted line.

THE GREATER SPLANCHNIC NERVE

At another time we expect to take up the more detailed consideration of all the splanchnic nerves of the cat, but the present paper would not be complete without some account of the structure of the first and largest of the series, the greater splanchnic nerve. A study of serial sections through the trunk at the point of origin of this nerve shows clearly that it is formed by the separation of a large part of the oval well myelinated fascicle from the rest of the trunk. The nerve has the same structure as this oval fascicle and consists of large and small myelinated and unmyelinated fibers in the same proportion and with the same arrangement as in that fascicle.

Usually in pyridine silver preparations it is possible to see that there are somewhat larger accumulations of unmyelinated fibers near the periphery or directly under the perineurium. These do not constitute well-defined fascicles such as one would expect to find if any large number of postganglionic fibers were present. They are probably of the same nature as those scattered through the nerve.

In two out of ten normal greater splanchnic nerves examined we found evidence of postganglionic fibers in the form of a well-defined and fairly good-sized fascicle composed chiefly of unmyelinated fibers. Preparations of the first lumbar segment of the sympathetic trunk and the greater splanchnic nerve taken

Fig. 9 Diagram of the upper lumbar portion of the sympathetic trunk of a cat in which there was an accessory ganglion at the origin of the greater splanchnic nerve. XIII. W., white ramus to the XIII thoracic nerve; I. G., gray ramus to the I lumbar nerve; I. W., white ramus of the I lumbar nerve; II. G., gray ramus to the II lumbar nerve.

from Cat 8 were especially instructive. Figure 9 shows that in the first lumbar segment of the trunk there was a ganglion, not connected with the spinal nerves by rami, located at the point of origin of the greater splanchnic nerve. The entire portion of the sympathetic trunk shown in the figure was cut in serial sections. A study of these sections shows that no branches, even of microscopic size, are given off from the trunk at the level of this ganglion except the splanchnic nerve. As this nerve leaves the trunk it carries with it a rather large bundle of peripherally placed unmyelinated fibers which closely resembles the crescentic area described in the trunk. It seems probable that this unusual bundle of fibers takes origin from the cells in this aberrant ganglion.

The observations so far recorded lead one to conclude that the greater splanchnic nerve is composed chiefly of preganglionic

autonomic fibers and visceral afferent fibers. In the majority of the specimens studied (eight out of ten) it was not possible to demonstrate any group of fibers that could be identified as post-ganglionic. We shall see that these conclusions agree with those of Langley. The statements which appear in the citation below will be found scattered through several pages of text (Schäfer's *Physiology*, vol. 2, pp. 644, 646, 648):

By dissection, it is easy to see that a large proportion of the splanchnic nerve fibers arise from the white rami communicantes, running in the sympathetic chain for a variable distance. In the cat and dog the fibers of the great splanchnic nerve can be traced upwards in the sympathetic chain as far as the sixth thoracic ganglion. And there is good reason to believe that all the splanchnic fibers are the direct continuation of the fibers of the white rami. It can easily be shown in the rabbit that the very great majority of the fibers running from the spinal cord to the abdominal viscera end in the prevertebral ganglia. After injection of a small amount of nicotine in the rabbit, the nerve roots, the splanchnics proper, and the inferior splanchnics have either no effect or a mere trace on the blood vessels or abdominal and pelvic viscera; but all the normal effects can be readily obtained by stimulating the fibers given off by the prevertebral ganglion. It has long been known that the major splanchnic contains a considerable number of non-medullated fibers, and it is in large part this fact which has led to the unquestioned belief that the ganglia of the sympathetic chain send fibers to the solar ganglia or to the abdominal viscera. If, then, the view which I have given above be accepted, namely, that very few if any fibers pass from the cells of the vertebral ganglia to the splanchnic nerves, we must take the non-medullated fibers to be preganglionic fibers which have lost their medulla.

According to Langley, the majority of the efferent fibers of the greater splanchnic terminate in the solar ganglion, though a few may pass on to more distal ganglia. He also admits the possibility that occasionally a few postganglionic fibers arising from cells in the ganglia of the trunk may run through the splanchnic to the coeliac plexus. The physiological experiments on which his conclusions are based are found in the papers by Langley and Dickinson ('89), Langley ('96 b), and Bunch ('97).

It will be seen that our histological results are in agreement with those obtained by physiological experimentation. We have seen reason to believe that the unmyelinated fibers in the splanchnic which Langley thought might be preganglionic fibers that had lost their sheaths, are instead afferent fibers. More convincing

evidence on some of these points will be presented in the paper which follows.

CONCLUSIONS

We shall make no attempt to summarize the detailed observations presented in the preceding pages, but will merely state a few general conclusions that seem warranted by the facts already given.

The segmental character of the sympathetic trunk is evident in its ganglia and gray rami. The fibers of each gray ramus arise chiefly, and sometimes exclusively, from the cells of its own segmental ganglion and are distributed through its associated spinal nerve. When two or more segmental ganglia are fused together the resulting compound ganglion gives rise to gray rami running to the corresponding spinal nerves. Except for compound ganglia like the cervical and stellate, the ganglia of the trunk are best designated by the number of the spinal nerve with which their gray rami are associated. The white rami have a restricted origin from the first thoracic to the fourth lumbar spinal nerves, inclusive, and their fibers are distributed through the sympathetic trunk to ganglia at higher and lower levels. A white ramus is in no special sense associated with its own segmental ganglion.

The gray rami contain in addition to the unmyelinated also a few, mostly fine, myelinated fibers. The latter are for the most part postganglionic. No preganglionic fibers run from the spinal cord to the sympathetic ganglia by way of these rami.

The white rami consist of myelinated fibers ranging from 1.5 to 13 μ , though fibers of more than 10 μ are rare except in the first two white rami and most of the large fibers have a diameter of about 6 or 7 μ . The majority of the myelinated fibers are small, measuring 1.5 to 3.5 μ . Most of these are preganglionic. The afferent components include myelinated fibers of all sizes, some of the very smallest as well as those of medium and large size, and also unmyelinated axons. The number of the large myelinated fibers varies greatly in the different white rami. They were found to be most numerous in the seventh to the tenth,

from which they run through the sympathetic trunk and the splanchnic nerves to the viscera.

The sympathetic trunk is to be looked upon as a series of more or less segmentally arranged ganglia bound together by fibers from the white rami. Above the sixth thoracic ganglion these fibers are chiefly ascending, below the tenth descending, but between the sixth and tenth both ascending and descending fibers are present. In addition to these fibers from the white rami, which make up the larger part of the cross-section of the trunk in the form of a large well myelinated oval field, there is also present throughout the thoracic sympathetic trunk a small well-defined bundle consisting chiefly of unmyelinated fibers. This in cross-sections appears flattened out like a crescent against the larger oval well myelinated field. Some of the fibers in the crescentic field are postganglionic, ascending or descending to reach adjacent gray rami. Others may be preganglionic fibers that have passed through one or more ganglia, giving off collaterals and losing their myelin sheaths.

In the upper part of the thoracic sympathetic trunk the oval well myelinated field is composed almost exclusively of fine myelinated preganglionic fibers, with very few large myelinated and unmyelinated afferent fibers. In the lower thoracic segments there are in addition to the preganglionic components also afferent fibers, both myelinated and unmyelinated, which increase steadily in number from the sixth internodal segment toward the origin of the greater splanchnic nerve.

The greater splanchnic nerve of the cat usually leaves the trunk at or just below the level of the thirteenth thoracic ganglion. It is formed by the separation of a large part of the oval well myelinated fascicle from the rest of the sympathetic trunk and is composed of fine myelinated preganglionic fibers, destined to end in the coeliac ganglion, and of both myelinated and unmyelinated afferent fibers. Occasionally it also contains a bundle of postganglionic fibers arising from cells in ganglia of the sympathetic trunk.

LITERATURE CITED

- BIDDER AND VOLKMAN 1842 Die Selbständigkeit des sympathischen Nervensystems. Leipzig, 1842.
- BUNCH, J. L. 1898 On the origin, course and cell-connections of the visceromotor nerves of the small intestine. *Jour. Physiol.*, vol. 22, p. 357.
- EDGEWORTH, F. H. 1892 On a large-fibered sensory supply of the thoracic and abdominal viscera. *Jour. of Physiol.*, vol. 13, p. 261.
- GASKELL, W. H. 1886 On the structure, distribution and function of the nerves which innervate the visceral and vascular systems. *Jour. Physiol.*, vol. 7, p. 1.
- LANGLEY, J. N., AND DICKINSON, W. L. 1889 On the local paralysis of peripheral ganglia, and on the connection of different classes of nerve fibers with them. *Proc. Roy. Soc. London*, vol. 46, p. 423.
- LANGLEY, J. N. 1891 a On the course and connections of the secretory fibers supplying the sweat glands of the feet of the cat. *Jour. of Physiol.*, vol. 12, p. 347.
- 1891 b Note on the connection with nerve-cells of the vasomotor nerves for the feet. *Jour. of Physiol.*, vol. 12, p. 375.
- 1892 a The origin from the spinal cord of the cervical and upper thoracic sympathetic fibers, with some observations on white and gray rami communicantes. *Phil. Trans. Roy. Soc. London*, vol. 183, p. 114.
- 1892 b On the larger medullated fibers of the sympathetic system. *Jour. of Physiol.*, vol. 13, p. 786.
- 1894 The arrangement of the sympathetic nervous system, based chiefly on observations upon pilo-motor nerves. *Jour. of Physiol.*, vol. 15, p. 176.
- 1896 a Observations on the medullated fibers of the sympathetic system and chiefly on those of the gray rami communicantes. *Jour. of Physiol.*, vol. 20, p. 55.
- 1896 b On the nerve cell connection of the splanchnic nerve fibers. *Jour. of Physiol.*, vol. 20, p. 223.
- 1900 The sympathetic and other related systems of nerves. Schäfer's *Physiology*, vol. 2, p. 616.
- 1903 a The autonomic nervous system. *Brain*, vol. 26, p. 1.
- 1903 b Das sympathische und verwandte nervöse Systeme der Wirbeltiere. *Ergebn. d. Physiol.*, vol. 2, p. 818.
- MÜLLER, R. L. 1909 Studien über die Anatomie und Histologie des sympathischen Grenzstranges, insbesondere über seine Beziehungen zu den spinalen Nervensysteme. 26. *Kongr. innere Med.*, Wiesbaden, p. 658. *Ref. in Jahres. Anat. u. Entwick.*, vol. 15, III, p. 731.