

SYMPATHETIC ELEMENTS IN THE CRANIAL AND SPINAL GANGLIA

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I. MATERIAL AND METHOD¹

THIS work is based on an anatomical examination of the cranial ganglia and their connections in all classes of vertebrates. The greatest variations were found in Mammals. In the present paper I shall refer only to such of my anatomical results as are essential for the interpretation of the histological part of my research.

Fresh human ganglia and those of different Mammals were examined by a new method, consisting essentially of subjecting series of sections to osmic acid for prolonged periods:

- (1) Fixation in 10 per cent. formol (4 per cent. formaldehyde) 24 hours.
- (2) Washing in distilled water 24 hours, shaking the water three or four times.
- (3) 1 per cent. osmic acid 5–8 days. The quantity of the solution must be adequate. The glass must always be thoroughly and carefully cleansed, otherwise the osmic acid will be reduced. The vessel must be slowly turned at least three to four times daily, otherwise the material will not be adequately exposed to the influence of the osmic acid.
- (4) Wash in distilled water 12–24 hours. The water must be slowly shaken with the material three or four times. Insufficiently washed materials contain osmic acid in the intercellular tissue, which will be reduced in the alcohol and produce a black precipitate.
- (5) Alcohol series (30–50–70–96 per cent., etc.).
- (6) Embedding into celloidin-paraffin (Apáthy's method). Careful double (celloidin-paraffin) embedding prevents shrinkage. Shrunken cells are useless for this study, both form and colour are influenced by shrinkage. I used for dehydration with good results 3–5 per cent. carbolic acid upward to the 96 per cent. alcohol (modified method of Barta).
- (7) Cut complete series of sections.
- (8) Some of the slides to be counterstained with eosin.

¹ The research was done in the Anatomical Department of University College, London, and in the Prosectorium of the Zoological Gardens (London), and I wish to express my thanks to Prof. Elliot Smith and Dr Zuckerman, as well as to Mr F. Pittock who made the microphotographs.

II. DESCRIPTION OF THE PREPARATIONS

By the prolonged osmic acid method two types of nerve cells can be differentiated in the cranial ganglia. Form, size and coloration of the two types are clearly distinct.

Type I (fig. 1, *a*) is apolar (or unipolar), the cell body (protoplasm) is pale with very fine granules; the size (diameter) is different (smaller or larger), the nucleus is uncoloured.

Type II (fig. 1, *b*) is always multipolar, the cell body (protoplasm) is dark (black), the granules are larger than in type I. Even the small forms of type I can easily be differentiated from type II.

To determine the two types I examined by my method different sensory and sympathetic ganglia. In human spinal ganglia (fig. 2) I found a great majority of type I (*a*) and scattered amongst the large pale cells single ones of type II. About the same proportion is found in the Gasserian ganglion of Man and Mammals (fig. 3).

In the sympathetic ganglia of Man (fig. 4) and different Mammals (monkeys and pigs), I found uniformly only small, dark, multipolar cells (type II). There were many unmyelinated bundles and fibres originating from ganglia with cells of type II. In my comparative anatomical study I often found that sensory and sympathetic nerves meet in the same ganglion (figs. 9 and 10). These three circumstances led me to the conclusion that the cells of type I are sensory elements, and that those of type II are sympathetic.

The different cranial ganglia are composed of different combinations of these two elements.

(1) CILIARY GANGLION (fig. 1)

Cells of the two types are represented by about the same numbers. The cells of type I (sensory) generally lie close to one another, those of type II (sympathetic) are in this as in the other ganglia usually scattered.

The proportion of the two types may be different in animals. In *Cercopithecus* (fig. 5) for instance the dark (sympathetic) cells form the great majority. I also found in the macaque that one part of the ciliary ganglion contains more sensory, the other part more sympathetic cells. It may be that new embryological investigations will explain these proportional differences¹.

I examined carefully a complete serial section of the roots and branches of the ciliary ganglion in Man and other Mammals. At the same time I studied the topography of this ganglion in different vertebrates.

(*a*) *Relation of the ciliary ganglion to the third nerve*

Like previous authors I found that the ciliary ganglion is situated in the trunk of the third nerve in Reptiles, Birds, and in some Mammals, for example, *Chiromys madagascarensis* (aye-aye), sloth bear (*Melursus ursinus* Shaw), etc.

¹ So far as I know embryological investigations hitherto have not taken cognisance of the two types of the cells described above.

The ganglion generally receives its largest (thickest) root from the third nerve, as in Man. I examined this connection on fresh human materials in serial sections, stained with osmic acid, and found that the trunk of the third nerve contains more thinly myelinated fibres, among the heavily myelinated fibres, than the fourth or sixth nerve. I also found that the ciliary ganglion receives, through the so-called short root exclusively, thinly myelinated fibres from the third nerve.

In my previous investigations¹ I confirmed Gaskell's observation that the thinly myelinated fibres of the anterior spinal roots are all pre-ganglionic, and that their number depends upon the size of the white ramus communicans, by which a spinal nerve is connected with a sympathetic ganglion. The larger number of the thinly myelinated fibres in the third nerve depends upon the connection with the ciliary ganglion. It seems that the sympathetic (dark) cells of the ciliary ganglion are in the same connection with the third nerve, as for example a thoracic sympathetic ganglion with the anterior (motor) spinal root of the same segment. It means also, that the short (or motor) root of the ciliary ganglion contains pre-ganglionic fibres. There is no morphological reason to differentiate this connection from the ordinary sympathetic system and call it "parasympathetic." Cells, pre-ganglionic fibres and connection to a motor (third) nerve have the usual sympathetic characters.

(b) *Relation of the ciliary ganglion to the trigeminus and to the sympathetic (carotid) plexus*

The long (sensory) root of the ciliary ganglion consists for the most part of thinly myelinated, with a minority of heavily myelinated, fibres. This agrees with a posterior spinal root. It seems also that the pale (round) cells of the human ciliary ganglion are in the same relation through the long root to the trigeminus, as a spinal ganglion to the posterior root. As I have already demonstrated (fig. 2) the human spinal ganglion also contains dark, multipolar (sympathetic) cells. The real function and connections of these cells is not yet known. Their pre-ganglionic fibres are probably in the posterior spinal roots. As efferent fibres, they should degenerate after section of the root in a direction opposite to that of the sensory (afferent) fibres. Hitherto these fibres have been ignored in the numerous experiments on posterior spinal roots.

The sympathetic root of the human ciliary ganglion contains for the most part unmyelinated fibres associated with a small number of finely and a few heavily myelinated fibres. I found in some cases two or three fine (microscopic) roots of this kind joined to the long root of the ganglion. This is the reason why sometimes, by anatomical dissection, the sympathetic root is not found at all.

¹ Kiss and Mihálik. "Ueber die Zusammensetzung der periph. Nerven und den Zusammenhang zwischen Morphologie und Funktion der periph. Nervenfasern." *Zeitschr. f. Anat. u. Entwicklungsgesch.* Bd. LXXXVIII, H. 2, 1928.

Kiss. "The relationship between vagus and sympathetic in the Vertebrates." *J. Anat.* vol. LXVI, p. 153, 1931.

The sympathetic root connects the ciliary ganglion to the fibres and small ganglia of the carotid plexus, and we can regard it as an ordinary inter-ganglionic part of the cranial sympathetic.

(c) *Branches of the ciliary ganglion (ciliary nerves)*

Examining the branches of the ciliary ganglion and its roots in series sections I found in the human ciliary nerves only two kinds of fibres: (1) a great majority of thinly myelinated and (2) a minority of unmyelinated fibres (fig. 6). The unmyelinated fibres form in *Macacus* unstained groups amongst the myelinated fibres (in transverse sections) or occupy (in Man) one side of the nerve (fig. 6, c, c). The ciliary ganglion also sends unmyelinated fibres to the trunk of the third nerve, which are distributed with the branches of this nerve.

On the basis of my previous investigations¹ I regard the thinly myelinated fibres as sensory, the unmyelinated as ordinary sympathetic (motor and secretory) fibres.

It seems that the sensory and sympathetic cells are, in the cranial ganglia, in a special combination which enables them to transfer sensory impulses directly to sympathetic cells and fibres (for example, secretion of tears through irritation of the conjunctiva, etc.).

(2) SPHENO-PALATINE GANGLION

I found in the human spheno-palatine ganglion two kinds of cells: a majority of dark, multipolar (fig. 7, b) and a minority of pale, round cells (fig. 7, a). The latter type is mostly of the smaller form. I found large unmyelinated nerves in the ganglion (fig. 7, c), and many thinly myelinated fibres between the cells.

The same ganglion of *Macacus* (fig. 8) is wholly composed of dark, multipolar cells. If these cells alone form the ganglion, they are dispersed in its stroma. The pale, round sensory cells, usually lay close to one another (fig. 1, a).

In my comparative anatomical study I found in different animals (figs. 9, 10) that the sympathetic trunk is continued above to the superior cervical ganglion, directly into the spheno-palatine ganglion. Very often in various animals this is enclosed in the palatine and nasal branches of the maxillary nerve. The ganglion is in such cases multiple. Figs. 9 and 10 show anatomically the meeting of sensory and sympathetic nerves in the ganglion.

The sympathetic trunk, which in the llama and in the tree kangaroo connects the superior cervical ganglion with the spheno-palatine ganglion, is represented in Man by the major superficial petrosal nerve (fig. 11, I). This nerve contains myelinated (d) and unmyelinated (c) fibres. The unmyelinated fibres connect the geniculate ganglion (fig. 16) with the spheno-palatine ganglion. The major superficial petrosal and the Vidian nerve are homologous to an inter-ganglionic part of the great sympathetic. The Vidian nerve also receives

¹ *Loc. cit.*

many unmyelinated fibres through the deep petrosal nerves (from the carotid plexus).

(3) OTIC GANGLION

This is one of the largest cranial ganglion. It is enclosed in the perineurium of the mandibular nerve, and its diameter is larger than the transverse section of the nerve (fig. 12).

The human otic ganglion is composed exclusively of small, dark, multipolar (sympathetic) cells. Many unmyelinated nerves are connected with this ganglion (fig. 13, c, c). They proceed to different organs, or join different branches of the mandibular nerve. The minor superficial petrosal nerve (fig. 11, II) contains myelinated and unmyelinated fibres. It represents an inter-ganglionic connection between the otic and the petrous ganglion of the ninth nerve (fig. 19), which also contains dark (sympathetic) cells.

The otic ganglion of the cat (fig. 14) is mixed; the majority of the cells belong to the round, pale (sensory) type.

In other animals the ganglion is subject to a wide range of variation. It seems that the proportions of sensory and sympathetic elements may be very different in the different families. Experimenters on living animals should not neglect these differences.

(4) SUBMAXILLARY GANGLION

I always found that the human submaxillary ganglion (fig. 15) contains exclusively dark, multipolar (sympathetic) cells. These are scattered in the stroma, as in an ordinary sympathetic ganglion. The human submaxillary ganglion is in fact an ordinary local ganglion.

(5) GENICULATE GANGLION

In the human geniculate ganglion (fig. 16) only dark, multipolar cells were found. These cells lay separated in the stroma. There are a few cells in fig. 16, which look rather pale than dark, but these are multipolar too.

This ganglion of *Cercopithecus* (fig. 17) contains both dark and pale cells. The cells generally lay closer than in Man.

(6) GANGLIA OF THE NINTH NERVE

The jugular ganglion of the ninth nerve in Man contains, mostly multipolar, dark (sympathetic) cells (fig. 18). The petrous ganglion of *Nasua* (fig. 19) contains a majority of round, pale (sensory) cells. The two ganglia of the ninth nerve are often united in different animals, or one of these ganglia is represented only by cells in the trunk of the nerve without any gangliform enlargement.

(7) THE GANGLIA OF THE TENTH NERVE

The ganglion of the root (jugular ganglion) of the human vagus nerve (fig. 20) contains a great majority of multipolar, dark (sympathetic) cells which lay scattered in the stroma. The kind of fibres which connect this ganglion to

other nerves (facial and spinal accessory), and to other ganglia (petrous and superior ganglion of the sympathetic), I have not yet investigated.

I found a very interesting section in *Nasua* (fig. 21). The preparation shows the lower end of the jugular ganglion (with sympathetic and sensory cells). Close to the ganglion is a nerve with mostly unmyelinated fibres (*c*). The spinal accessory has two parts, one of them (*d*₁), which lies close to the vagus, is composed mostly of thinly myelinated fibres. This is the internal branch of this nerve. The other portion (*d*₂) is composed principally of heavily myelinated fibres. This is the external (motor) branch of this nerve.

The ganglion of the trunk (ganglion nodosum) is different from the previous ganglion. It is more like a spinal ganglion (fig. 22). The round, pale cells (*a*), which form the great majority, lie close to one another. The single, multipolar, dark cells (*b*) are dispersed among the pale cells.

The ganglion nodosum of *Cercopithecus* (fig. 23) agrees with that of Man. The same ganglion of the pig (fig. 24) very distinctly shows the two types (*a* and *b*) of cells. The vagus, therefore, receives unmyelinated fibres not only through the anastomoses with the cervical sympathetic, as I claimed in my previous paper on this subject ("Le rapport entre le pneumog. et le grand symp." 1931), but also from the sympathetic cells of its own ganglia.

III. DISCUSSION OF THE LITERATURE

The multipolar, dark cells of some cranial and spinal ganglia are mentioned in the literature under different names. Some writers described them as pathological or senile forms of the ganglionic cells, others regarded them as argyrophyl cells. They represent one of the eleven groups of Dogiel. Some of the authors saw single multipolar cells and described them as sympathetic, but no author and no method described and demonstrated them as systematically and distinctly as I have attempted to do in the present paper.

Tangential sections of type I or type II may give the appearance of intermediate forms, but serial sections always prove that these forms belong either to type I or type II. This is the explanation of the intermediate cells of some authors.

Most writers describe the cranial ganglia as homologous to the spinal ganglia, but several authors found single multipolar cells in this or in that ganglion. Thus G. Retzius (1880), His (1888-90), F. Martin (1890) and M. Lenhossék (1893) described the geniculate ganglion as a real spinal ganglion of the intermedius nerve. Gaskell (1889) thought that the ganglion nodosum is a sympathetic ganglion; Van Gehuchten (1897) regarded the same ganglion as analogous to the spinal ganglion. In this communication it has been shown that we cannot generalise as to the nature of any cranial ganglion.

Disse (1893) found multipolar cells in the spinal ganglia of frog embryos. M. Lenhossék (1893) found multipolar cells in the spinal ganglia of chick embryos. He described the processes of these cells as dendrites. Lenhossék also

examined the spinal and cranial ganglia of Mammals, but he could not find multipolar cells in them. Van Gehuchten agreed with Lenhossék. Ramón y Cajal (1893) also saw multipolar cells in the spinal ganglia of chick embryos. He described the processes as short dendrites which later disappear through a regressive metamorphosis. Retzius (1894) described multipolar cells in the spinal ganglia of the rat and of snakes (*Ophidia*). Kölliker (1896) illustrates in his manual a multipolar cell from the Gasserian ganglion of the calf. Spirias (1896) found, by means of Golgi's method, multipolar cells in the spinal ganglion of Mammals. Dogiel (1896) described multipolar cells in the spinal and Gasserian ganglia of the dog, cat, rabbit and guinea-pig. Huber (1896), described the same cells in the tortoise (*Chelydra*) and in chickens. Van Gehuchten (1897) found multipolar cells in the 10 cm. embryos of the snake (*Tropidonotus natrix*), Dogiel (1898) in the spinal ganglia of Man and other Mammals, Retzius (1898) in embryos of the chicken, rabbit and snake. Barratt (1898) regarded the two ganglia of the vagus as similar to one another ("The cells of the two ganglia were not obviously distinct in character," p. 426). Cannieu (1898) described multipolar cells in the cranial ganglia of different mammals.

Herrick (1899) illustrates in his monograph how the sympathetic crosses over the cranial nerves in fishes, which I also described in the cod (*Gadus*). Comparative anatomical studies like these show distinctly that the cranial part of the sympathetic is in immediate connection with many cranial nerves and ganglia. This relation is clearly illustrated in a teleostean fish (*Uranoscopus scaber*) by J. Z. Young (1931). Holmgren (1899), found multipolar cells in the spinal ganglia of another teleostean (*Lophius piscator.*), Levi (1903, 1906) in tortoises and selachians. Ramón y Cajal (1906) again described multipolar cells in the sensory ganglia of adult Man, donkey, horse and cattle, without the physiological characteristics of these cells. Nageotte (1907) found the same cells in transplanted spinal ganglia of the rabbit; he regarded them as transformed unipolar cells. Lenhossék (1907) found, in the human spinal ganglia, cells which had multiple axons (Cajal's method). Marinesco, Parhon and Goldstein (1908) found by the silver method of Cajal three different types of multipolar cells in the ciliary ganglion of Man, monkey and dog. The authors suggested the sympathetic nature of this ganglion. Dogiel (1908) regarded the multipolar cells in the spinal ganglia as embryonic forms, which later replace the old cells. Takeda (1924) found, in the Gasserian ganglion of cattle, several multipolar cells. He regarded the processes partly as dendrites, partly as axons.

This list of investigations reveals how individuals of the numerous multipolar (dark) cells emerged through the silver and methylene-blue methods, but none of the above-mentioned authors by these methods, and on the basis of isolated, and not serial, preparations was able to obtain a general view of the multipolar (sympathetic) cells in the cranial and spinal ganglia.

Riquier (1914) found that the otic ganglion of cattle and of Man is similar to a sympathetic ganglion.

It is more interesting to follow some clinical and experimental observations in recent literature.

Stewart and Lambert (1930) found that pain or circulatory and secretory troubles of the nasal cavity are dependent upon the sphenopalatine ganglion. Anaesthesia, or extirpation of this ganglion, helped in many cases. It was also observed that the disturbed function of the sphenopalatine ganglion was in relation with sympathetic diseases of other organs, for example, the stomach. These observations suggest the sensory and sympathetic characters of this ganglion.

Yungoro Takagi (1931) cut the posterior spinal roots in cats. Like other authors he obtained very contradictory results. He often found that many fibres were not degenerated in the central portion of the operated posterior root. Like previous writers he came to the conclusion that the posterior root contains efferent fibres. These efferent fibres are, according to my investigations, most probably the pre-ganglionic fibres of the sympathetic cells in the spinal ganglia.

Ken Kuré (1928-31) published, with his fellow-workers, a series of experiments on dogs. They made radicotomies on the posterior spinal roots, and found numerous thinly myelinated fibres in the central stump without degeneration. These are called by Kuré "spinal parasympathetic nerves." The authors do not mention any sympathetic cells in the spinal ganglia. The undegenerated fibres are probably simple pre-ganglionic fibres. There is no reason for the supposition of a "spinal parasympathetic" system. Kuré and his fellow-workers impute to this system tonic, trophic, vaso-dilatory, stimulating and vaso-constrictory functions. The suppositions of these authors only increase the great confusion about the morphology and physiology of the vegetative nerves.

S. W. Ranson and H. K. Davenport (1931) published a paper on the "Sensory unmyelinated fibres in the spinal nerves." They extirpated in cats the lumbar and sacral part of the sympathetic trunk. Thirty-nine to eighty-four days after the operations they still found unmyelinated fibres in the saphenous nerve and in a motor branch of the femoral nerve. They call them "sensory unmyelinated fibres." The authors do not mention the sympathetic cells in the spinal ganglia; the unmyelinated fibres (of Ranson and Davenport) are probably the simple post-ganglionic fibres of the sympathetic cells in the spinal ganglia. The supposition that the sympathetic has some (sensory) function, other than effective (motor or secretory), only adds another great element of confusion to the literature of the vegetative nervous system.

F. Rossi (1931) found in human embryos multipolar cells in the central portion of the rami communicantes of the lumbar and sacral region. He regards them as small sympathetic ganglia and describes them as different from the "microsympathetic, hypospinal ganglia" of Marinesco and Minea (1908).

It is a common phenomenon to find in the cranial ganglia that multipolar, dark (sympathetic) cells are located in the central portion of the branches, which contain sympathetic (unmyelinated) fibres (for example ciliary nerves). The ganglia described by Rossi and those described by Marinesco and Minea

are the same groups of cells and they are simple sympathetic cells of the spinal ganglia exposed in the rami communicantes. H. Streckfuss claimed in a recent paper (1931) that the greater splanchnic nerve contains in its roots and trunk many small ganglia. He therefore calls this nerve a splanchnic ganglionated cord.

The sympathetic cells are not located exclusively in the ganglionated cord, but partly in their embryonal places in the cranial and spinal ganglia. There is, as yet, no morphological evidence that all the local ganglia of the organs are not common sympathetic elements.

IV. SUMMARY

1. The prolonged osmic acid method differentiates two types of cells in the cranial and spinal ganglia.

2. Cytological characters, histological circumstances (unmyelinated branches) and comparative anatomical evidence prove that the multipolar, dark, small cells (type II) are sympathetic, the round, pale and generally larger cells (type I) are sensory.

3. The human ciliary, sphenopalatine, Gasserian and both ganglia of the ninth and tenth nerves are composed of sensory and sympathetic cells.

The otic, submaxillary and geniculate ganglia in Man contain only sympathetic cells.

4. The proportions of the sensory and sympathetic cells in the same ganglion are also variable in the different Mammals.

5. Human spinal ganglia also contain a few sympathetic cells.

6. Sympathetic cells emigrate, not only between the second dorsal and fourth lumbar segments (Gaskell), but also through the cranial ganglia.

7. There is no morphological foundation for the supposition of a cranial "parasympathetic system." The cranial parasympathetic of literature is a part of the cranial sympathetic.

8. The ganglia of the cranial sympathetic are in the same relation to the cranial nerves (through communicating branches) as the ganglia of the great sympathetic to the spinal nerves.

9. The terminal member of the cranial sympathetic is the ciliary ganglion. The ganglia of the cranial sympathetic are linked together through interganglionic fibres, like the ganglionated cord.

10. The mixed (sensory and sympathetic) ganglia may be the transformers of sensory (centripetal) affects into vegetative (centrifugal) effects; for example, irritation of the cornea, secretion of the lachrymal gland, etc.

11. The effective (centrifugal) fibres of the posterior spinal roots, "spinal parasympathetic" of Ken Kuré, are at least partly pre-ganglionic fibres of the sympathetic cells in the spinal ganglia. The "sensory unmyelinated fibres" of Ranson and Davenport are simple post-ganglionic fibres of the same cells.

12. My investigations afford no evidence for the existence of a "cranial parasympathetic."

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EXPLANATION OF PLATES

(Microphotos of the same magnification.)

PLATE I

- Fig. 1. Ciliary ganglion of Man.
- Fig. 2. Fourth spinal thoracic ganglion of Man.
- Fig. 3. Gasserian ganglion of Man.
- Fig. 4. Thoracic sympathetic ganglion of Man.
- Fig. 5. Ciliary ganglion of *Cercopithecus*.
- Fig. 6. Ciliary nerves of Man. I=transverse, II=longitudinal section.
- Fig. 7. Sphenopalatine ganglion of Man.
- Fig. 8. Sphenopalatine ganglion of *Macaca*.

PLATE II

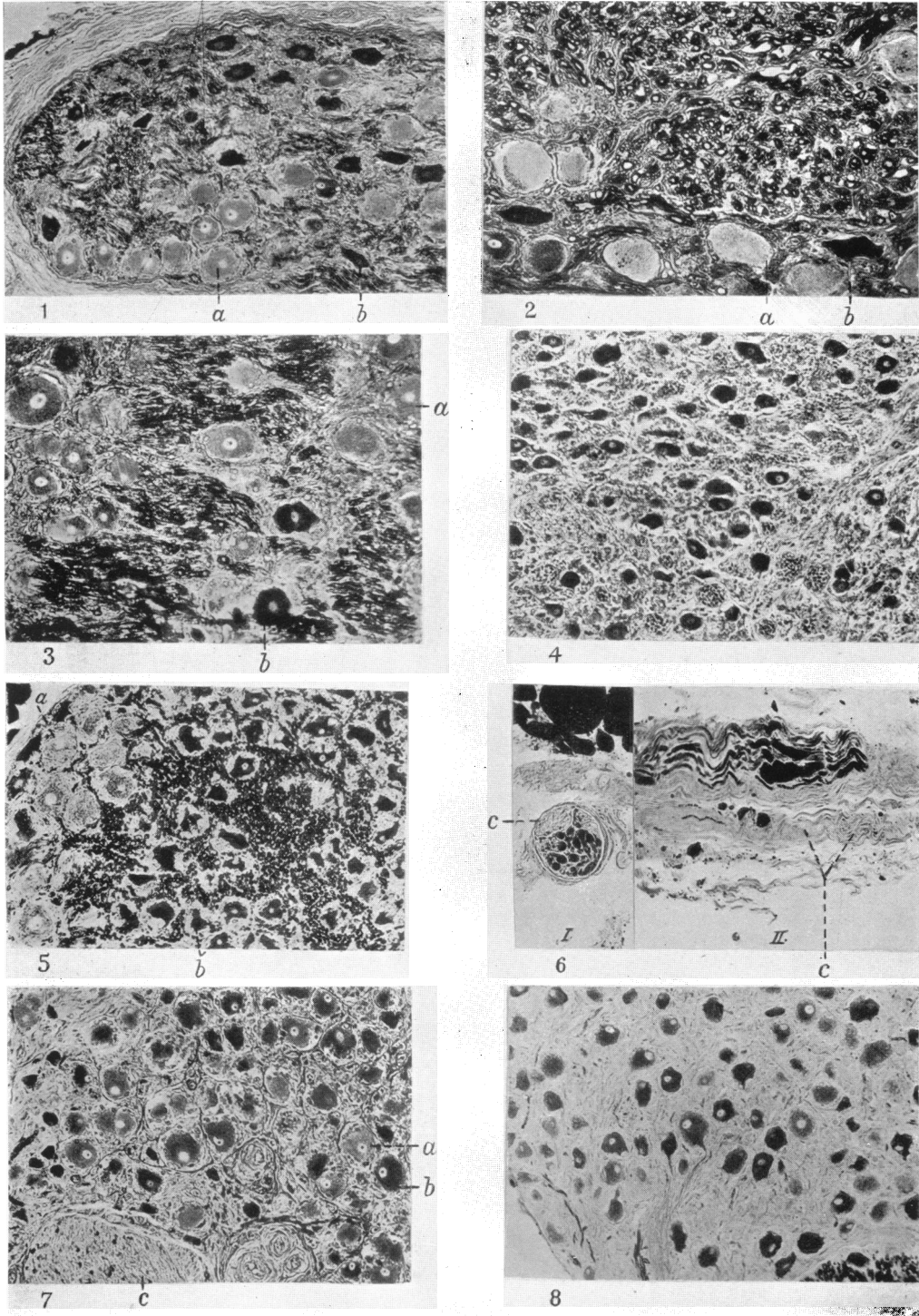
- Fig. 9. Llama: roots of the sphenopalatine ganglion.
- Fig. 10. Tree Kangaroo: roots of the sphenopalatine ganglion.
- Fig. 11. Superficial petrosal major (I) and minor (II) nerves of Man.
- Fig. 12. Otic ganglion of Man (transverse section with mandibular nerve).
- Fig. 13. Otic ganglion of Man.
- Fig. 14. Otic ganglion of cat.
- Fig. 15. Submaxillary ganglion of Man.
- Fig. 16. Geniculate ganglion of Man.

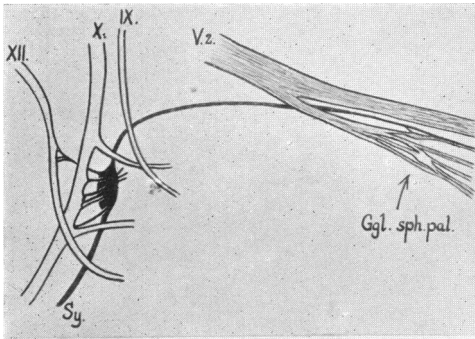
PLATE III

- Fig. 17. Geniculate ganglion of *Cercopithecus*.
- Fig. 18. Jugular ganglion of the ninth nerve in Man.
- Fig. 19. Petrous ganglion of the ninth nerve in *Nasua*.
- Fig. 20. Jugular ganglion of the tenth nerve in Man.
- Fig. 21. Jugular ganglion of the tenth nerve in *Nasua*.
- Fig. 22. Ganglion nodosum vagi of Man.
- Fig. 23. Ganglion nodosum vagi of *Cercopithecus*.
- Fig. 24. Ganglion nodosum vagi of pig (*Sus scrof. dom.*).

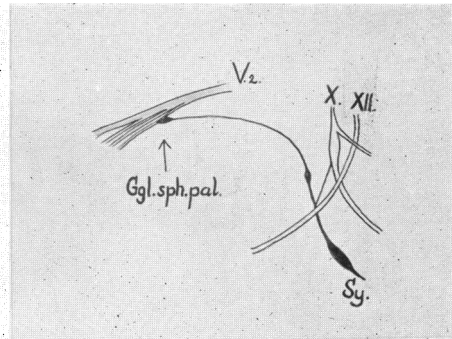
Letters on the figures:

a=sensory, b=sympathetic cells, c=unmyelinated, d=myelinated fibres.

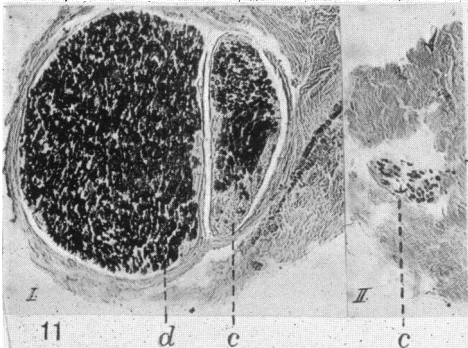




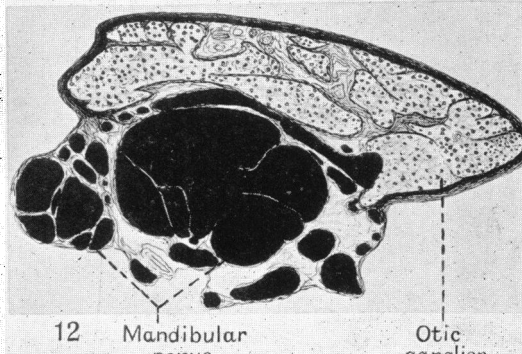
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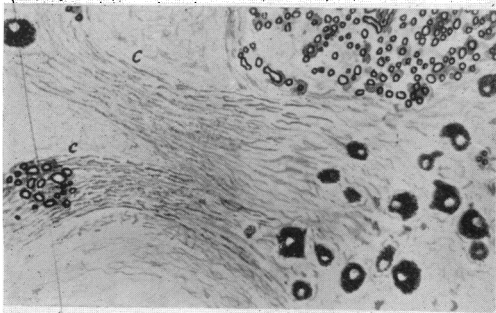
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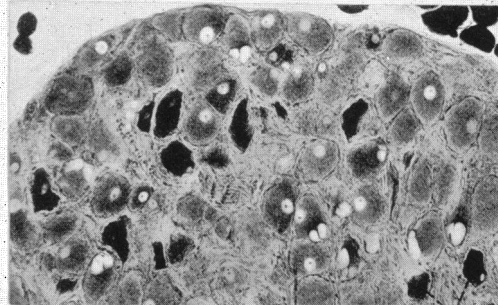
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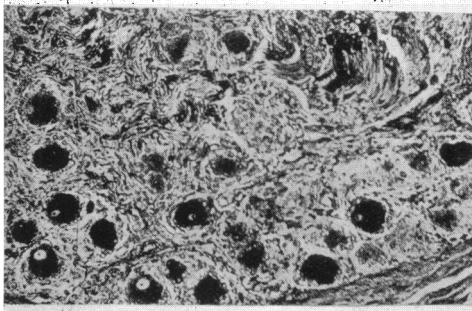
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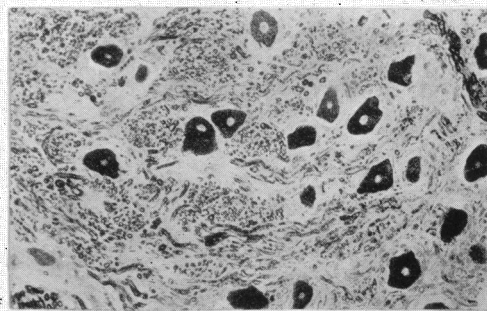
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