THE PROBLEM OF THE INNERVATION OF THE DENTINE

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I. INTRODUCTION

The question as to whether the dentine is supplied with nerve fibres is of great importance to the dental surgeon. In his clinical work he is continually treating carious teeth, in which the dentine is extremely sensitive to pain, and in his efforts to relieve it he is hampered by having no definite information as to its etiology.

This problem has interested workers for many years, and the literature is fairly extensive. In this communication an elaborate description of this literature will not be given, as it has been frequently reviewed in the past. Only the more important papers will be discussed, and several hypotheses, which are now of purely historical interest, will not be considered.

When the more modern views are studied it will be found that they fall into two distinct groups. The members of the first believe that the nerve fibres of the tooth pulp end around the odontoblast cells; those of the second group claim to have traced the nerve fibres into the dentinal tubules.

Retzius, who was one of the earlier advocates of the hypothesis that the fibres terminated among the odontoblasts, published a series of papers (33, 34, 35), in which he described the course of the dentinal nerves in the different classes of the Vertebrates. In every case he used Golgi's stain. In the Fish he found that the nerve fibres branched repeatedly, and finally invested the inner surface of the dentine, giving off free-ending lateral branches. The nerves did not appear to extend to the tip of the pulp. In the Amphibians the arrangement was similar to that in the Fish, except that fibres in the periodontal membrane could be traced as far as the epithelium of the mouth. In the Reptiles fine nerve fibres were given off from the nerve trunks in the middle of the pulp, and ran to its sides and top. They passed through the odontoblast layer and ended in the inner surface of the dentine in knotty points. In the Mammals Retzius had great difficulty in following the nerves to their destination, but finally in the tooth of a young mouse he traced them to their termination, which was similar to that of the Reptiles except that on arriving at the dentinal surface, they ran tangentially for a short distance.

Huber (16) appears to have been more successful with mammalian teeth, for which purpose he used the pulps of rabbits' teeth stained with Ehrlich's *intra-vitam* methylene blue. He states that when the nerves approach the

surface of the pulp they lose their medullary sheaths, divide repeatedly, and form a network under the odontoblasts, but the individual fibres do not anastomose. From this network fibres pass between the odontoblasts to end in the manner described by Retzius.

Professor Hopewell-Smith, the leading British advocate of this school, published, as far back as 1894 (8), a paper in which he put forward the idea, that the dentine is formed by small round cells, and not by the odontoblasts, which, he considered, were solely for the transmission of nervous impulses. At that time he was unable to establish any connection between the nerve fibres and the odontoblasts. In 1903 (9) he was able to describe such a connection, for he says that the nerve fibres of the pulp "terminate in a basket-work of varicose fibres, embracing and often closely attached to the cell walls of the individual odontoblasts." Since that time Hopewell-Smith has apparently seen no reason to alter his views on this subject, and has been a strong antagonist of the views of Mummery, to be described later, as can be seen by consulting different papers written by him during the last few years (10–14). Other authorities who consider that the nerve fibres end in association with the odontoblasts are Hoehl (7), Walkoff (38, 39), Fischer (4), Noyes (32), and Gysi (6).

The hypothesis that the nerve fibres actually enter the dentine has had numerous adherents since the time of Boll (1), in 1868; among the more prominent are Dependorf, Mummery, and Carol Montfort.

Dependorf (2, 3), found that the non-medullated nerves formed a sub-odontoblastic plexus, and then passed through the odontoblasts in the most diverse manner, giving off lateral branches to the cells. Near the dentinal margin their course became straighter. Using Lowitz's, Bielschowski's and Held's stains, he found two types of nerve fibres in the dentine; one group in the dentinal tubes had club-shaped endings, the other in the ground substance terminated in a fine plexus at the dentino-cemental margin.

The late Mr J. Howard Mummery, up to the time of his death in the autumn of 1926, was the leading British supporter of the view that the dentine contained nerve fibres. Towards the end of the last century he stained some teeth with iron and tannin, and was able to trace fibres which appeared to be nerves to the dentinal margin, but could not definitely satisfy himself that they entered the dentine (23, 37). In 1910 he re-examined these sections and found that he could now follow the fibres into the dentine (23). A little later he published two papers (24, 26) containing the results of some experiments in which he had stained sections of teeth with Beckwith's gold chloride; his conclusions were as follows: "The nerves of the dental pulp lose their medullary sheaths, and neurolemma just beneath the odontoblast layer, and are seen to form an intricate plexus of neuro-fibrils in this situation, the plexus of Raschkow; from this plexus they pass in approximately straight lines between and around the odontoblast cells and form another much narrower plexus at the inner margin of the dentine, which I have called the 'marginal plexus.'

They very closely envelop the cells and the dentinal fibrils and enter the dentine in company with the latter. They can be traced as fine beaded fibrils all along the tubes and their very numerous branches, and are seen to terminate in the fine ramifications of the dentinal tubes beneath the enamel and cementum."

In a short supplementary paper (25) he announced that he was now able to trace the nerve fibres from the nerve trunk to the dentine without interruption. In 1916 he had some doubts as to the existence of the marginal plexus, as he then stated (27) that it is very small, being formed only by a few of the fibrillae, and that in the most completely reduced specimens nearly all the main fibrils pass directly to the dentine.

In 1919 (28, 29) Mummery found structures interposed in the course of the nerves, which he considered were nerve cells. These were placed in a row along the bases of the odontoblast cells. Fig. 1, which is reproduced from Mummery's *Microscopic Anatomy of the Teeth*, p. 22, shows the connection of the cells with the nerve fibres. There is one point mentioned by the author, which this diagram does not illustrate, which is that the peripheral process of the nerves have a markedly wavy cork-screw-like course. It will be noticed that in the diagram there is no indication of the "marginal plexus," which he described in his earlier papers. Mummery's reasons for omitting it are as follows: "Small enlargements or nodes are seen upon the fibres distributed around the odontoblasts, but are not present in the distal or dental process. It is these enlargements that were considered by Huber, Guido Fischer and others to form the terminations of the nerve fibres of the pulps and which are similar to those shown by Retzius in the mouse, and in fish and reptiles. It is these strongly beaded fibres which I first described as the marginal plexus, but although my first preparations appeared to indicate that the neurofibrils which pass into the dentinal tubes arise from this plexus, the later ones show that this is not the case, for these fibres pass direct to the dentine as the distal processes of the nerve-end cell with which they are continuous. What I had formerly described as the marginal plexus is evidently a portion of the network of fibres surrounding the odontoblasts and extending to the dentine margin; it is derived from the dendritic processes of the nerve cells."

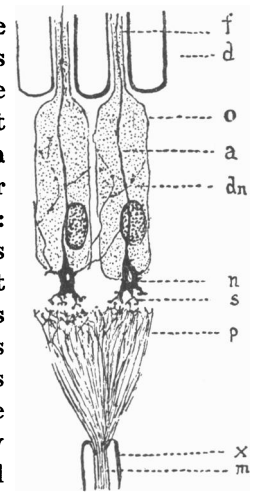

Fig. 1.

The work of Mummery has been dealt with rather fully, as it formed the starting-point of the investigation, a description of which is contained in this paper.

Carol Montfort in 1914 apparently published in a Spanish dental journal, which I have been unable to obtain, the results of some experiments with Bielschowski's stain, by which means he claims to have found nerve cells

within the dental pulp. In 1920(20) and 1923(21) he published two further papers in the *Dental Cosmos*, in which he described an elaborate system of nerves in the pulp cavity.

It consists of

(1) Non-myelinated nerve fibres which end in knotty expansions around the odontoblasts.

(2) Medullated nerves which lose their myelin and end in the plexus of Raschkow.

(3) Sub-dentinal nerve cells, which have two dendrons entering the dentinal tubes.

(4) Nerve cells in the central part of the pulp.

He also claims to have found neuroblasts in the dental follicules of the new-born cat.

It should be noted that Montfort's nerve cells correspond in no way to those of Mummery, which as we saw in fig. 1 had only one process running to the dentine, and which in form, if not in function, resembles an axon fibre.

A serious criticism of Montfort's work is that he relied mainly on Bielschowski's stain, which is uncertain in its actions, so that many of the cells which he thought were of nervous origin were probably only impregnated connective tissue cells.

Among other workers who consider that the dentine is innervated are Fritsch(5), Morgenstern(22), Latham(18), Law(19), Römer(36) and Welling(40).

It will be noticed, from this review of the literature, that those workers who believe that the nerve fibres enter the dentine have given such differing accounts of the arrangement and course of these fibres that it is impossible to reconcile their results with each other. On the other hand, there is no insurmountable difference in the description given by those who consider that the nerve fibres end around the odontoblast cells. This conclusion, however, at least implies that sensory stimuli from the dentine are in the first place conducted along the dentinal fibres of the odontoblasts, and Hopewell-Smith advocated this view. There is a difficulty in accepting such a hypothesis, as the odontoblasts are of mesodermic origin.

From this summary of the results of earlier workers it will be seen that our knowledge of the termination of the dentinal nerves is unsatisfactory. It therefore appeared desirable that a further investigation should be carried out on the subject and with this aim in view I repeated the work of Mummery. The reasons for this choice were:

(1) It was the latest work on the subject and had been very favourably received by a large number of British dental histologists. Professor Hopewell-Smith however had strongly dissented, and written several papers stating his belief that Mummery's conclusions were unsound.

(2) Mummery's description of a special end neurone at the end of a somatic sensory nerve, differed entirely from the conditions found anywhere else in the body. It might be considered that they were end organs of some de-

scription, but during an investigation into the tactile sensibility of the teeth, I found evidence, which has not yet been published, which suggested that the fibres of the pulp carried only painful stimuli, and such nerves are believed to end as branching fibrils.

(3) Mummery's papers were easily accessible and were freely illustrated with very excellent microphotographs, which assisted greatly in comparing his results with my own.

II. HISTOLOGICAL OBSERVATIONS

In this portion of the investigation, the various methods employed by Mummery were carefully followed. In his earlier work in which he claimed to have traced the course of the nerve fibres into the dentine, he used freshly extracted normal human teeth (removed mainly from children who were under orthodontic treatment). These he divided transversely into two parts and then fixed them in formol and afterwards decalcified them in 30 per cent. formic acid. They were cut into sections with a freezing microtome, and finally stained with gold chloride by Beckwith's method. A full account of the technique is given in his original paper (24). As it was by means of this technique that Mummery claimed to have discovered the nerve fibres, and did not advance the hypothesis of the presence of nerve cells in the pulp until a later date, it was considered better to deal with the fibres in the first place and leave the problem of the cells until a later date.

Sections stained by the above method were made and examined. They were found to show, very clearly, the fibres described by Mummery, for these stood out as black lines against the general red background of the pulp. About 250 sections from human teeth were prepared by this method, and in the great majority of cases the fibres were seen.

Fig. 2 illustrates a transverse section from the root of a bicuspid of a female aged 42 and was one of the earliest preparations made. It demonstrates several of the characteristics of these fibres which Mummery noted and described. They run through the odontoblast zone in a direction more or less parallel to the long axis of those cells. In the actual section the odontoblasts are not nearly as conspicuous as in the photograph and are stained faintly pink. The beaded appearance of some of the fibres will be noticed; in the actual specimen a large number of the fibres exhibit this appearance if examined with a sufficiently high magnification. Mummery attached considerable importance to this beading, as being characteristic of non-myelinated nerves. It will be seen that some of the fibres have the markedly wavy course described by their discoverer, and that most of them appear to begin immediately internal to the odontoblasts in the region of Raschkow's plexus, which is not clearly stained in this preparation. Some of the fibres can be traced inwards towards the centre of the pulp; Mummery also noted this, and claimed to have followed some of the fibres to their origin from a medullated nerve; in

none of my specimens was it possible to establish such a connection. At their distal extremity the fibres ended suddenly at the edge of the dentine as if they entered it, but in this specimen none of them could be traced actually into that tissue. The fibres do not give off side branches to the odontoblasts and in some of Mummery's photographs the same lack of branching will be noticed.

Fig. 3 represents a longitudinal section from the crown of an incisor from a female aged 26. In this section the fibres pass through the odontoblast layer and can then be traced into the dentine.

Although the last two sections do not show the sub-odontoblastic plexus, it has been seen frequently. Another feature of the fibres of Mummery which that author noted is their elasticity. During the preparation of specimens it frequently happens that a portion of the pulp is torn away from the dentine, leaving a gap which is often bridged over by some of these fibres. These are seen to be under tension, as they are now quite straight instead of wavy, and the beaded appearance is more conspicuous than usual. The above condition has been seen quite commonly during the present research.

Teeth from the monkey, cat, dog, sheep, hedgehog, rabbit and guinea pig were treated with Beckwith's stain, and Mummery's fibres were found in every case. They showed all the characteristic features seen in man, and therefore require no further description.

The repetition of Mr Mummery's earlier work confirmed the existence of fibres which entered the dentine, and which in many of their histological characters resembled non-myelinated nerves. His statement that they were continuous with the myelinated nerves was not confirmed; neither were any structures resembling nerve cells seen. The next step therefore was to repeat his later work and employ the method of staining with which he claimed to have demonstrated these cells. The technique adapted by that author can be found in his paper on this subject(29) and need not be described in detail here. It consisted essentially of a modification of the original method, so that portions of teeth could be stained in bulk before being sectioned. The teeth were suspended in a 1 in 5000 solution of gold chloride for a week or longer and afterwards reduced in the ordinary Beckwith way.

This technique proved to be very disappointing; out of twenty-six different pieces of teeth which were treated in this way, in only five were sections found which showed the fibres definitely, and in none of these were the details as clearly seen as in those sections which had been treated with Beckwith's stain. None of them contained any structures which even resembled nerve cells.

I had some correspondence, and afterwards an interview, with Mr Mummery on this subject, and he informed me that he had experienced the same difficulty, and that by far the greater part of his preparations were failures. I gathered that only one section (which he kindly allowed me to examine, and afterwards sent on to me at Manchester for a few days) showed the cells

at all clearly. After receiving this information, I carried out some experiments, to see if any modification could be found which would make Mummery's technique more satisfactory. The results of these experiments suggested certain alterations which gave markedly improved results. The strength of the gold chloride solution was increased from 1 in 5000 to 1 in 1000, and was acidulated by the addition of four drops of concentrated hydrochloric acid to every 100 c.c. of the gold solutions. These modifications practically stopped the precipitation of the gold on to the tooth while it was being stained. The portion of tooth being stained was left in the gold solution for three weeks and afterwards treated with the ordinary Beckwith reducing reagents for the following periods:

20 per cent. sodium hydrate	1 hr.
10 per cent. potassium carbonate	24 hrs.
10 per cent. potassium iodide	24 hrs.

The specimens were then sectioned with a freezing microtome, dehydrated and mounted.

By the above technique sections were obtained which closely resembled those obtained by Beckwith's original stain. The fibres were clearly demonstrated, but no nerve cells were found in any of the three hundred sections examined.

Beckwith's and Mummery's stains and the modification of the latter, which I devised, are so closely related, that if nerve cells can be picked out by one method, they ought also to be found with the others, but in no case has this been possible, although 1034 sections were prepared and examined, which showed Mummery's fibres. As mentioned above, I have seen that investigator's preparation in which the cells were found, and after careful examination am of the opinion that they are not nerve cells. Professor Stopford has also examined this preparation, and agrees with my conclusions. As Mummery stated that very complete reduction is required to show these cells, some of the sections stained by Beckwith's method were left for several hours in potassium iodide solution, but the only results were that all the fibres of the pulp became black, and no nerve cells were found.

Other metallic impregnation methods, Bielschowski's and Nabias', were tried; when successful they gave results similar to those described above, but a very much larger proportion of failures was obtained with these stains. With Bielschowski's stain, which had been used by Carol Montfort, no structures resembling those described by that worker as nerve cells were seen.

At that stage it became clear that no further information could be expected from methods depending upon impregnation with gold or silver. They stained fibres which resembled nerves, but on account of the unreliability of these methods, in that they are liable to stain all sorts of tissues, it was impossible to say with certainty that the fibres were of nervous origin.

A variety of other stains were now tried and the results obtained are briefly described in the following paragraphs.

Van Giesen, haemalum and eosin, Weigert's resorcin fuchsin, rubin and orange G, Mallory's haematoxylin ammonium molybdate or phospho-tungstic did not stain Mummery's fibres. Nissl's stain failed to reveal any structure which resembled nerve cells.

Stroebe's stain (Mallory and Wright's *Pathological Technique*, 7th ed., p. 134) brought out a few fine blue fibres in the position usually occupied by those of Mummery, and that author considered this to be an additional argument in favour of these structures being nerves. Unfortunately the dentinal fibres and tissues of the pulp stain quite as deeply as these fibres, consequently the stain cannot be considered as specific for nerve fibres, and does not therefore give any assistance in solving the problem of the nature of Mummery's fibres.

Mallory's connective tissue stain gave interesting results. If the sections were not thoroughly washed after immersion in the aniline blue and orange G solution, the fibres of Mummery were stained dark blue. In those cases where the washing had been carried out more carefully the fibres disappeared or became so pale that it was impossible to say with certainty that they were present. It must be remembered that Mallory's stain colours connective tissue blue and nerve fibres red, so that the result obtained in this case casts grave doubt on Mummery's hypothesis that his fibres are of nervous origin.

The results of this histological investigation into the nature of Mummery's fibres may be summarised as follows: They are stained by metallic impregnation methods, but not by Mallory's nerve stains. On the other hand, they are stained by Stroebe's method, but so are the other tissues. The ordinary stains for white fibrous and elastic tissue do not seem to affect them, but with Mallory's connective tissue stain they respond like white fibrous tissue. These different results must lead to the conclusion that the nature of Mummery's fibres cannot be settled finally by purely histological approach, without the assistance of other methods of research.

III. THE RESULTS OF SECTION OF THE INFERIOR DENTAL NERVE

The account in the last section of the results obtained from different histological stains showed, that those stains left it very doubtful whether the fibres of Mummery are of nervous origin. As we have said, it seemed improbable that a definite decision, as to the nature of the fibres, would ever be arrived at by such means. It was therefore decided to attempt to elucidate the problem by the experimental method. For this purpose it was considered that the study of the effect on the pulp, of section and degeneration of one of the nerves to the teeth would be of great value, and would provide a new means of approach to this question.

The inferior dental nerve was chosen in preference to one of the superior ones, as it is more accessible, and on account of there being only one nerve on either side in the lower jaw, there is less overlapping of their areas of dis-

tribution than in the upper. There is only one objection to the use of this nerve, and that is due to the fact that the nerve on one side is believed (on clinical grounds) to extend for some distance into the opposite half of the jaw. How far this distribution is carried is at present uncertain and requires investigation, but the nerve is not believed to supply teeth farther back than the opposite canine. Consequently it seems possible to exclude fallacies due to overlap by using for examination, teeth posterior to the canine.

The experiments were performed on the cat in preference to the rabbit or guinea-pig, on account of various peculiarities in the nerve supply of these teeth, which are still being investigated, and a description of which will be published at a later date.

In carrying out the operation the line of approach selected was *via* the mouth, and in each case the left nerve was divided. Six cats in all were operated upon, two (Nos. 1 and 4) were killed on account of sepsis, No. 2 was killed at the end of a fortnight, No. 3 after three weeks and Nos. 5 and 6 after a month. In cat No. 5 it was found, post-mortem, that the nerve had not been divided, but in the other three cases the operation had been successful. In the successful cases the teeth were disposed of in the following manner. The canine and the three teeth posterior to them on each side of the lower jaw, were hardened and decalcified in the usual way, and cut into sections with the freezing microtome. These teeth were numbered 1 to 4 from before backwards. At the same time those parts of the inferior dental nerve of both sides which lay in the mandibular canals were stained with Marchi, embedded in paraffin, and cut into sections. In each case therefore the structures on the normal side could be used as controls for those on the abnormal side.

Sections from tooth No. 4 of cat No. 2 were first of all stained with haemalum and eosin, and on examination no difference could be seen in the sections from the two sides. This confirms the results of Hopff (15) who cut the inferior dental nerve in ten rabbits, and could find no structural changes in the pulp tissues after this operation. He did not however study the state of the nerves of the pulp.

The inferior dental nerves which had been stained with Marchi were now examined, and it was found that degenerative changes had occurred in each case on the affected side. No alteration had taken place in the normal nerves.

The decalcified sections were now stained in the usual way by the Beckwith method, and the results obtained in one of the teeth of cat No. 2 are shown in figs. 4 and 5 which are sections from the corresponding teeth from the opposite sides of the mouth. It will be noticed that the fibres of Mummery are present, and are equally abundant upon both sides. In fact the sections from the various teeth on the denervated side cannot be distinguished by any histological alteration from the corresponding ones on the normal side. The teeth of cats Nos. 3 and 6 were treated in the same way with Beckwith and in spite of the increased time allowed for degenerative changes to take

place, the appearance of the sections from the opposite sides of the jaw is identical. This can be seen in figs. 6 and 7 which are from the farthest back teeth of cat No. 6, in which the degenerative changes were allowed to continue for four weeks.

A few sections were treated with Bielschowski's method, but as it had been very unreliable in the earlier part of this research it was only used for one pair of teeth (No. 4 of cat No. 2). Only 12 per cent. of the sections previously stained had shown the presence of fibres, so it was considered that if fibres were found only in one or two of the sections of the denervated side the result would be satisfactory; actually the percentage on that side was better than on the normal one, being 20 per cent. to 11·4 per cent. In no case however were the fibres clearly seen.

IV. DISCUSSION

The results of these denervation experiments show that whatever else Mummery's fibres may be, they are not the terminal fibres of the dental nerve. The experiments do not rule out completely the possibility of the fibres having a nervous origin, as it could be argued that they formed part of a separate neurone, or arose from the sympathetic plexus around the inferior dental artery, which was not divided at the operation.

The validity of the first argument rests upon the hypothesis that nerve cells as described by Mummery and Carol Montfort are present in the pulp. In regard to these structures however we must recall the following facts:

(1) The above-mentioned authors have described two entirely different structures as nerves.

(2) The stains they employed are, for teeth at least, extremely unsatisfactory in their action, being liable to stain all manner of tissues.

(3) Mummery's cells do not resemble nerve cells in appearance.

(4) Throughout this research, in which a large number of sections were examined, no structures in any way resembling nerve cells were found.

(5) No such arrangement has been found at the termination of any somatic nerve.

From these facts, therefore, we can safely say that there is no evidence to support the belief that nerve cells occur in the pulps of mammalian teeth.

The question as to whether these fibres might not arise from the sympathetic plexus around the inferior dental artery is one of greater difficulty, and cannot be finally settled with the evidence at present in our possession. On account of the large number of Mummery's fibres found in each tooth it is unlikely that they arise from the periarterial plexus which must be relatively extremely small. It is also probable that the inferior dental nerve gives off branches at intervals to the plexus, and if this is the case, when that nerve is divided the plexus will be still further diminished in size. However, to settle this point finally it will be necessary to divide the artery along with

the nerve in order to exclude every source of nerve supply to the pulp. I hope to carry out this experiment during a later investigation.

The question which now arises is, what is the nature of Mummery's fibres if they are not nerves? At present it is impossible to give any definite opinion on this matter. Professor Hopewell-Smith has put forward the view that they may be the same as the fibres of Korff. v. Korff(17) in 1906 saw fibres which stained with connective tissue stains in the same position as those of Mummery, and they had the same cork-screw like appearance. They were found however only in embryonic teeth and never in fully developed ones. An attempt was made, during this investigation to find these fibres in sections taken from teeth in which Mummery's fibres had been seen in large numbers. This was unsuccessful, although the same stains as v. Korff employed were used. From these facts it seems rather difficult to believe that the fibres of Mummery and v. Korff are identical. One suggestive observation was made however: in some of the sections stained by one of the impregnation methods a piece of bone was present and Sharpey's fibres could be seen, which, although much thicker, resembled Mummery's fibres in their staining properties. It is therefore possible that there may be some morphological relationship between them.

This portion of the investigation has been confined to checking the work of those authors who believe that the dentine is innervated with fibres from the pulp and it has shown that there is at present no evidence that it obtains a somatic supply from this source. At present further work is being carried out with other methods, and will be published when they are completed.

No attempt has been made to study the nerve endings in the periodontal membrane, as the methods employed stained that tissue so densely that it was impossible to trace nerve fibres into it. It must be borne in mind however that it is possible that the dentine receives nerves from that tissue, and certain experiments which I have made on the power of teeth to locate pressure stimuli suggest that this may possibly be the case.

V. SUMMARY AND CONCLUSIONS

(1) Gold impregnation stains demonstrate fibres described by Mummery which resemble nerves in certain of their characters.

(2) Section and degeneration of the inferior dental nerve does not cause these fibres to disappear from the teeth which it supplies, consequently they are not the terminal fibres of that nerve.

(3) Nerve cells as described by Mummery and Carol Montfort are not present in the pulps of teeth, therefore the fibres of Mummery cannot be a part of an end neurone on the somatic sensory tract.

(4) Mummery's fibres may possibly arise from the periarterial plexus associated with the inferior dental artery. This is improbable, but the difficulty can only be solved by division of the artery along with the nerve.

(5) The tentative suggestion is put forward that there may be a relationship between the fibres of Mummery and those of Sharpey.

I have to acknowledge my indebtedness to Professor Stopford for many helpful suggestions. Professor Raper kindly allowed me to use the laboratory of the Physiology Department of Manchester University to carry out the nerve section experiments. The following gentlemen have supplied me with material: Messrs Campion, Fish and Matthews. Mr Gooding of the Anatomy Department has prepared the microphotographs, and I have received great assistance from my wife in preparing the paper for publication.

I have to thank the Oxford University Press for permission to use the diagram in fig. 1.

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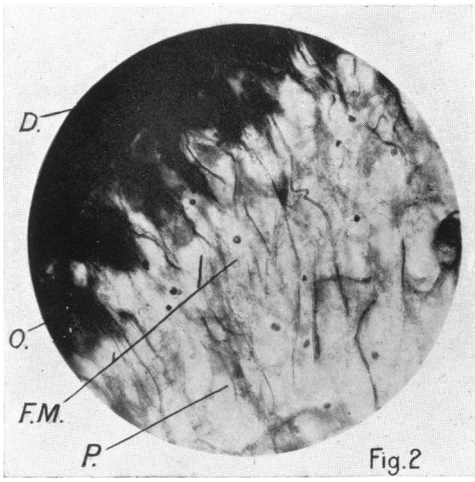

Fig.2

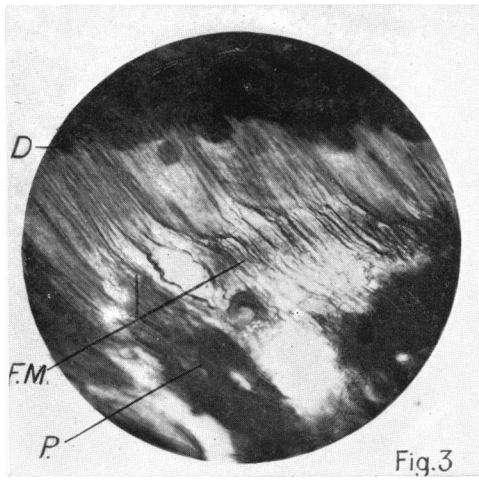

Fig.3

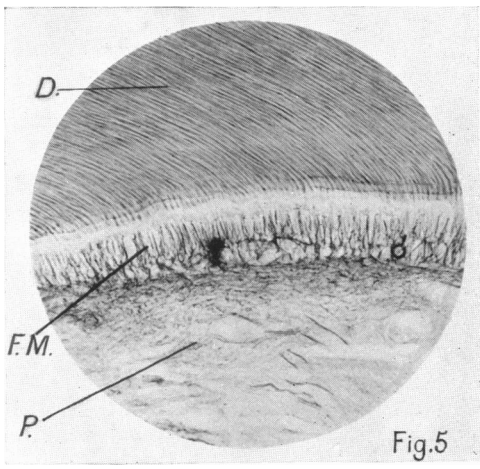

Fig.5

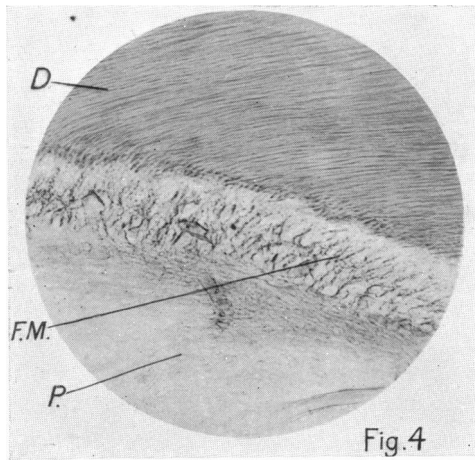

Fig.4

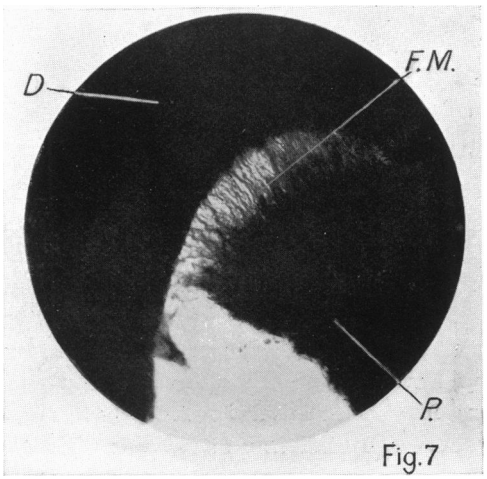

Fig.7

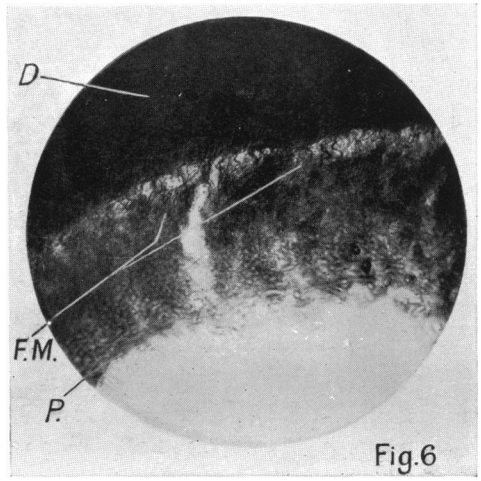

Fig.6

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INDEX OF ABBREVIATIONS

D = dentine.	*O* = odontoblasts.
P = pulp tissue.	*FM* = fibres of Mummery.