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Observations on the connexions between myelin sheaths and glial cells in the optic nerves of young rats

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INTRODUCTION

During the past few years, evidence has been accumulating to show that the lamellae of the myelin sheaths of the central nervous system have a spiral arrangement, similar to that of the sheaths of peripheral nerves (Geren, 1954). A spiral arrangement within the sheaths of central nerve fibres was first proposed by Fernández-Morán & Finean (1957), but such a structure was doubted by Luse (1956) and by De Robertis, Gerschenfeld & Wald (1958). Later, however, Maturana (1960) and Peters (1960*a*), examining the optic nerves of amphibians, produced evidence in favour of a spiral by showing that the counts of lamellae in different parts of the same myelin sheath are consistent with such an arrangement. They believed that the spiral commenced on the inside of the sheath at the internal mesaxon and terminated on the outside of the sheath at the external tongue (Peters, 1960*a*) or loop (Maturana, 1960), of cytoplasm. In transverse sections of central sheaths, the external tongue process is usually confined to only a small part of the circumference of a sheath and does not surround the sheath completely as does the Schwann cell cytoplasm in peripheral sheaths. This is the essential difference between peripheral and central sheaths. External tongues of cytoplasm and internal mesaxons have since been demonstrated in the sheaths from the diencephalon of the frog (Metuzals, 1960, 1963), from the optic nerve of rats and mice (Peters, 1960*b*, 1962*a*), from the spinal cords of cats (Bunge, Bunge & Ris, 1961), from the inferior olives of cats (Walberg, 1963) and from tissue cultures of the cerebellum of rats, mice and kittens (Perier & de Harven, 1961; Ross, Bornstein & Lehrer, 1962). The results obtained by all of these authors are consistent with the existence of a spiral arrangement of the lamellae in central sheaths and a direct demonstration of a spiral has recently been given in the myelin sheaths from the optic nerves of mice (Peters, 1963).

Stages in the formation of central myelin sheaths have been examined (Peters, 1960b, 1962*a*) and the existence of a spiral arrangement of the lamellae, together with the presence of the nodes that have now been demonstrated by both light (Feindel, Allison & Weddell, 1948; Hess & Young, 1949; Perier & de Harven, 1961) and electron microscopy (Gray, 1959; Maturana, 1960; Peters, 1960*b*; Metuzals, 1960, 1963; Bunge *et al.* 1961) lead to the conclusion that central sheaths are formed in internodal lengths, as are those of the peripheral nervous system (see Hild, 1959).

In peripheral nerves, the internodal lengths of myelin are formed by Schwann cells, whose nuclei are to be found in the cytoplasm surrounding the sheaths. In mature sheaths from the central nervous system, however, nuclei have never been observed in the cytoplasm of the tongue process on the outside of the sheath. These

tongues are generally even free of such characteristic cytoplasmic organelles as mitochondria and endoplasmic reticulum (Bunge *et al.* 1961). This suggests that the myelin-forming glial cells of the central nervous system are situated some distance away from the site of myelin formation, and that continuity between the cytoplasm on the outside of the sheath and that of the perikaryon of the glial cell is established through a glial cell process. Such connecting processes have recently been demonstrated by Bunge, Bunge & Pappas (1962) in the spinal cords of kittens, and the purpose of the present paper is to show that connecting processes are also present in the optic nerves of young rats.

MATERIALS AND METHODS

The optic nerves of 7-, 11- and 14-day post-natal rats and of adult rats and mice were removed and fixed for 1–2 hr., at 4°C., in the chromate-osmium tetroxide mixture of Dalton (1955). The optic nerves were then cut into short lengths, washed in 10% alcohol and dehydrated in absolute ethanol, before embedding in Araldite (Glauert & Glauert, 1958). Sections were cut on a Servall Porter-Blum microtome. Most of the sections were mounted on grids without the use of supporting films and stained with potassium permanganate (Lawn, 1960), but when serial sections were used they were mounted on wide-mesh grids with supporting films and stained with an alcoholic solution of uranyl acetate. The sections were all examined in a Metropolitan-Vickers, EM 6, electron microscope.

DESCRIPTION

In the optic nerves of adult rats and mice, all of the nerve fibres appear to be myelinated. The tongue of cytoplasm on the outside of each sheath is generally quite small and in transverse sections usually occupies only about 5% of the circumference of the sheath, and rarely more than 25%. The large tongues of cytoplasm sometimes extend for a short distance between neighbouring sheaths, but it is exceptional for them to contain anything beyond a few small, smooth vesicles and a few electron dense particles. Despite an intensive search, no outer tongues of cytoplasm have yet been found that are in continuity with the cytoplasm of the perikaryon of a glial cell in an adult nerve. As pointed out earlier (Peters, 1962*b*), intimate contacts that lead to the formation of quintuple-layered structures are frequently formed between the cell membrane of a tongue process and that of a glial cell, but in all cases so far observed, the separation between the cytoplasm on both sides of these contacts has always been complete.

Because of this failure to find connexions between the cytoplasm of glial cells and that associated with the sheaths of adult nerves, the optic nerves of younger animals have been examined. In these optic nerves, from 7-, 11- and 14-day post-natal rats, the majority of nerve fibres are still unmyelinated, but around those that have begun to myelinate the outer tongues of cytoplasm are usually both much larger and more electron dense than in adult nerves. Consequently, the tongues of cytoplasm are identified more readily than in adult nerves.

In young optic nerves, particularly those from 7-day post-natal rats, it is not unusual to find sheaths in which the cytoplasm on the outside is so extensive that it

completely encircles the sheath, giving it an appearance similar to that of a peripheral nerve. In other cases, the sheaths have extensive tongue processes that extend away from the sheath to pass between the adjacent nerve fibres, as in Plate 1, figure 1. The process (P), related to this axon is about 0·3 μ wide and extends away from the sheath for a distance of 3 μ. Near to the sheath, the cell membrane on the left of the process becomes apposed to that enclosing the cytoplasm in the outer turn of the sheath, so that an external mesaxon (EM) is formed that soon runs on to the outside of the sheath. At X, the cell membrane of the right side of the process also becomes continuous with the lamellae of the sheath and it is at this point that the cytoplasm is excluded from the cell membrane and the sheath. Apart from its size, the relation between this process (P) and the sheath is similar to that existing between the majority of the sheaths and the more commonly observed, smaller, external tongues of cytoplasm (T, Pl. 1, fig. 1). The cytoplasm of the smaller tongues is usually more electron-dense than that of the adjacent axons, but, as in the adult sheaths, it is uncommon for them to contain more than a few vesicles and granules. In contrast, the more extensive tongues, or processes of cytoplasm, frequently contain a well-developed endoplasmic reticulum and mitchondria. Further, when these processes are traced through a series of sections it is sometimes found that they approach, and ultimately join, a process of the same type of cytoplasm extending from the perikaryon of a glial cell. In this way, connexions are established between the cytoplasm on the outsides of sheaths and that of the perikarya of glial cells. Such connexions are quite frequently found in sections of the optic nerves of 7- and 11-day post-natal rats, and it is upon observations of these nerves that the following account is based.

A typical connexion between a sheath and glial cell is shown in Plate 2, figure 2. In this micrograph, a process (P) extends from the body of the glial cell (G_1), which contains a nucleus (N), to the myelinated nerve fibre, 1, on the left. As it extends towards the nerve fibre, the process also passes close to the body of a second glial cell (G_2), but in higher power micrographs it is apparent that there is no continuity between the two. The sheaths of two other nerve fibres, 2 and 3, are also in close proximity to the perikaryon of the first glial cell (G_1) but there is no connexion between the cytoplasm of the sheaths and that of the glial cell. A higher power micrograph of the relation between the glial cell process (P) and the sheath around fibre 1, is given in Plate 2, figure 3.

As pointed out by Bunge *et al.* (1962), to establish that a connexion exists between a glial cell and a myelin sheath, it is necessary to show that the cell membrane of the glial cell is in continuity with the membrane forming the lamellae of the sheath. Such a continuity is present in Plate 2, figure 3. The glial cell process, P, approaches the sheath, encircles it in a clockwise direction (arrows), and forms an external mesaxon (EM) which has a quintuple-layered structure. Initially, this external mesaxon is separated from the lamellae of the sheath by a layer of cytoplasm, but this cytoplasm is lost as the external mesaxon turns on to the sheath to form the outer lamella. The lamellae of this sheath therefore run inwards in a clockwise direction and ultimately terminate on the inside of the sheath at the internal mesaxon (IM).

Another example of a connexion between a sheath and a glial cell is given in

Plate 3, figure 4. Here, the process, P, derived from the glial cell (G) is much shorter than that described above and contains a number of relatively large mitochondria (MIT). This process does not form a complete layer of cytoplasm on the outside of the sheath, but as before, the cell membrane of the process is in continuity with the lamellae of the sheath. In Plate 3, figure 4, the cell membrane on the right side of the process appears to run directly on to the sheath without the formation of a distinct external mesaxon and the cytoplasm is lost from the process at Y, where its cell membranes form the lamellae of the sheath. In this case, the membranes turn on to the outside of the sheath to form an anti-clockwise spiral that terminates on the inside of the sheath at the internal mesaxon (IM).

Not all of the connexions between glial cells and myelin sheaths are effected through distinct processes of the type described above, for in some instances connexions are formed with sheaths that abut directly on to the perikaryon of a glial cell. Such a connexion is shown in Plate 3, figure 5. In this example, the process (P) of the glial cell (G), which is surrounded by unmyelinated nerve fibres (U), extends in a clockwise direction (arrow) from a region of the perikaryon that is close to the nucleus (N). The process gives rise to three loose turns (1, 2 and 3) before forming the compact myelin that terminates at the internal mesaxon (M). The presence of such loose turns on the outside of a sheath is unusual for, in other examples in which the sheath indented the perikaryon of a glial cell, compact myelin was formed by the cell membrane as soon as the short connecting process reached the outside of the sheath. At one point, indicated by an asterisk, there appears to be a break in the continuity of the second loose turn of the spiralling glial cell process. This is a site of contact between the first and second turns, however, and in adjacent sections, where the loose lamellae of this region of the sheath are separated, the continuity of cytoplasm is readily visible.

It should be emphasized that although many sheaths indent the perikarya of glial cells at all stages of development of the central nervous system, very few of these have been observed to form direct connexions with the glial cells. In the majority of cases, the cytoplasm of the perikaryon of the glial cell is quite definitely separated from that on the outside of the sheath by intervening cell membranes (see Peters, 1962*b*).

In the optic nerves of young rats, many of the sheaths are in an early stage of development when, although the axon is enclosed by a glial cell process, compact myelin has not yet started to form (see Peters, 1960*b*, 1962). Such an early stage in sheath formation is shown in Plate 4, figures 6 and 7. In Plate 4, figure 6, the process (P) of a glial cell (G) extends towards, and encloses, a small (A). The manner in which this enclosure is effected is apparent in Plate 4, figure 7, where it will be seen that as the process (P) of the glial cell reaches the axon, it divides into small processes (P_1 and P_2), which pass on each side of the axon. One of these smaller processes (P_1) encircles the axon and its cell membrane becomes apposed to that on the inside of the second small process (P_2) to form a mesaxon (M). It is worth while at this point to consider briefly how such a mesaxon might be elongated, and further turns added to the spiral that the glial cell process has begun to form around the enclosed axon, to form a mature myelin sheath. In the present example, it seems that this could be achieved most readily by the growth, or elongation, of the end of

the process P_1 inside the space between the axon and the glial cell process itself. Adding turns to the outside would appear to necessitate either a rotation of the axon and its sheath in an anti-clockwise direction relative to the present position of the glial cell body, or a rotation of the glial cell around the enclosed axon. This point will be considered more fully in the discussion.

From this account, it will be appreciated that there is a considerable variation in the sizes of the connexions between glial cells and myelin sheaths and some measurements are given in Table 1. This table gives the minimum distance, along the connecting process, between the outside of the sheath and the nuclear membrane of the myelin-forming cell, as well as the minimum width of the connecting process. These measurements, although arbitrary, have been taken in order that a direct comparison may be made with the results obtained by Bunge *et al.* (1962) in their study of the connexions in the spinal cords of kittens.

Table 1. *Dimensions of connecting processes between myelin sheaths and glial cells in the optic nerves of* 7- *and* 11-*day post-natal rats*

No.	Distance between sheath and nuclear membrane of glial cell (μ)	Minimum width of connecting process (μ)
1	0·1	Sheath indents perikaryon
2	0·2	Sheath indents perikaryon (Plate 3, figure 5)
3	0·3	Sheath indents perikaryon
4	1·2	0·5 (Pl. 3, figure 4)
5 (*a*)	1·5	0·03
(*b*)	2·1	0·23
6	3·1	1·0
7	3·3	0·3
8	4·2	0·5
9	4·6	0·5 (Plate 4, figure 6)
10	4·8	0·2 (Plate 2, figure 2)
11	6·4	0·2
12	9·5	0·3
13	10·2	0·1

It will be seen from Table 1, that in only one case, No. 5, have connexions been found between two separate sheaths and the same glial cell. These two connexions only became apparent by examination of a series of sections and both could not be demonstrated in the same micrograph.

The longest connecting process observed was 10·2 μ, but it is apparent that the lengths and widths of the processes are both very variable, although on the whole, it seems that the longest processes are the most narrow. The impression has been gained, especially from serial sections, that the connecting processes have a slender, rounded form; in other words, that they are not sheets of cytoplasm. Thus, as mentioned by Bunge *et al.* (1962), in serial sections it is often found that one part of a connexion may disappear while another part becomes visible, a finding which would not be expected if the connexions are composed of sheets of cytoplasm. Further, rounded processes, which have a cytoplasm similar to that of the connecting processes, have been observed between the axons in sections of these optic nerves.

One very important point is the identification of these myelin-forming cells. In the present osmium fixed and potassium permanganate or uranyl acetate stained

material, the main characteristics of these cells are shown in Plate 2, figures 2, 3, Plate 3, figure 4 and Plate 4, figure 6. The cells have a relatively electron-dense cytoplasm with many dense particles, both free in the cytoplasm and associated with the endoplasmic reticulum (Plate 2, figure 3, Plate 3, figure 4) which is often well-developed and takes the form of parallel cisternae. Stacks of agranular reticulum (Plate 4, figure 6, R) also occur within the cytoplasm, which sometimes contains relatively large mitochondria (Plate 3, figure 4, MIT). The outlines of these cells are very irregular and in any one section a number of processes may extend from the cell body where only a thin rim of cytoplasm surrounds the rather dark, homogeneous nucleus (Plate 2, figure 2; Plate 3, figure 4; Plate 4, figure 6, N). These characteristics suggest that the myelin-forming cells are oligodendroglial cells. These cells are easily recognized in young rat optic nerves and can be readily distinguished from a second, definite type of glial cell, that has a lighter cytoplasm and more numerous processes containing a fibrillar component (Plate 1, figure 1; Plate 4, figure 6, F). The processes of this second type of glial cell are often found in groups (Plate 4, figure 6) and their appearance is similar to that of the fibrous astrocytes previously described in the optic nerves of adult rats, mice and toads (Gaze & Peters, 1961; Peters, 1962*b*) and in the spinal cords of cats (Bunge *et al.* 1961). In addition to these two definite types of glial cell, however, there are others that fall into neither category. These latter are usually more rounded, do not possess processes and frequently occur either in groups or in pairs. Their identification is uncertain, but it is probable that they are immature glial cells.

DISCUSSION

The connexions between myelin sheaths and glial cells that have been described in the present account of the optic nerves of 7- and 11-day post-natal rats are similar to those found by Bunge, *et al.* (1962) in the spinal cords of kittens. They also note a great variation in the length of the connecting processes. The most extensive process that they record is 12·3 μ long, compared with 10·2 μ observed in the present investigation, while the shortest connexions are also those effected with myelin sheaths indenting the perikarya of the myelin-forming glial cells. Further, the glial cells forming the connexions have a similar appearance to those observed in young optic nerves and they also come to the conclusion that these are oligodendroglial cells.

There is no doubt that the cytoplasm of the connecting process of the glial cell is in continuity with that of the tongue, or loop, of cytoplasm seen on the outside of central myelin sheaths since this continuity can be observed in transverse serial sections of sheaths. Except at the level of the connecting process, the outer tongue of cytoplasm is consistently present on the periphery of each sheath, so that it is envisaged as a ridge, or process of cytoplasm, that extends along the entire internodal length of a sheath. Therefore, as indicated by Bunge *et al.* (1962), if it were possible to stain the cytoplasm of the connecting process and of the outer tongue of cytoplasm in light microscope preparations, one would expect to see a process emerging from the body of the myelin-forming glial cell that branched dichotomously as it reached the nerve fibre and then ran along the entire internodal length of the myelin sheath. This is almost exactly the type of picture that Penfield

(1924) produced after staining oligodendrocytes of white matter by the method of Del Rio-Hortego. In his description of oligodendroglia, Penfield (1924, p. 438, figure 2) shows a drawing of oligodendroglia giving off processes that then divide to give branches running parallel to the surrounding nerve fibres. A similar picture is also given by Del Rio-Hortego (Penfield, 1932, p. 441, figure 13).

Unfortunately, neither the present study, nor that of Bunge *et al.* (1962) give any information about the number of connexions that exist between glial cells and each internodal length of myelin in the central nervous system. However, in both studies examples have been found of glial cells that form connexions with more than one myelin sheath. Thus, it seems likely that each oligodendroglial cell is responsible for the formation of myelin around a number of nerve fibres and this is consistent with the light microscope appearances of these cells. Further evidence in favour of this suggestion was put forward earlier (Peters, 1962*a*) when it was observed that the number of glial cells related to a given number of nerve fibres in the central nervous system is much less than that of Schwann cells in the peripheral nervous system, where it is generally believed that one Schwann cell is responsible for the formation of each internodal length of myelin. This difference in the relative numbers of cells occurs despite the fact that the internodal lengths of peripheral (Vizosi & Young, 1948) and central (Hess & Young, 1949) nerve fibres are similar.

Further evidence for the participation of oligodendroglial cells in the formation of central myelin has been put forward by Penfield (1924, 1932), who points out that oligodendroglial cells first appear in the fibre tracts of the central nervous systems of new-born animals at the time of onset of myelination, while they are not seen before myelination. He also remarks that oligodendroglial cells are especially numerous in white matter and are arranged in columns between the myelinated nerve fibres around which their expansion wrap.

An important point, as yet unexplained, is the failure to find connexions between sheaths and glial cells in both the spinal cords of adult cats (Bunge *et al.* 1962) and in the optic nerves of adult rats and mice. It seems unlikely that these connexions are formed during development and disappear later, since in the adult animal cytoplasm is still present both on the outside of the sheath, as well as within the terminal helix at the node (Maturana, 1960; Peters, 1960*b*; Bunge *et al.* 1961; Metuzals, 1963). Processes of cytoplasm that do not contain the characteristic fibrils of astrocytes are sometimes seen to pass between the closely packed myelinated fibres of adult optic nerves and it may be that these represent parts of the connecting processes. If so, these connecting processes may be slender and tortuous, with the result that it is not possible to follow them in electron microscope sections. Certainly the sheaths of many nerve fibres abut on to the surfaces of recognizable oligodendroglial cells in adult optic nerves (Peters, 1962*b*), but in all cases so far examined the cytoplasm of the sheath and that of the glial cell have been completely separated. Profiles of small myelinated nerve fibres embedded in the cytoplasm of oligodendroglial cells have been observed by Metuzals (1963) in the diencephalon of adult frogs, but while he suggests that this may indicate a relationship between the two, no continuity was demonstrated between the sheaths and cells.

Assuming, as the present investigation and that of Bunge *et al.* (1962) suggest, that each oligodendrogial cell is connected to the myelin sheaths of a number of

separate nerve fibres, how is this myelin formed? It has now been shown that each myelin sheath of the central nervous system is composed of a continous spiral of lamellae (Peters, 1963), similar to that of peripheral nerves, and the stages in the formation of this spiral have been described (Peters, 1960*b*, 1962*a*). Nevertheless, the mechanism of the formation of this spiral of lamellae is unknown. During myelination in tissue cultures of peripheral nerves, where one Schwann cell is responsible for the formation of one internodal length of myelin, Crain & Peterson (see Murray, 1959) have observed that the nuclei of the Schwann cells move in such a manner as to suggest rotation around the enclosed axon. Such a rotation would of course account for the formation of a spiral of lamellae in peripheral myelin sheaths. In the central nervous system, however, the rotation of an oligodendroglial cell around each of a number of axons at the ends of its connecting processes is geometrically impossible if a continuous spiral of lamellae is to be produced in each sheath. Further, this would involve the glial cell in a tortuous passage between many hundreds of neighbouring axons. In the present state of our knowledge, it is most easy to envisage that the spiral is produced by a growth or elongation of the process of cytoplasm, and consequently the internal mesaxon, on the inside of the sheath between the sheath and the axolemma.

SUMMARY

An electron microscope study of the connexions between glial cells and myelin sheaths has been made in osmium fixed optic nerves from 7- and 11-day post-natal rats. The connexions are effected through processes of the glial cells, but the lengths and widths of the connecting processes are variable, so that while they may be as long as 10 μ, in other instances they are very short, particularly when a connexion is established with a myelin sheath that indents the perikaryon of the glial cell. In all cases, the cytoplasm of the glial cell process is in continuity with the cytoplasm on the outside of the sheath and the cell membrane of the process turns on to the outside of the sheath to form the myelin lamellae. Each myelin-forming cell has a number of processes and one cell was found to form connexions with two separate sheaths, so that it appears likely, both from this evidence and from the small number of oligodendroglial cells related to the nerve fibres, that each of these cells forms myelin around more than one nerve fibre. The myelin-forming cells have irregular shapes and their cytoplasm, which is relatively electron-dense, contains many small granules. Frequently both well-developed endoplasmic and agranular reticula are present. From their characteristics it is suggested that the myelin-forming cells are oligodendroglia.

Despite an intensive search, no connexions between glial cells and myelin sheaths have yet been observed in the optic nerves of adult rats.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. Transverse section of part of the optic nerve of a 7-day post-natal rat. One of the axons is surrounded by a myelin sheath whose lamellae turn off from the outside to form an external mesaxon (EM) and to enclose an extensive process (P) of cytoplasm. Such extensive processes of cytoplasm are usual, for the cytoplasm on the outsides of the majority of sheaths is confined to a small tongue process (T), such as that present on the outsides of the other sheaths. The internal mesaxons (IM) on the insides of the sheaths are indicated and passing between the nerve fibres are the fibril-containing processes (F) of glial cells. Section stained with potassium permanganate. × 70,000.

PLATE 2

Fig. 2. Transverse section of part of the optic nerve of a 7-day post-natal rat. One of the glial cells (G_1), whose nucleus (N) is on the right, has a process (P) that passes towards, and surrounds, the myelin sheath of a nerve fibre (1). As it extends towards the myelin sheath, this process passes close to a second glial cell (G_2). Two other myelinated nerve fibres, 2 and 3, abut against the body of the first glial cell (G_1), but do not form connexions. Section stained with potassium permanganate. × 20,000.

Fig. 3. Higher power micrograph of part of Pl. 1, fig. 1 to show the connexion between the glial cell process (P) and myelin sheath. The glial cell process (P) completely surrounds the myelin sheath in a clockwise direction (arrows) and the membranes of the process form an external mesaxon (EM) that runs on to the outside of the sheath and gives rise to the lamellae. The lamellae terminate on the inside of the sheath at the internal mesaxon (IM). Section stained with potassium permanganate. × 100,000.

PLATE 3

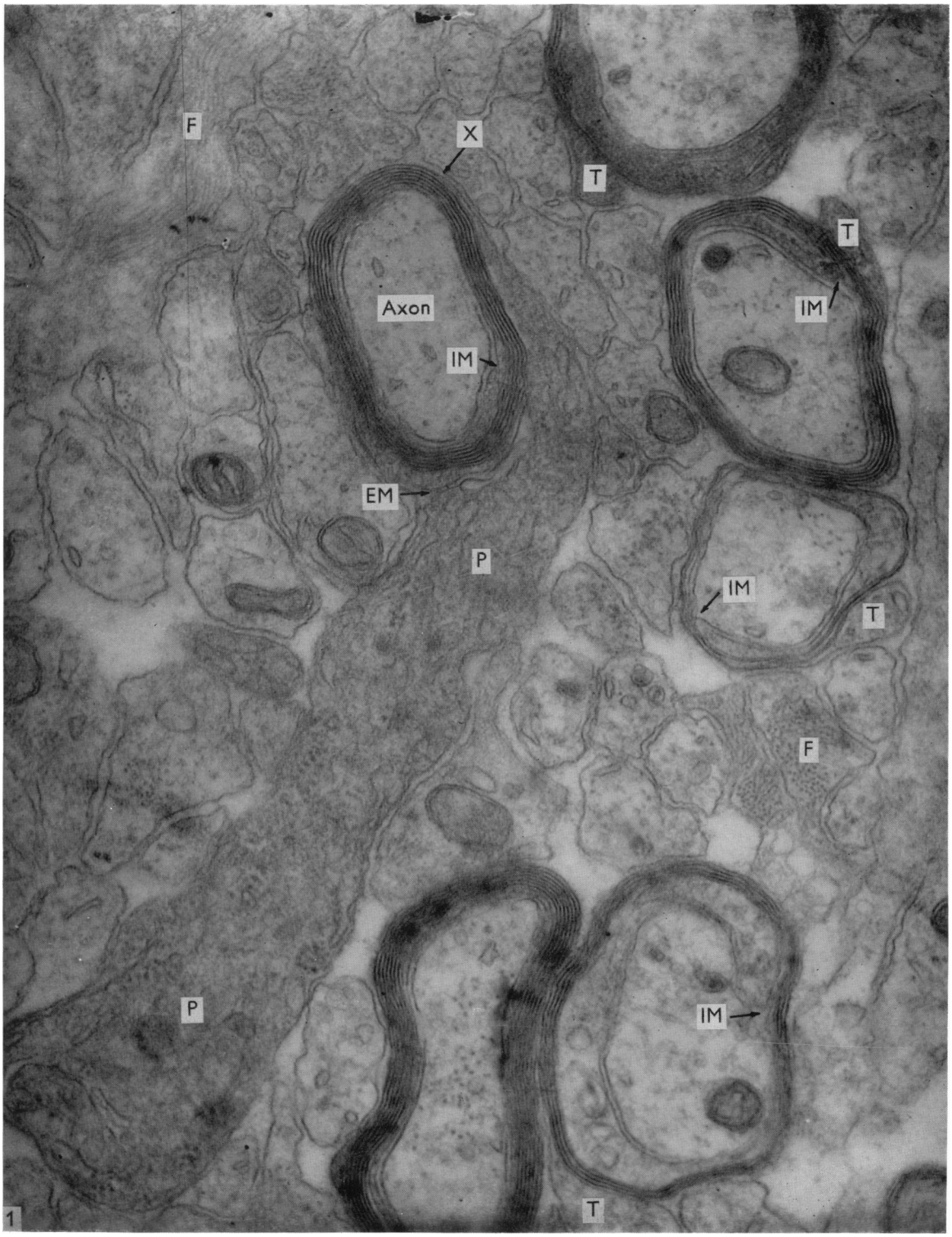
Fig. 4. Part of the optic nerve of a 7-day post-natal rat. The glial cell (G), whose nucleus (N) is visible at the top of the micrograph, has a short process (P) that contains mitochondria (MIT) and extends towards the myelin sheath surrounding an axon. At Y, the cytoplasm is excluded from the glial cell process and its cell membranes become continuous with the lamellae of the sheath. The lamellae run inwards in an anti-clockwise direction and terminate on the inside of the sheath at the internal mesaxon (IM). Section stained with potassium permanganate. × 44,000.

Fig. 5. Part of the optic nerve of an 11-day post-natal rat. In this micrograph the myelin sheath of an axon indents the perikaryon of a glial cell (G) in the region of the nucleus (N). A process (P) of the glial cell turns on to the outside of the sheath (arrow) to form three loose turns (1, 2 and 3), before forming the more compact myelin lamellae that terminate on the inside of the sheath at the internal mesaxon (IM). The other axons (U) surrounding this part of the glial cell (G) are unmyelinated. Section stained with uranyl acetate. × 90,000.

PLATE 4

Fig. 6. Part of the optic nerve of a 7-day post-natal rat to show an early stage in the formation of a myelin sheath. The nucleus (N) of the glial cell is almost as electron-dense as the surrounding cytoplasm, which contains stacks of agranular reticulum (R). From the cell body of the glial cell a process (P) extends towards, and surrounds, an axon (A). Close to the body of the glial cell (G) are the fibril-containing (F) processes of a second type of glial cell. Section stained with potassium permanganate. × 28,000.

Fig. 7. Enlargement of part of Pl. 4, fig. 6 to show the manner in which the glial cell process (P) surrounds the axon. As it approaches the axon, the glial cell process (P) divides into two smaller processes (P_1 and P_2) that surround the axon and form a mesaxon (M). Section stained with potassium permanganate. × 130,000.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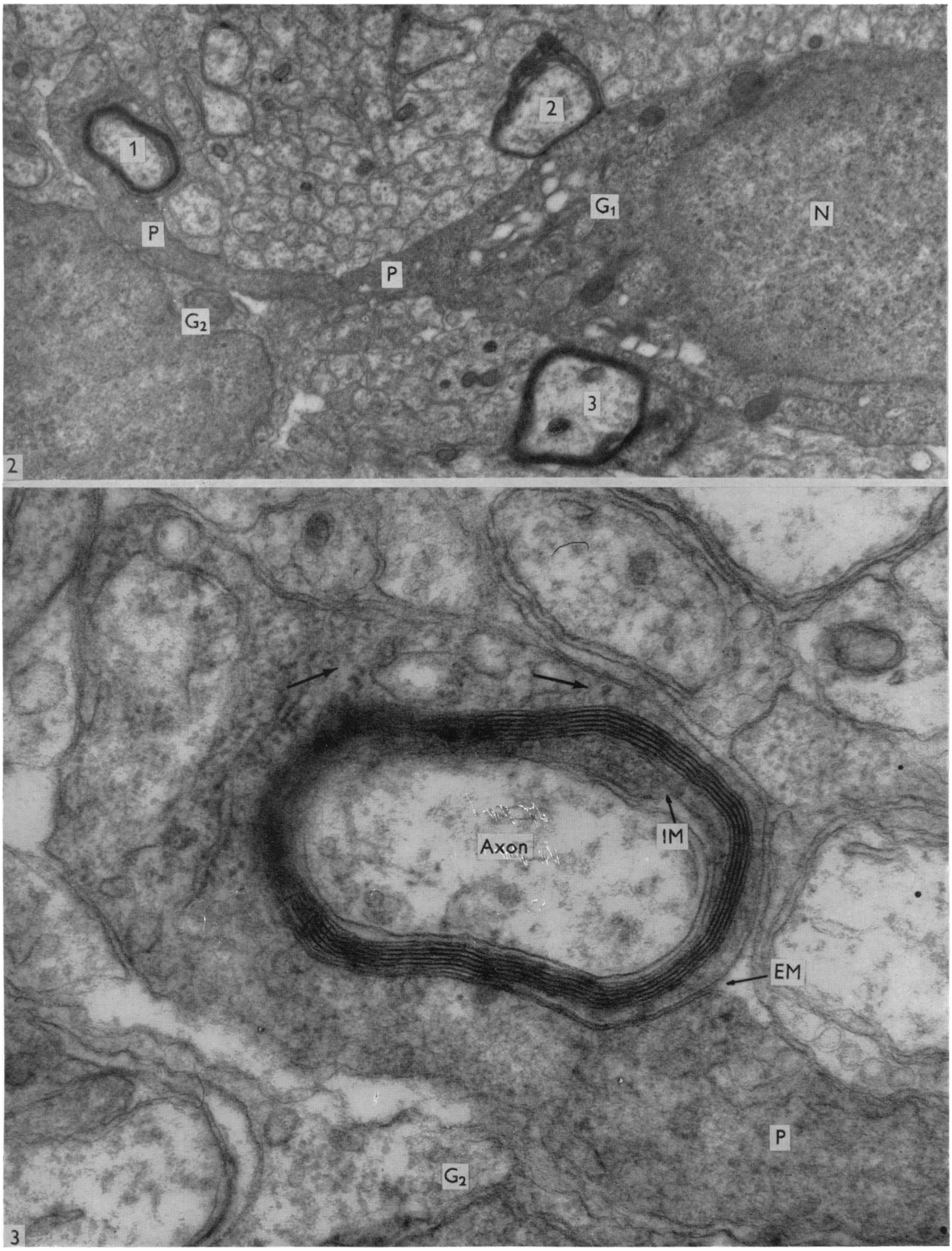

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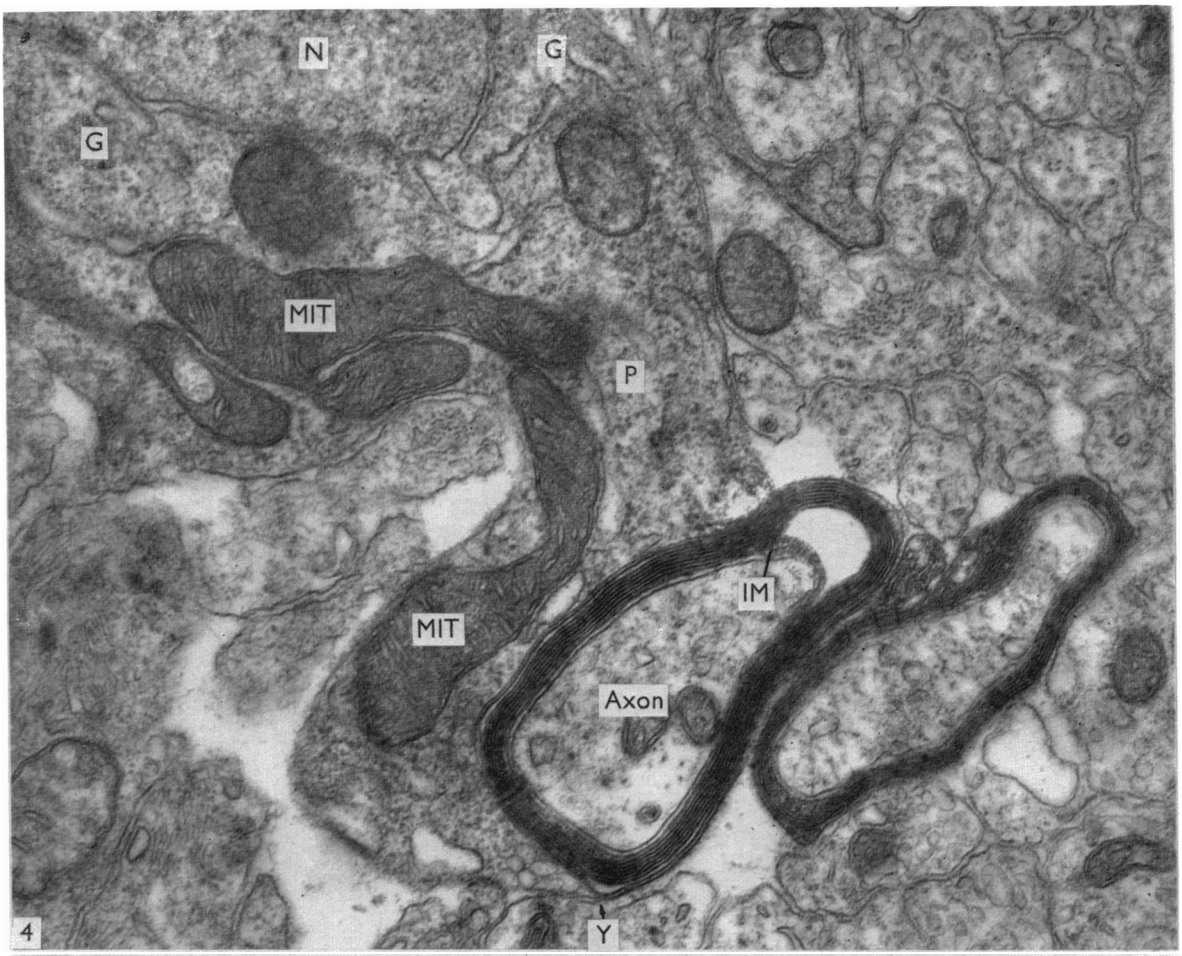
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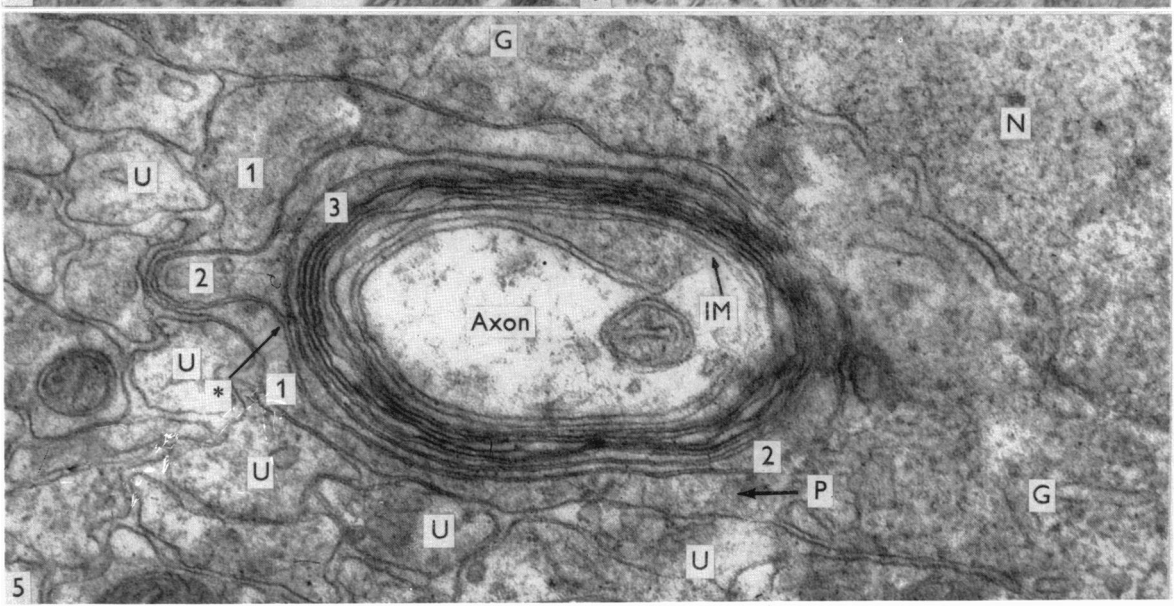
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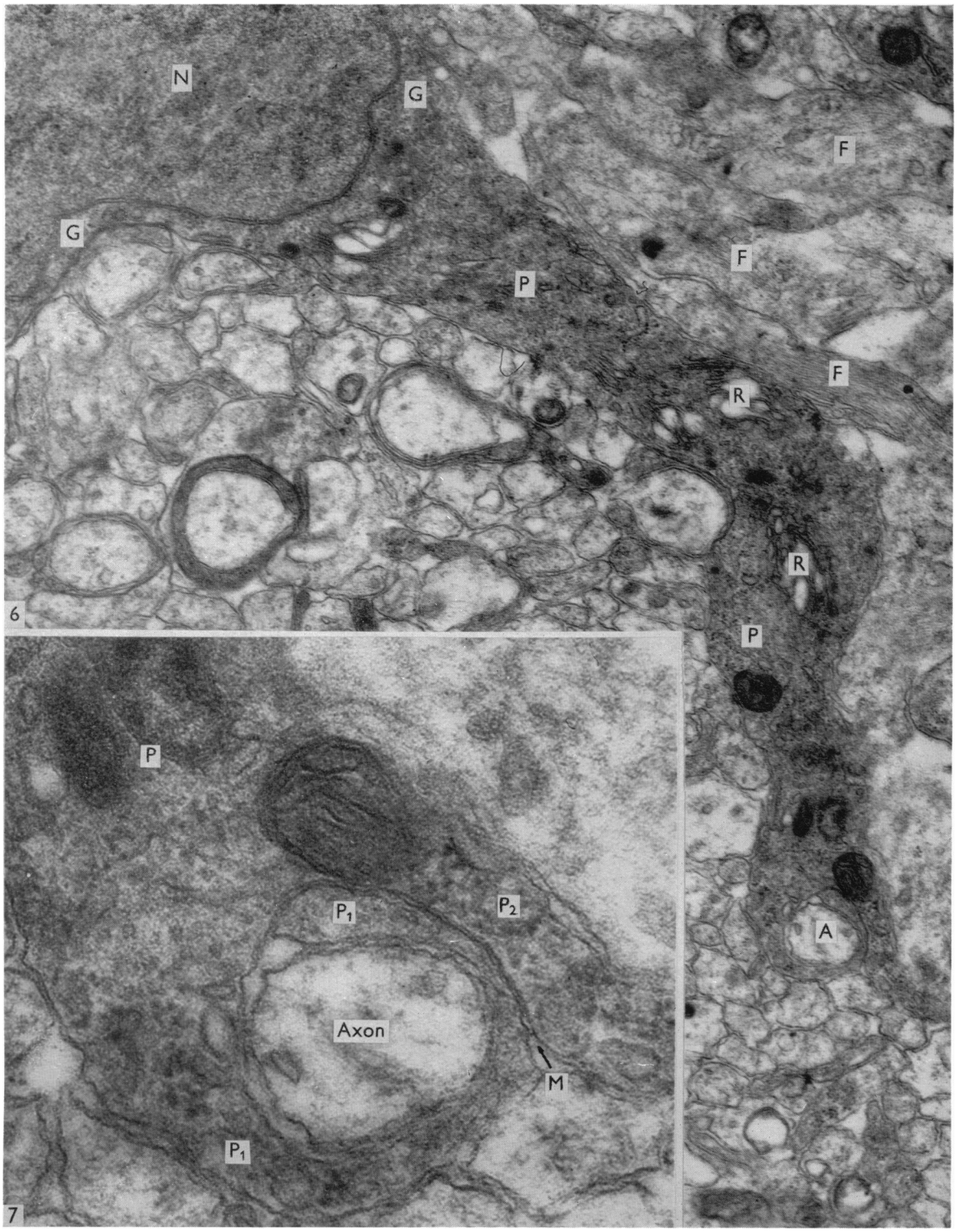
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