CILIATED SCHWANN CELLS IN THE AUTONOMIC NERVOUS SYSTEM OF THE ADULT RAT

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Recently several papers have appeared reporting the discovery of cilia on cells where they have not been suspected before, such as fibroblasts (20), chromaffin cells (6, 22), neurons (14, 22), tumor cells (3, 12), smooth muscle (20), renal epithelium (11), the parenchymal cells of the adenohypophysis (2) and the islets of Langerhans (13), and unidentified cells in the spleen of the chick embryo (3). These examples fall into three categories: (*a*) those in which the fine structure of the cilia is similar to that of ordinary motile cilia (12), (*b*) those in which the reports give insufficient detail for the analysis of the fine structure (3, 6, 11, 22), and (*c*) those which have one atypical feature in common—the absence of the axial pair of fibers characteristic of motile cilia (2, 13, 14, 20). Since none of these cilia has been observed in living preparations, it is unknown whether they are motile. Their significance cannot be ascertained merely by examining electron micrographs. Barnes (2) has collected examples from the literature which suggest to her that the absence of the axial filaments can be correlated with sensory function, but it must be recalled that most of these examples do not involve known receptor cells.

The present paper reports still another example of modified cilia attached to cells where they have not been noticed before. These cilia were encountered on the surfaces of Schwann cells in autonomic nerves and ganglia of the adult rat. Because their internal structure differs somewhat from that of all other vertebrate and invertebrate cilia so far reported, a brief description of them seems warranted.

MATERIALS AND METHODS

The superior cervical and sphenopalatine ganglia, the cervical vagus nerve, and the gastrointestinal tract were obtained from young adult male rats of the Osborne-Mendel strain, weighing approximately 150 gm. The tissues were fixed *in situ* in the living anesthetized animal by the intravascular perfusion of a 1 per cent solution of OsO_4 buffered to pH 7.35–7.4 in Veronal acetate and containing 5.4 or 0.13 mg of $CaCl_2$ per ml of solution (15). The tissues were then dehydrated in a graded series of methanol, embedded in Epon 812, and sectioned with glass knives on a Porter-Blum microtome. Sections mounted on copper grids with a Formvar-carbon substrate and stained with a saturated aqueous solution of uranyl acetate were examined in an RCA EMU-3D microscope.

OBSERVATIONS

Isolated cilia were encountered on 9 Schwann cells in the autonomic nerves and ganglia studied. Each cilium originates deep in the cell, close to the nucleus, and projects away from the axon into a narrow channel of extracellular space formed by a deep invagination of the cell membrane. In unmyelinated nerve fibers the basement lamina, which separates the Schwann cell plasmalemma from the connective tissue space, covers only the distal portion of the cilium and does not extend into the depths of the invagination to coat the shaft of the cilium (Fig. 1). In ganglia, the cilia of satellite cells[1] project inward toward the surface of the neuron.

The shaft of the cilium appears to bend sharply at its base, for in thin sections only a short portion of the shaft attached to a longitudinal section of its basal body is often seen (Fig. 2). Fig. 3, which shows a nearly transverse section of a cilium in proximity to a nearly longitudinal section of its basal body, suggests that the angle of the bend is close to 90°.

The ciliary shaft measures about 270 mμ in diameter, and at least 950 mμ in length. In transverse sections nine double fibers are discernible arrayed peripherally in a circle about a circular profile 90 mμ in diameter (Figs. 3 and 4). The uniformity in size and shape of this axial component indicates a tubular or cylindrical structure of some length.

The peripheral fibers of the cilium appear to be continuous with those of the basal body. As in most mammalian cilia (8), the central cavity of the basal body does not contain any formed structure (Figs. 2 and 3), and is not closed off from the ciliary shaft by a basal plate. The basal body is surrounded by a cloud of fine dense granules or filaments which are not well resolved in our micrographs. In some specimens (Fig. 2) coarse appendages can be made out extending for short distances from the wall of the basal body into the surrounding cytoplasm (also illustrated in Fig. 5 which, however, shows a basal body in a neuron). In one of these (Fig. 3) a cross-striated rootlet is evident. A more detailed analysis of the structure of the basal bodies detached from their ciliary shafts by the plane of section was based upon the nature of the associated appendages; for example, the cross-striated rootlets in Fig. 3 were taken to mark a basal body, whereas the satellite body and its connecting bridge in Fig. 7 were taken to indicate a centriole.

In their orientation and site of origin the cilia of Schwann cells resemble the cilia of neurons in the superior cervical ganglion (Fig. 5). Properly oriented sections of the nerve cell cilia have not yet been obtained to determine whether the central component resembles the tubular structure of Schwann cell cilia or the non-fibrous structure of cilia on the neurosecretory cells of *Carassius auratus*

[1] The term "satellite cell" is being used to designate a Schwann cell which partially or completely envelops a neuron of the peripheral ganglia. A morphological distinction from the Schwann cells of unmyelinated nerve fibers is not intended.

(14). The fiber pattern of cilia on sympathetic neurons in the frog has only recently been analyzed, and it appears that the axial pair of fibers is missing here also (Taxi, personal communication). The fiber pattern of nerve cell cilia in the sympathetic ganglia of the lizard is still unknown (22).

Centrioles in both Schwann cells and neurons bear satellite bodies (Figs. 6 and 7) similar to those observed in mammalian leucocytes (3, 4).

DISCUSSION

Since the observations reported in this paper were incidental findings in a study of autonomic ganglia and nerves, the small number of cilia noticed probably represents an inadequate sample of the number present. It should be pointed out that centrioles, which presumably occur in all Schwann cells, were not encountered more frequently than cilia. The statistics of thin sectioning and sampling in electron micrography militate against finding small, isolated structures like single cilia and centrioles in the extensive and highly attenuated cytoplasm of the Schwann cell. Hence, although our study uncovered only a token number of ciliated cells, it would not be surprising if a thorough study of serial sections revealed a single cilium on each Schwann cell.

The cilia of Schwann cells possess 9 pairs of peripheral fibers arranged concentrically about a tube approximately 90 mμ in diameter. Although the peripheral doublets are similar to those described in other cilia (7, 8, 10, 16, 17), with one exception (18), the central component differs from the usual two-filament axial structure found in most motile cilia and flagella, as well as from the unusual single fiber axial structure found in the sperm tails of *Haematoloechus*, a parasitic flatworm (19). The central unit differs from that found in *Haematoloechus* by its larger size, by the non-fibrillar structure of its limiting membrane, and by the absence of a dense core. Since this central component is absent from the other modified cilia previously described (1, 2, 5, 9, 13, 16, 20), it appears to be a distinctive feature of Schwann cell cilia.

The meager observations on ciliated Schwann cells reported here form a rather insubstantial basis for understanding their structure or function. Nevertheless, some speculations may be ventured concerning their significance. The existence of cilia on Schwann cells of adult unmyelinated nerves indicates that these cells are still so close to embryonic ectodermal cells that they can construct some of the appendages of typical surface epithelium. The scanty evidence available on the

FIGURE 1

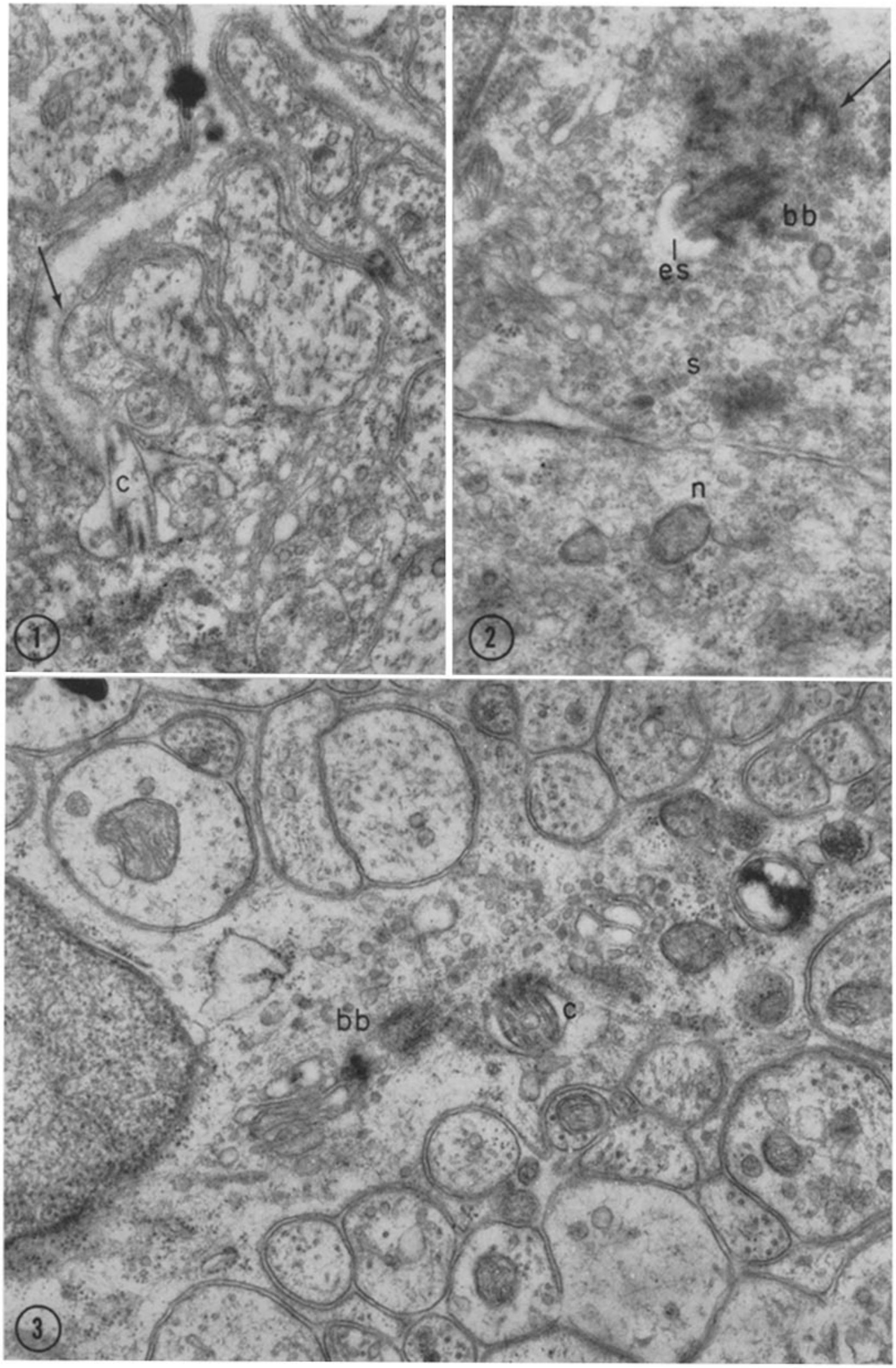
Ciliated Schwann cell enveloping a number of unmyelinated axons in the sphenopalatine ganglion. Only a few fibers are visible in the swollen ciliary shaft (*c*). The basement lamina (arrow) coats the Schwann cell cytoplasm and only the distal portion of the cilium. × 29,000.

FIGURE 2

Ciliated sheath cell (*s*) embracing a neuron (*n*) in the superior cervical ganglion. Projecting from the basal body (*bb*) into the extracellular space (*es*) is a short ciliary stub. At the arrow is indicated either the basal body of another cilium or a centriole surrounded by an unresolved cloud of osmiophilic material. A portion of the Schwann cell nucleus is included in the upper left corner. × 33,500.

FIGURE 3

A ciliated Schwann cell in a myenteric ganglion of the pylorus. In the center of the micrograph can be seen a nearly transverse section of a cilium (*c*) containing 9 pairs of fibers arranged peripherally around a membranous profile of circular outline. Cross-striated rootlet fibers extend from the basal body (*bb*) to the surface membrane delimiting a narrow channel of extracellular space in which the cilium is located. Enveloped singly or in groups by cytoplasmic processes of the Schwann cell are numerous unmyelinated axons which contain filaments, canaliculi, elements of the endoplasmic reticulum, mitochondria, and osmiophilic granules of various sorts. × 33,500.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ontogeny of cilia (21) is inadequate for the purpose of comparing the fine structure of these cilia with stages in the development of the ordinary motile cilia and flagella. The Schwann cell cilia could result from arrested development, abnormal deviation, or degeneration in the morphogenesis of complete cilia. Ciliated Schwann cells appear only in the sheaths of unmyelinated nerves. This difference in morphology suggests that the formation of myelin not merely constitutes a complex alteration in shape but reflects a profound change in the nature of the Schwann cell and that it should be considered as a further stage in the progressive differentiation of the Schwann cell.

The peculiar cilia of the Schwann cell might also be the products of specialization. But for what function? As Sorokin (20) has pointed out, there are no compelling reasons for assigning a sensory function as Barnes has done (2) to those modified cilia which lack the usual axial filaments. If these cilia are motile it is reasonable to expect their pattern of motion to differ from that of ordinary cilia. But in the absence of observations on living cells, we cannot determine whether Schwann cell cilia are motile or stationary.

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Figure 4

Section of a Schwann cell cilium in the superior cervical ganglion, showing the central component. × 33,500.

Figure 5

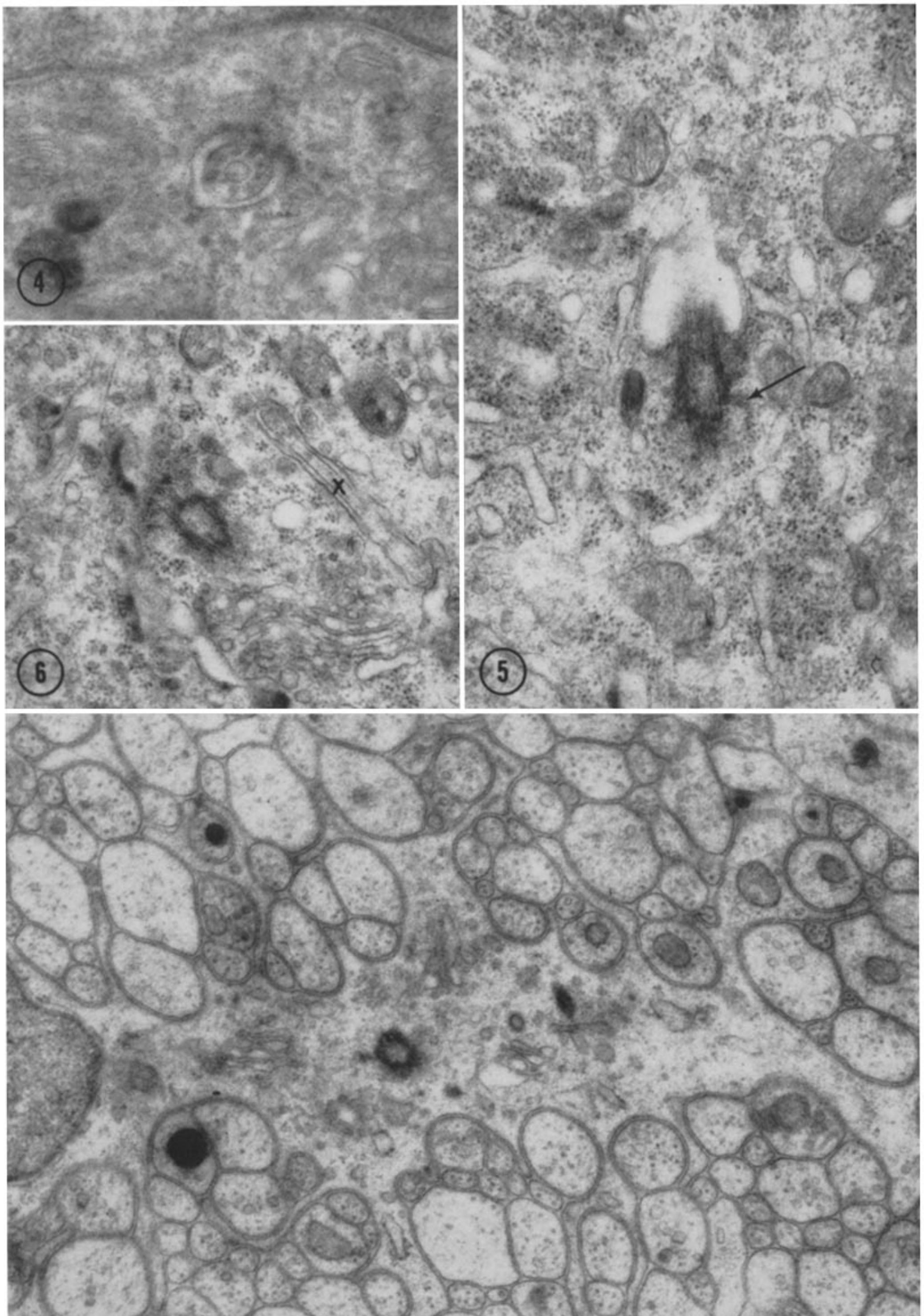
A basal body and the proximal portion of a cilium in a neuron of the superior cervical ganglion. Similar radially arranged coarse appendages (arrow) also occur on the basal bodies of cilia in Schwann cells. In the lower left corner is part of the nucleus. × 33,500.

Figure 6

Centriole and associated satellite bodies in a neuron in the superior cervical ganglion. The slender mass of cytoplasm at *x* probably belongs to a satellite cell which has penetrated deeply into the perikaryon. × 33,500.

Figure 7

Oblique section through a Schwann cell centriole and associated satellite body in the neuropil of a ganglion of Auerbach's plexus. Duodenum. × 21,000.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