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The ultrastructure of the sensory nerve endings in the articular capsule of the knee joint of the domestic cat (Ruffini corpuscles and Pacinian corpuscles)

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INTRODUCTION

Numerous authors have studied the innervation of articular capsules (See Gardner, 1950; Barnett, Davies & MacConaill, 1961). Polacek (1966) provides a wide-ranging and detailed review of light microscope studies up to that time. He studied the innervation of articular capsules in various mammals and birds noting the structure and variability of the sensory nerve endings. Goglia & Sklenska (1969) described the ultrastructure of Ruffini corpuscles in the articular capsule of the knee joint in the domestic rabbit. The ultrastructure of the Pacinian corpuscles in articular capsules has not yet been described.

The functions of the various nerve endings in articular capsules have been discussed by Boyd & Roberts (1953), Boyd (1954), Ecklund & Skoglund (1960), Skoglund (1956; 1973) and Burgess & Clark (1969).

Freeman & Wyke (1967) and Wyke (1973) have published detailed light microscope studies of the nerve endings in the knee joint capsules of the domestic cat.

The current paper examines the ultrastructure of the nerve endings of the knee joint capsule in the domestic cat and compares them with the mechanoreceptors of the skin (Halata, 1975).

MATERIAL AND METHODS

Five adult cats (*Felis silvestris f. catus L.*) were anaesthetized by intraperitoneal injection of Nembutal® (80 mg/kg body weight). The animals were perfused via the left ventricle with a glutaraldehyde solution (6 % in 0·05 M Millonig phosphate buffer, pH 7·2). After preparation of the knee joint the articular capsule was diced (length of edge approximately 2 mm), fixed in a glutaraldehyde solution for one hour and post-fixed in 1 % OsO_4 solution in 0·1 M Millonig phosphate buffer with the addition of 1 % saccharose, at a temperature of 2–4 °C for 2 hours. The material was embedded in Epon 812 by the method of Luft (1961).

Semithin sections for light microscopy, and ultrathin sections for electron microscopy, were cut on either a Reichert (OmU2) or a Porter–Blum ultramicrotome. The semithin sections were stained with toluidine blue and pyronin by the method of Ito & Winchester (1963), and the ultrathin sections were contrasted with uranyl acetate and lead citrate by the method of Reynolds (1963). Sections were visualized in a Philips 300 electron microscope working at 60 kV.

RESULTS

Two types of sensory nerve corpuscle were seen in the knee joint capsule of the domestic cat – Ruffini corpuscles and encapsulated corpuscles with an inner core (Pacinian corpuscules).

Ruffini corpuscles are found chiefly in the stratum fibrosum of the capsule. They occur in the vicinity of blood vessels and are very variable. They are 300–800 μm long and approximately 300 μm wide. They are composed of 2–6 cylinders, each consisting of an afferent axon with its dendritic processes and terminal processes, Schwann cells, endoneural connective tissue and capsule (Figs. 1–4*d*).

The afferent axon of a cylinder is myelinated and has a diameter of 3–4 μm. It is a process of a stem axon, the diameter of which is 8–12 μm.

After a short course inside a cylinder, the afferent axon loses its myelin sheaths and, at the last node of Ranvier, divides into 2–4 non-myelinated dendrites. These non-myelinated branches take a spiral course parallel to the longitudinal axis of the cylinder, ramify, and develop various kinds of swellings – discs, grooves and loops. Each of the swellings contains clumps of mitochondria, vesicles with a diameter of 60–80 nm, neurotubules and neurofilaments, and in some cases clumps of glycogen granules. The swellings give rise to digitate processes of varying length, with a width of approximately 0·5 μm. They contain only vesicles and occasional glycogen granules. In the Ruffini corpuscles the digitate processes form a system of loops which are contiguous to fascicles of collagen fibres. The nerve endings and their digitate processes are enveloped by Schwann cells and their lamellar processes.

The Schwann cells may envelop the nerve swellings with up to three lamellae (Figs. 4*a–c*). The number of cytoplasmic lamellae is unrelated to the size of the swelling. The lamellae may be absent in some parts of the nerve endings (Fig. 4*b*, *c*). Schwann cells, their processes, and the lamella-free areas of the nerve swellings are enveloped by a basal lamina. Desmosome-like membrane contacts occur not only between two cytoplasmic lamellae of Schwann cells, but also between a nerve ending and a Schwann cell (Fig. 4*c*). The Schwann cells form lamellar septa between the collagen fibre fascicles of the cylinder in a Ruffini corpuscle. The septa are not in contact with the nerve swellings and their digitate processes. The septa-forming processes of the Schwann cells are enveloped by a basal lamina, unlike the processes of the fibrocytes. The nuclei of the Schwann cells are in the centre of a cylinder.

The endoneural connective tissue of a cylinder consists of bundles of collagen fibres and fibrocytes. The cytoplasm of the fibrocytes contains clumps of glycogen granules. Bundles of collagen fibres run parallel with the longitudinal axis of the nerve ending inside the tubules of the cylinder formed by the septa of Schwann cells.

The capsule of each cylinder of a Ruffini corpuscle is a continuation of the perineurium of the axon (Figs. 3*c* and 4*d*). The number of layers making up a capsule ranges between two and eight. Most corpuscles possess a capsule consisting of four layers of thin, flat cells. In the region of the myelinated axon the capsule is complete and forms capsular septa between the individual cylinders of the nerve endings. The septa consist of one to two layers of perineural capsular cells.

The layers of the capsule are formed by flat cells which are interconnected with desmosome-like contacts. The thickness of a layer is 0·5–3·0 μm. The outer surfaces of the cytoplasmic membrane are covered by a basal lamina. The basal laminae of two adjacent layers of the capsule are separated by a 0·2–5·0 μm gap in which

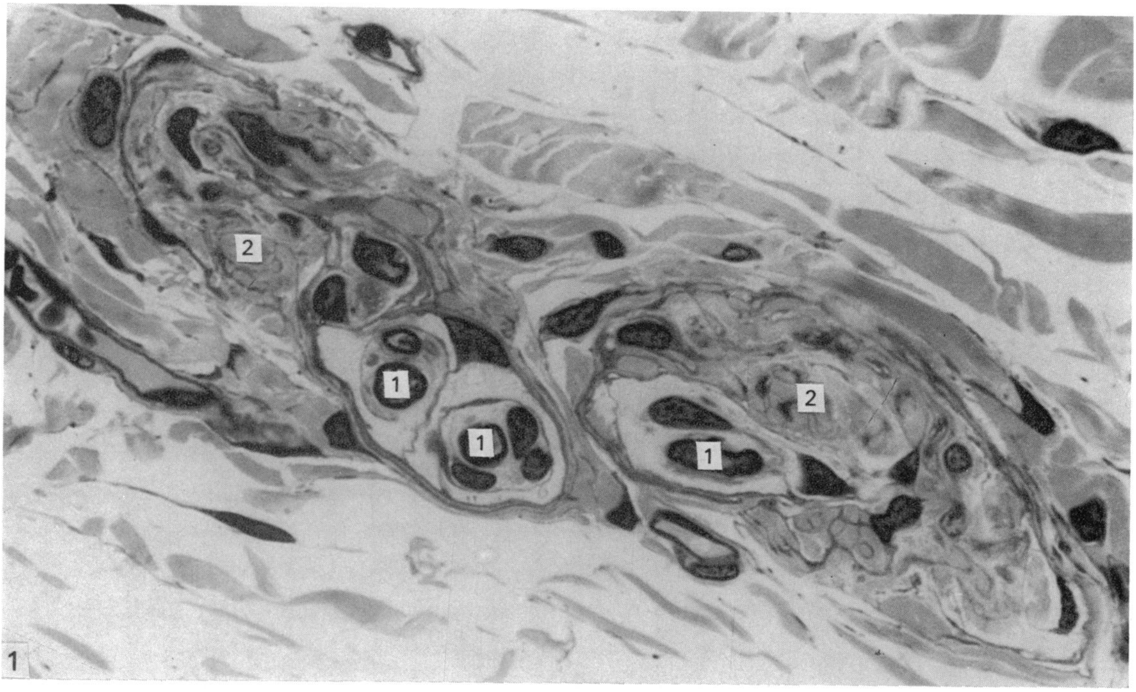
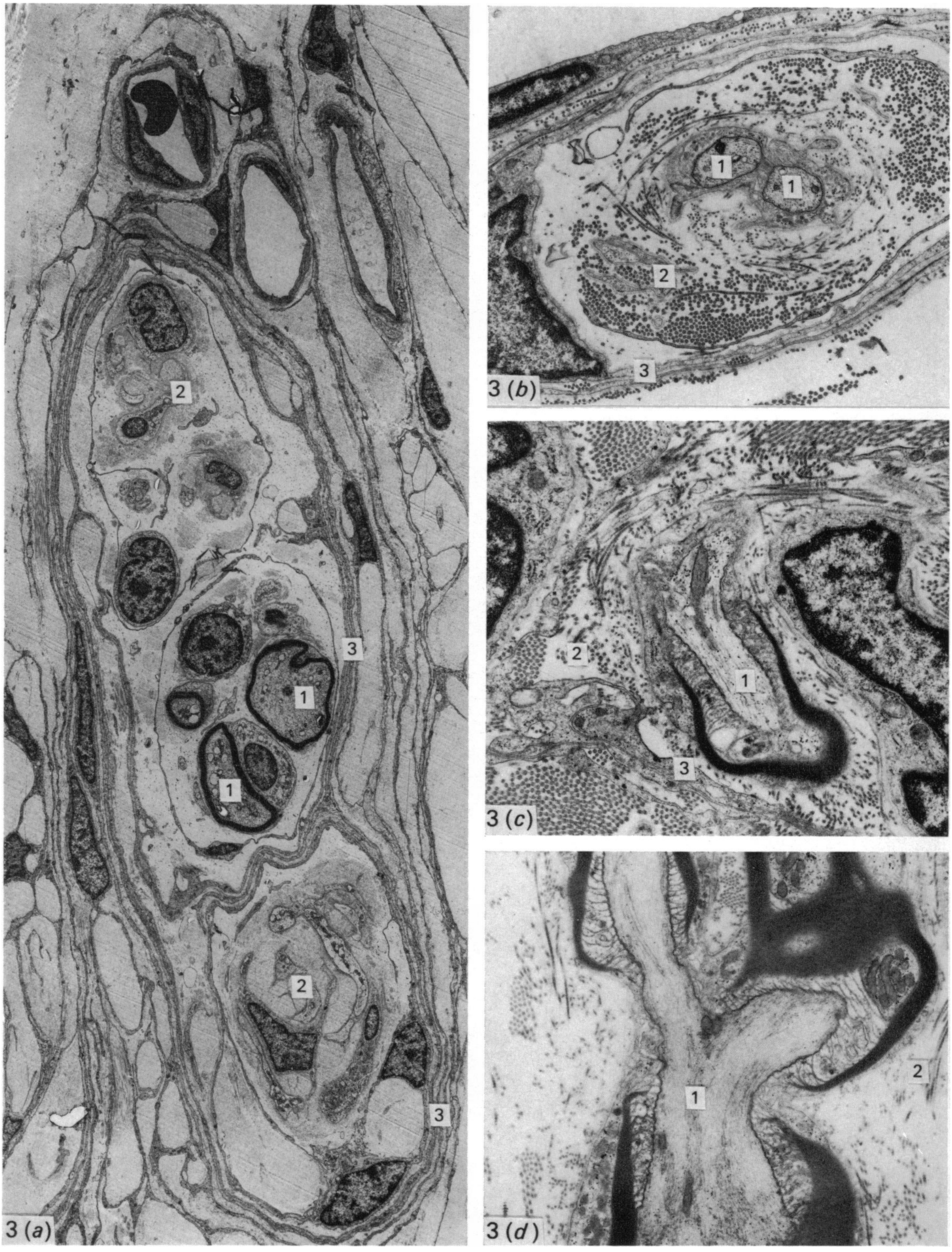


Fig. 1. Ruffini corpuscle of the stratum fibrosum of the knee joint capsule; cross section. 1, afferent myelinated axon; 2, non-myelinated nerve fibres with Schwann cells. Semithin section. ×900.

Fig. 2. Ruffini corpuscle; cross section. 1, afferent myelinated axon; 2, cylinder of the Ruffini corpuscle with nerve swellings and Schwann cells; 3, blood vessels; 4, capsule of the cylinder. ×2000.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collagen fibres run parallel to the longitudinal axis of the corpuscle. The cytoplasm of the capsule cells contains mitochondria, ergastoplasm, free ribosomes and clumps of glycogen granules. The membrane vesicles have a diameter of 80 nm. The capsule of a Ruffini corpuscle frequently shows openings at the distal pole of the cylinder through which the collagen fibres leave the nerve ending and mingle with the collagen fibres of the stratum fibrosum in the articular capsule. In addition to the collagen fibres, some of the digitate processes of the nerve swellings leave the cylinder at the pole, and occasionally the nerve swellings themselves also leave. These terminal portions of the nerve endings have a similar structure to the free nerve endings in the skin of the cat. They are situated between the collagen fibres of the stratum fibrosum of the articular capsule, and are enveloped by Schwann cells with a basal lamina.

The second type of nerve ending in the knee joint capsule is represented by simple encapsulated corpuscles with an inner core (Pacinian corpuscles). They are situated near blood vessels at the boundary between the stratum synoviale and the stratum fibrosum. The corpuscles lie singly or in groups of up to five. In rare cases a corpuscle is actually inside a nerve fibre fascicle (Fig. 5*b*). In such cases the corpuscles do not have a capsule of their own but are enveloped in the perineurium of the nerve.

The encapsulated corpuscles with an inner bulb are oblong, being 20–40 μm wide and 150–250 μm long. Each corpuscle consists of an afferent axon, a lamellar system of Schwann cells (inner core), a space between the inner bulb and the capsule (subcapsular space) and a capsule which is a continuation of the perineurium of the nerve fascicle.

The afferent nerve fibre is myelinated and has a diameter of 3–5 μm. The last node of Ranvier is inside the inner core of the corpuscle (Figs. 5*a* and 6*c*). In the last node of Ranvier the cytoplasmic processes of the Schwann cells are connected by desmosome-like structures. The Schwann cell of the node of Ranvier is overlapped by the cytoplasmic lamellae of the inner core cells, and the basal lamina of the Schwann cell of the afferent axon passes into the basal membrane of the inner core. After losing its myelin sheath, the axon runs in the centre of the inner core. In cross section the axon is oval and the axoplasm contains mitochondria and neurotubules at the periphery and neurofilaments in the centre. The axon extends digitate processes of varying length into the spaces of the inner core. The processes contain clumps of vesicles with a diameter of 60 nm. The final portion of the axon in the inner core shows a bulbous swelling, and contains a large number of mitochondria. The terminal swelling extends processes, resembling those of the axon, into the spaces between the lamellae of the inner core.

The inner core of the Pacinian corpuscle is formed by a lamellar system of modified Schwann cells. The outer lamellae of the inner core are wider (4–6 μm) than the inner ones. Cell nuclei are confined to the outer cytoplasmic lamellae of the

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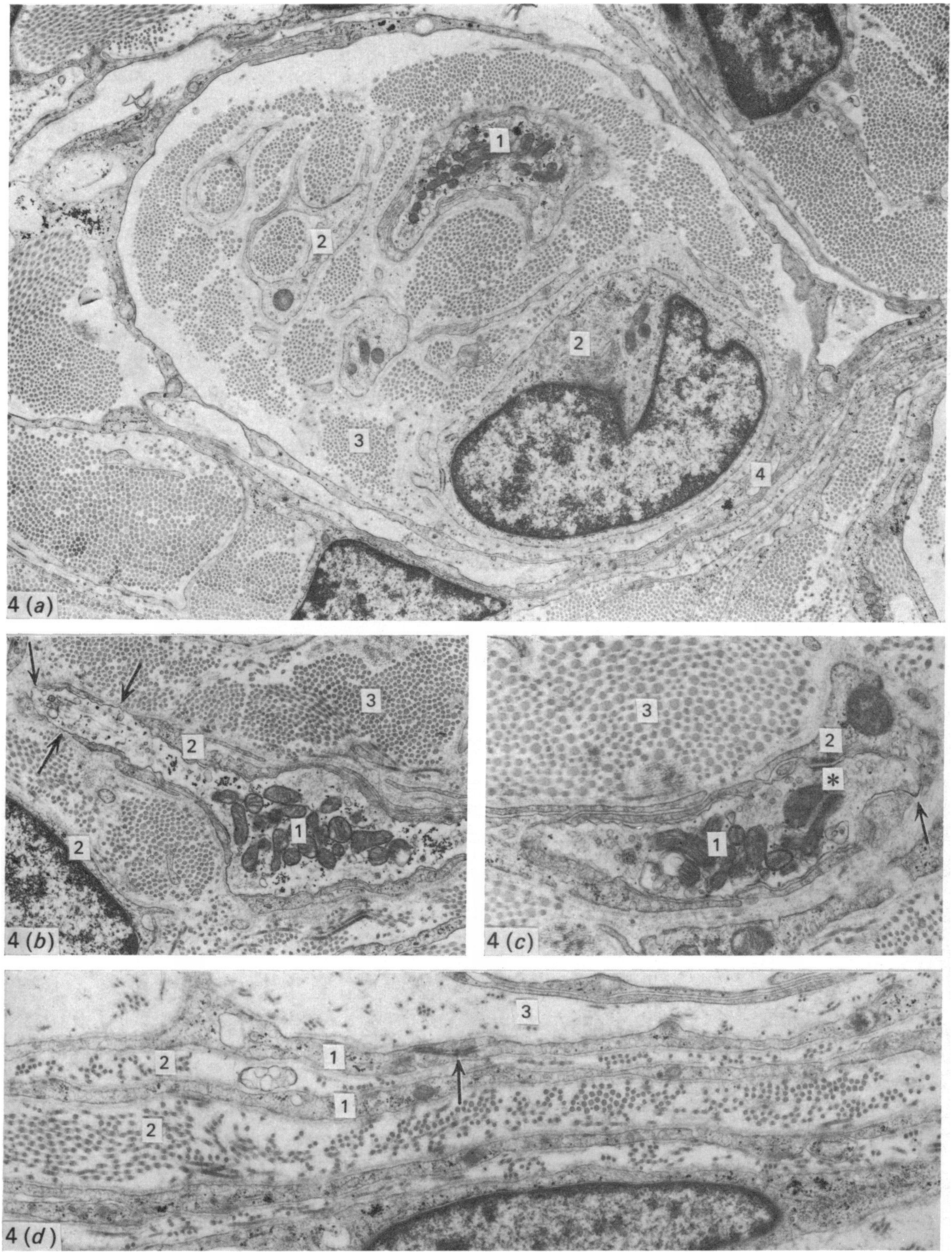
Fig. 3 (*a*). Ruffini corpuscle; cross section. 1, afferent myelinated axon; 2, cylinder of the Ruffini corpuscle which shows a swelling of a nerve, and Schwann cells with cytoplasmic lamellae; 3, capsule of the cylinder. ×2500. (*b*). Two non-myelinated afferent axons in the cylinder of a Ruffini corpuscle; cross section. 1, non-myelinated branches of the afferent axon; 2, endoneural connective tissue with processes of the Schwann cell; 3, capsule of the cylinder. ×7600. (*c*). Last node of Ranvier of the cylinder of the Ruffini corpuscle; longitudinal section. 1, afferent myelinated axon; 2, endoneural connective tissue; 3, perineurium. ×9000. (*d*). Last full node of Ranvier and the branching of a stem axon, longitudinal section. 1, stem axon; 2, endoneural connective tissue. ×8500.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inner core. In the vicinity of the flat cell nuclei the cytoplasm contains the Golgi apparatus, mitochondria, ergastoplasm, free ribosomes and microfilaments. The inner cytoplasmic lamellae lying close to the axon are thinner (0·2–2·0 μm). Their cytoplasm contains only free ribosomes and filaments. The outer as well as the inner lamellae exhibit rich membrane vesiculation.

A cross section through the inner core shows that cytoplasmic lamellae are arranged around the axon in two concentric semicircles. The semicircles are separated by two longitudinal spaces which extent from the outer surface of the inner core to the axon. The lamellar system of the inner core is enveloped by a basal lamina. Collagen fibres run between the lamellae of the inner core parallel with the longitudinal axis of the corpuscle. In some areas we have found desmosome-like structures between the cytoplasmic lamellae of the inner core. The collagen fibres of the longitudinal gap reach to the processes of the axon.

The subcapsular space of the Pacinian corpuscle is 3–10 μm wide and lies between the basal lamina of the inner core and the inside layer of the capsule. The subcapsular space contains collagen fibres and fibrocytes. The collagen fibres run either spirally or parallel to the longitudinal axis of the corpuscle. The fibrocytes extend long, discoid processes between the collagen fibres. The cytoplasm of the fibrocytes is more electron-dense than that of either the inner core cells or the cells of the capsule. The cytoplasm of the fibrocytes frequently contains clumps of glycogen granules.

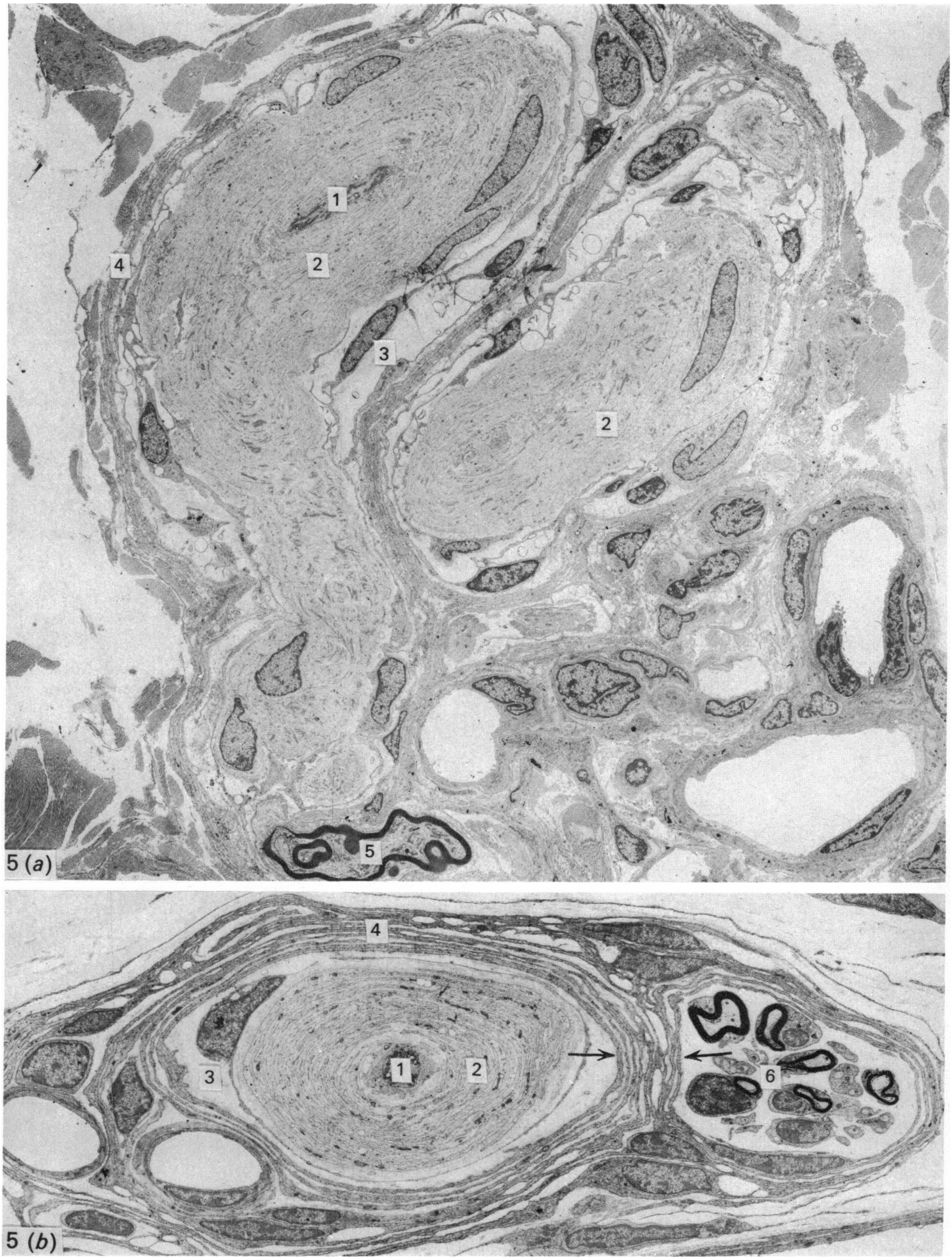
The capsule of the corpuscle is a continuation of the perineurium of the afferent nerve. Like the perineurium, the capsule consists of 4–8 layers of flat cells, with the individual layers being joined by desmosome-like structures. The outer side of the cytoplasmic membrane of the capsule cell is covered by a basal lamina. Collagen fibres run between the layers of the capsule cells parallel with the longitudinal axis of the corpuscle. The capsule cells show rich microvesiculation, similar to those of Ruffini corpuscles (Fig. 6*d*).

DISCUSSION

The articular capsule of the knee joint of the domestic cat is richly innervated. The nerves consist of both myelinated and non-myelinated nerve fibres (Hagen-Torn, 1882; Samuel, 1952; Polacek, 1966). The myelinated nerve fibres are afferent, the non-myelinated ones vegetative and are thought to innervate the blood vessels of the capsule (Polacek, 1966). Most of the nerves follow the blood vessels and form nerve plexuses. One plexus is found between the muscle layer and the capsule (periarticular nerve plexus), another is in the stratum fibrosum of the articular capsule (Polacek, 1966).

The afferent myelinated axons terminate in different types of mechanoreceptors, the general function of which is, according to Skoglund (1956; 1973) and Wyke

Fig. 4 (*a*). Cylinder of a Ruffini corpuscle; cross section. 1, nerve swelling with mitochondria; 2, Schwann cells with cytoplasmic processes; 3, endoneural connective tissue; 4, perineural cells of a capsule. ×7600. (*b, c*). Nerve swellings of a Ruffini corpuscle; cross section. 1, nerve swelling with mitochondria, vesicles, and granules of glycogen; 2, cytoplasmic processes of Schwann cells; 3, endoneural connective tissue; (arrows), lamellae-free areas of the nerve swelling are enveloped by a basal lamina; (*), desmosome-like contacts between a nerve ending and a Schwann cell. 4*b*, ×11000; 4*c*, ×17000. (*d*). Capsule of a Ruffini corpuscle. 1, flat perineural cells of the capsule with a basal lamina; 2, layers of collagen fibrils; 3, subcapsular space with endoneural connective tissue; (arrow), desmosome-like contacts between two capsule cells. ×13000.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(1967; 1973) to receive information concerning the tension and the changes in tension of the collagen fibres in the capsule. According to Wyke (1973) this information may regulate the activity of the articular musculature.

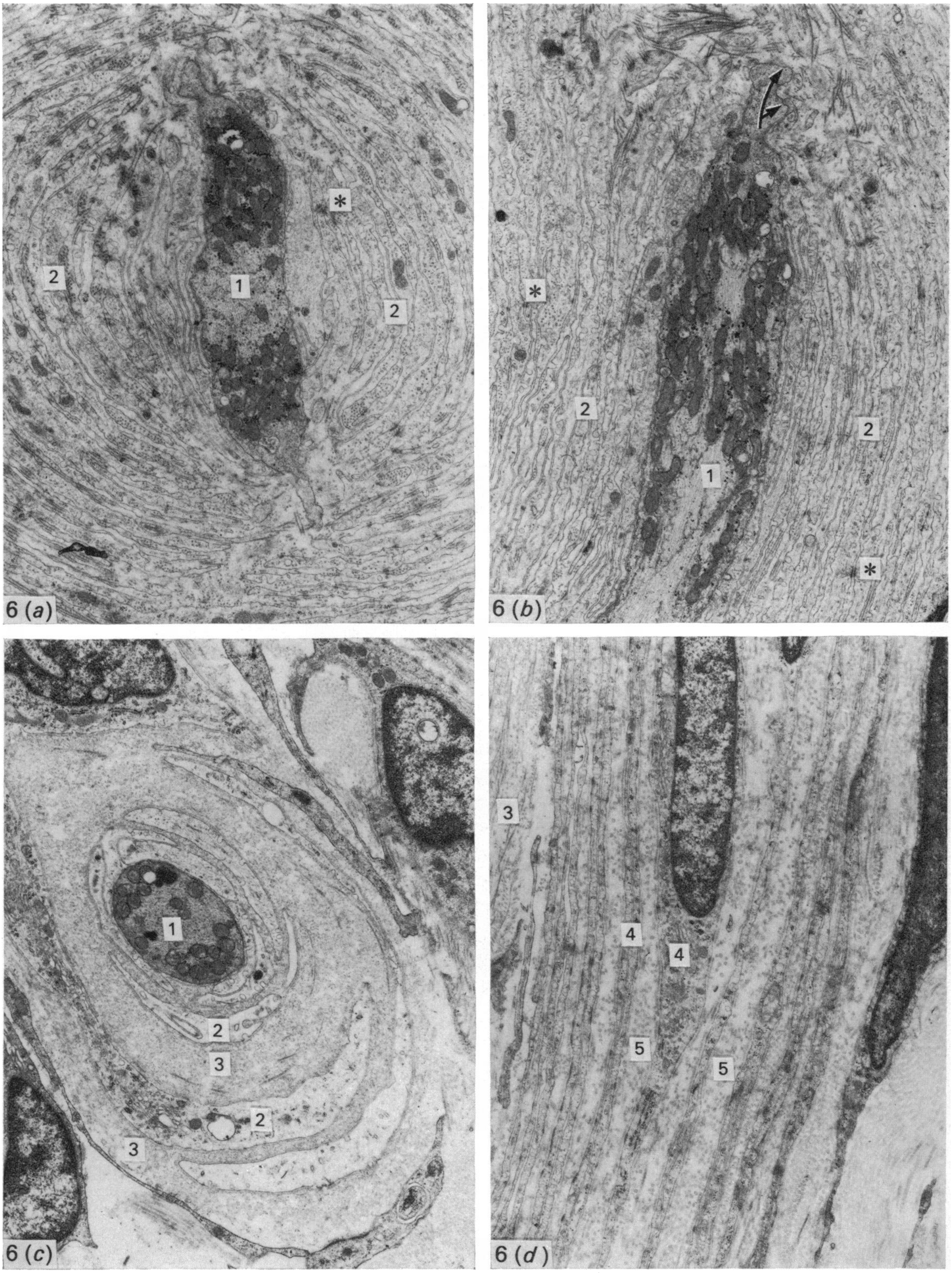
According to Polacek (1966) there are three types of nerve endings in articular capsules, namely free nerve endings, Ruffini corpuscles, and simple corpuscles with an inner core. These nerve endings frequently occur in groups and, according to Stilwell (1957) form proprioceptive triads. Polacek (1966) calls such triads 'receptive fields'. The majority of receptors are situated at the boundary between the stratum fibrosum and the stratum synoviale. In the stratum synoviale Polacek found only a few axons accompanying blood vessels and terminating as free nerve endings. Like Freeman & Wyke (1967), the author has found only non-myelinated axons near blood vessels in the stratum synoviale, none of which terminated as free nerve endings. Free nerve endings were only found in the stratum fibrosum in the immediate vicinity of Ruffini corpuscles and it is believed that these arise from the cylinders of these corpuscles.

Ruffini corpuscles were found chiefly in the stratum fibrosum. They showed very great variability. Ruffini (1893) himself describes them as 240–1350 μm long and 50–200 μm wide. Polacek (1966) has given a detailed description of the different types of Ruffini corpuscle. He distinguishes five variants: simple sprays, encapsulated sprays, myelinated sprays, encapsulated spirals and sprays with concentrically arranged auxiliary cells. With the electron microscope, the author has found that Ruffini corpuscles are made up of several unit cylinders, each being supplied by a myelinated axon. Corpuscles vary not only in the number of cylinders but also in the structure of their capsule. Most corpuscles have a capsule which is complete at the proximal end but has gaps at the distal end. Some of the nerve swellings leave the cylinder through these gaps and extend into the connective tissue of the stratum fibrosum. Such corpuscles belong to the first two variants described by Polacek (1966) – simple sprays and encapsulated sprays. The corpuscles that Polacek (1966) described as myelinated sprays and encapsulated spirals have not been observed.

The longitudinal axis of a cylinder runs parallel to the fascicles of collagen fibres of the stratum fibrosum. Where a corpuscle is situated between several bundles of collagen fibres running in different directions, the directions of the longitudinal cylinder axes vary accordingly. By this means a Ruffini corpuscle is probably able to monitor the tension of several bundles of collagen fibres in the stratum fibrosum.

The afferent axon of a Ruffini corpuscle is myelinated. As described by Freeman & Wyke (1967), there is a stem axon with a diameter of 13–17 μm which gives several branches each with a diameter of 4–5 μm. These divide again and supply individual cylinders of the corpuscle. The nerve fibres serving individual cylinders of a Ruffini corpuscle have diameters of only 2–3 μm. This agrees with the more recent measurements of Novotny (1973). The fibres branch dichotomously at the last node of Ranvier, within the cylinder. The non-myelinated fibres may divide repeatedly in their further course and extend in wide spirals to the distal end of a cylinder. These fibres form discoid swellings in their course, and the latter contain numerous

Fig. 5 (*a*, *b*). Pacinian corpuscles from the subsynovial boundary layer of a joint capsule. 5*a*, longitudinal section, 5*b*, cross section. 1, non-myelinated axon inside the inner core; 2, cytoplasmic lamellae of Schwann cells of the inner core; 3, subcapsular space with endoneural connective tissue; 4, cells of the capsule; 5, afferent myelinated axon of the last node of Ranvier; 6, nerve with myelinated and non-myelinated nerve fibres; (arrows), perineurium which forms the capsule of the Pacinian corpuscle. $\times 1700$.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mitochondria, and vesicles which appear empty under the electron microscope. Similar swellings were seen by Goglia & Sklenska (1969) in Ruffini corpuscles in the joint capsules of the rabbit, and by Chambers *et al.* (1972) in the Ruffini corpuscles of the hairy skin of the domestic cat. Hanker, Dixon & Moore (1973) interpret the clumps of mitochondria as indicating high energy consumption associated with sensory transduction. These swellings give rise to digitate processes which do not contain mitochondria but often contain vesicles. These processes increase the surface area of the nerve swelling and are anchored firmly in the endoneural connective tissue. Every axon inside a cylinder contains several consecutive swellings. These swellings are enveloped by 1–3 Schwann cell lamellae and their basal laminae. Some areas lack Schwann cells and are covered only by a basal lamina. The author shares the view of Chambers *et al.* (1972) and Andres (1974) that these sites may serve to transmit tension from the connective tissue fibres of the articular capsule to the nerve swellings. A similar relationship between nerve endings and connective tissue is shown by the lanciform nerve endings of the sinus hairs of the cat (Halata, 1975), and Meissner's corpuscles in the digital skin of men and monkeys (Chouchkov, 1972, 1973; Andres & v. Duering, 1973). The structure of Ruffini corpuscles resembles that of the genital corpuscles of rat (Patrizi & Munger, 1966) and man (Polacek & Malinovsky, 1971). Corpuscles of similar structure are also found under the papillae fungiformes of various mammals (Beckers & Eisenacher, 1975).

Functionally (Freeman & Wyke, 1967; Wyke, 1973; Skoglund, 1973), Ruffini corpuscles are slowly adapting mechanoreceptors. According to Wyke (1973) they have a very low threshold, react to changes in pressure within the joint, and signal static and dynamic tensile stresses in the articular capsule.

The simple encapsulated corpuscles with an inner core in the knee joint capsule of the domestic cat are often regarded as small Pacinian corpuscles. Their structure is discussed in detail in a review by Freeman & Wyke (1967). Like Polacek (1966), the present author found these corpuscles chiefly in the vicinity of blood vessels at the boundary between the stratum fibrosum and the stratum synoviale. They are arranged in groups of up to 5 corpuscles. Two corpuscles are frequently seen with a common perineural capsule. Occasionally a corpuscle lies within a nerve bundle.

The afferent axon of a Pacinian corpuscle is always myelinated. According to Freeman & Wyke (1967) there is a stem axon with a diameter of 8–12 μm, which gives branches of 4–5 μm diameter to each corpuscle. This agrees with the present findings, and also with those of Novotny (1973), who found the diameters of corpuscles from the knee joint capsule of the cat to be between 4 and 5·75 μm. The last node of Ranvier lies inside the inner core, and the basal lamina of the Schwann cells of the axon fuses with the cells of the inner core.

The axon runs in the centre of the inner core and extends digitate processes into the gaps between the lamellae; the processes may be in contact with the collagen

Fig. 6 (*a*). Inner core of a Pacinian corpuscle; cross section. 1, final portion of an axon with digitate processes in the spaces of the inner core; 2, cytoplasmic lamellae of the inner core with desmosome-like contacts (*). ×9000. (*b*). Inner core of a Pacinian corpuscle; longitudinal section. 1, final portion of an axon with mitochondria, vesicles and granules of glycogen; (arrows), digitate processes of an axon in the spaces of the inner core; 2, cytoplasmic lamellae of the inner core with desmosome-like contacts (*). ×9300. (*c*). Inner core near the last node of Ranvier; cross section. 1, non-myelinated axon; 2, Schwann cells; 3, endoneural connective tissue. ×9000. (*d*). Capsule of a Pacininian corpuscle; longitudinal section. 3, endoneural connective tissue; 4, perineural cells of the capsule; 5, layers with collagen fibrils. ×9000.

fibres of the inner core. The structure of the corpuscle resembles that of the corpuscle from the hairless skin of the cat (Halata, 1975). The variation in the size of corpuscles, described by Polacek (1966), results from differences in the number of Schwann cell lamellae in the inner core and in the number of layers in the perineural capsule.

According to Boyd (1954), Freeman & Wyke (1967), Wyke (1973) and Skoglund (1973), the Pacinian corpuscles of the articular capsule are rapidly adapting mechanoreceptors. According to Wyke (1973), they have a very low threshold, and work as dynamic mechanoreceptors at the beginning and end of a movement.

SUMMARY

Two types of mechanoreceptor have been found in the articular capsule of the knee joint of the domestic cat – Ruffini corpuscles and Pacinian corpuscles.

Ruffini corpuscles are situated in the stratum fibrosum and consist of 2 to 6 cylinders. Each cylinder is made up of an afferent axon (diameter 3–4 μm), its swellings and terminal processes, Schwann cells enveloping the nerve swellings and terminal processes, endoneural connective tissue and a perineural capsule. The nerve swellings of a cylinder extend digitate processes into the endoneural connective tissue. Schwann cells form septa in the cylinders. The perineural capsule is incomplete in Ruffini corpuscles.

The Pacinian corpuscles are 20 to 40 μm wide and 150–250 μm long. They are situated in groups of up to five at the boundary between the stratum synoviale and the stratum fibrosum. The afferent axon is myelinated (diameter 3–5 μm). Its terminal portion is inside the inner bulb which is formed of modified Schwann cells. Each corpuscle is enveloped by a perineural capsule (4–8 layers). The ultrastructure of the Pacinian corpuscles is compared with the ultrastructure of the skin receptors in the cat.

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