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# THE STRUCTURE OF HUMAN DIGITAL PACINIAN CORPUSCLES (CORPUSCULA LAMELLOSA) AND ITS FUNCTIONAL SIGNIFICANCE

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## HISTORICAL

The lamellar corpuscles were first seen by Vater (1741) who found them attached to the digital nerves in large numbers. Without describing their structure or function he called them Papillae nerveae. The corpuscles were shown in a drawing and the specimens were preserved in the anatomical museum (Göttingen), yet Vater's discovery was forgotten until a hundred years later when Pacini (1835, 1840) rediscovered them and described their lamellar structure. He found that spaces between the lamellae contained a quantity of fluid and that the lamellae were connected by a ligament (ligamentum intercapsulare) at the distal pole of the corpuscle. Pacini thought that the structures were terminal ganglia concerned with animal electricity and magnetism. Lacouchie (1843) suggested that Pacinian corpuscles belonged to the lymphatic system and that the 'central canal' opened into a lacteal. Henle and Kölliker (1844) found that the lamellae of the corpuscle consisted of cells and two layers of fibrillar tissue, the outer layer being transverse and the inner longitudinal. They also found blood vessels around and inside the corpuscle and observed that a medullated fibre ended by an enlargement inside it, often after a division. They suggested that Pacinian corpuscles were electric organs comparable with those of some fishes. Mayer (1844) found that the corpuscle consisted of an outer fibrous part and an inner glandular portion with a duct leading out of it. Herbst (1848), in his monograph, rejected the suggestion that the Pacinian corpuscles were terminal ganglia, electric organs or glands and firmly stated that they represented nerve endings. He described the corpuscle as consisting of four systems: peripheral, middle and inner capsules and the central cavity; the latter containing a nerve fibre which frequently after some ramification ended in a swelling. He gave an extensive account of variations of the corpuscles and their distribution among mammals.

Although the lamellar corpuscle was the first general nerve receptor organ recognized by anatomists and is easily demonstrated by most histological methods, yet, as is apparent from the review of the literature, its structure, nerve supply and functions have been and are still in dispute.

#### Structure

#### LITERATURE

Hassall (1849) suggested that each lamella of the corpuscle consisted of two layers fused together, with the cells placed between them. Huxley (1854) stated that

\* On study leave from the East Pakistan Government.

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human Pacinian corpuscles neither possessed a central cavity nor true lamellae with spaces between them, but they consisted of a fibrillated granular substance containing nuclei arranged in layers. A nerve fibre occupied the central solid substance which had 'almost the appearance of cartilage'. Virchow (1858) suggested that the Pacinian corpuscles represented nerve endings with 'enormous development of perineural elements' around them. Engelmann (1863) considered that the substance of the inner bulb surrounding the nerve ending was myelin and that the outer bulb was derived from the neurilemma. Ciaccio (1864) considered that nuclei in the outer bulb of the Pacinian corpuscle were those of connective-tissue cells and that the streak between the lamellae described as a ligament by Pacini was, in fact, a blood vessel. Hoyer (1864), using a silver nitrate technique on mesenteric corpuscles, found that the inner surface of each lamella was lined with polygonal cells of an epithelial type. Michelson (1869) suggested that the lamellae were composed entirely of endothelial cells and that the inner bulb consisted of a cytoplasmic substance devoid of cell nuclei. Key & Retzius (1876), in their monograph on nerves and Pacinian corpuscles, supported Hassall's view that the lamellae of the outer bulb were double layers and suggested that they were derivatives of the perineural membrane with which they were continuous. They believed that both surfaces of the lamellae were lined by cells of irregular shape and that the inter-cellular spaces contained fine fibrils and some free cells which they termed 'Wanderzellen'. The inner bulb was derived from the fibrillar sheath of the nerve fibre with which it was continuous. A fibrous extension (ligamentum intercapsulare) of the inner bulb was sometimes observed towards the distal end of the corpuscle. Krause (1881) supported Virchow's view on the nature of the receptor organ and suggested that all terminal corpuscles consisted of a cellular inner bulb derived from the neurilemma or Schwann sheath and a fibrous outer envelope or bulb derived from the perineurium. He did not recognize two layers within the lamellae. Michailow (1908), on examining injected specimens of cat's mesentery, found that the inner bulb contained a glomerulus of blood capillaries and he believed that nuclei visible within the inner bulb belonged to wandering cells, while the outer bulb was devoid of blood vessels. Further, the corpuscle was surrounded by an elastic capsule to prevent its overdistension. Van de Velde (1909) observed a network of elastic fibrils surrounding the inner bulb and small vessels entering the corpuscle at its basal pole. Dogiel (1910) found that cell nuclei were not situated on the surfaces but lay within the lamellae which consisted of fine fibrils; small apertures were found as communications between the inter-lamellar spaces. He stated that small arteries entered the corpuscle along with the nerve and formed capillaries between the lamellae while a vein left the corpuscle at the same pole. Contrary to Michailow he found no blood vessels within the inner bulb. Schumacher (1911) found that each lamella of the mesenteric corpuscles consisted of two layers with cells enclosed between them. The corpuscle as well as the deeper lamellae were surrounded by a fine network of elastic fibrils which became fewer towards the inner bulb. He found blood vessels entering the corpuscle at various positions, but denied that they formed capillaries near the inner bulb, which he said also consisted of lamellae; they were, however, not circular as in the outer bulb, but formed symmetrical half-circles around the axon. Schäfer (1912) considered that the lamellae consisted of collagen

and elastic fibrils and were covered by endothelial cells, a single capillary accompanying the nerve as far as the core. Glees, Mohiuddin and Smith (1949) observed in injected Pacinian corpuscles of cat's mesentery that blood vessels entered the corpuscle at the same place as the nerve fibre and supplied the central core with capillary loops almost to its end.

# Nerve supply

Most observers have found that the Pacinian corpuscle is supplied by a single thick medullated fibre. Pappenheim (1846) found that the nerve ramified inside the corpuscle and its branches ended by union with one another. Jakubowitch (1860) supported by Ciaccio (1864) suggested that nerve fibres inside the corpuscle ended on nerve cells fusing with their nuclei. Beale (1867) observed that nerve fibre divided into 'lobes' inside the axis of the corpuscle, the lobes being connected to the nuclei of the lamellar cells; but some 'return fibres' being prolonged downwards to join the sheath of the main nerve so forming a closed circuit. Schäfer (1875) found that the nerve fibre ended in a swelling inside the central core and that the Schwann sheath was usually lost on entering the corpuscle, but the myelin sheath sometimes accompanied the nerve for some distance. Ranvier (1875) found, however, that the Schwann sheath extended farther into the corpuscle than the myelin sheath and that the inner bulb consisted of a granular substance with concentric zones and a few nuclei. Key & Retzius (1876) found that the corpuscle was supplied by one or two medullated fibres which lost their myelin and expanded showing fibrillation and ended by bulbous swellings, usually after ramification. Sala (1899), a pupil of Golgi, and Sokolow (1899), a pupil of Dogiel, using supravital methylene blue techniques, found that the cat's mesenteric Pacinian corpuscles had a dual nerve supply: a thick medullated fibre supplied the inner bulb whereas an independent fine beaded fibre formed a network around it similar to that which Timofeew (1896) described in the lamellar corpuscles of mammalian genitalia. Dogiel (1905), using Cajal's silver method on human and cat's Pacinian corpuscles, found that a medullated axon ramified repeatedly within the inner bulb; the branches twisted around each other showing swellings with neurofibrillar structure and ended by expansions of neurofibrils; but he did not find the Timofeew's apparatus. Michailow (1908), using the methylene blue technique, once more found the pericorpuscular network, but Van de Velde (1909), using Bielschowsky's silver impregnation method, did not see it and suggested that a network of elastic fibrils may have been mistaken for nerves. He found that the medullated nerve fibre ramified within the inner bulb and ended in a swelling which showed neurofibrils in its structure. He did not observe cells within the inner bulb. Botezat (1912) also denied the presence of cells in relation to nerve endings in mammalian Pacinian corpuscles, but found them in those of birds, describing them as 'tactile cells'. Boeke (1926), using Bielschowsky's technique, found syncytial continuity between the neurofibrillar system of the nerve ending and the texture of the surrounding lemmoblastic elements of the inner bulb-this finding being in conformity with Boeke's general view on the nature of nerve endings. Quilliam & Sato (1955), using osmic acid and gold chloride on the cat's mesenteric corpuscles, found it was supplied by a single medullated fibre; the myelin sheath

with recognizable Ranvier's nodes surrounding the proximal part of the intracorpuscular axon, the fibre ending at the distal segment of the central core, in branches with terminal swellings.

## Function

To the various historical views already mentioned, we have to add that of Palladino (1866) who suggested that the Pacinian corpuscles in man were electric multipliers subserving a tactile function and that the nerves entering the corpuscle from all directions ended on special nerve cells. Rauber (1865, 1867), in his extensive studies on the distribution of the Pacinian corpuscles, suggested that they served to measure muscular power and pain when found in relation to muscles, or the extent of movement when situated near a joint. Arndt (1875) found that the corpuscles were associated with blood vessels and had nothing to do with ordinary sensation, while Krause (1881) suggested that by their situation they were protected against changes of temperature and so were receptors of deep pressure and general sensation and that in the mesentery they reported its tension or the weight of the viscera. Thoma (1884), finding a considerable number of corpuscles in all parts of the aortic system, suggested that they were concerned with the regulation of blood pressure while Grosser (1901), observing a series of large Pacinian corpuscles near the arterio-venous anastomoses in the limbs of the bat, suggested that these might play some part as indicators of the activity of the anastomosis. Ramström (1908), studying the position of Pacinian corpuscles in human parietal peritoneum of the anterior abdominal wall, found them aggregated in groups along the line where transversus abdominis muscle becomes aponeurotic. In order to gain information about their function, he performed a series of experiments on patients undergoing abdominal operations under local anaesthesia and found that pressure of a spatula over the peritoneal surface of the anterior abdominal wall was not felt by the patient, whereas even a light touch over the same area of the skin was immediately recognized; repetition of the experiment with cooled or warmed instruments on the peritoneal surface did not produce the slightest sensation whereas a very exact sensation occurred when the overlying area of the skin was stimulated. On this evidence he rejected the suggestions that Pacinian corpuscles were pressure or temperature receptors. Michailow (1908) argued that the extensive distribution of the corpuscles in subcutaneous tissue, muscles, in the vicinity of joints, periosteum, in viscera and adventitia of blood vessels, showed that their function could not be connected with their position and suggested that they were concerned with the pressure of the peripheral circulation. Schumacher (1908) found that groups of Pacinian corpuscles were situated in the vicinity of the human glomus coccygeum which he described as a collection of arterio-venous anastomoses and suggested that here they might represent moisture regulators (eine Art von Feuchtigkeitsregulatoren) -the corpuscles would take up moisture and expand when tissue fluid was increased due to the enlarged capillaries and, as a result, the nerves of the inner bulb would be compressed and cause the arterio-venous anastomoses to open so that capillary circulation and tissue fluid is reduced. Later (1911) he enlarged his previous theory suggesting that adventitial Pacinian corpuscles of blood vessels were stimulated by the pressure of arterial pulsation and reported that mesenteric Pacinian corpuscles of the cat expanded when soaked in saline or when arterial pressure in the mesentery was increased by injection of its arteries. Schade (1923) suggested that Pacinian corpuscles were osmosensitive ('Schwellsinnesorgane') since they shrink in hypertonic and expand in hypotonic solutions. Clara (1925), investigating lamellar corpuscles of birds, came to the same conclusion as Schumacher, viz. that the corpuscles recorded changes of osmotic pressure and ionic concentration and that they were not associated with tactile functions in the ordinary sense. Adrian & Umrath (1929), in experiments with Pacinian corpuscles from the cat's toe, found that changes of temperature did not excite the receptor, while pressure gave an immediate discharge of impulses, the frequency of which varied with the pressure and declined gradually under a constant stimulus; they concluded that the corpuscles were organs responding to pressure stimuli and considered it possible that changes of blood pressure might sometimes provide an adequate stimulus, but since movements of joints and muscles and external pressure must occur so often, it was unlikely that the corpuscle could have any specific function in connexion with blood pressure and fluid regulation. Sheehan (1933b) studied Pacinian blood vessels in the cat's mesentery and suggested that impulses originating in the corpuscles might cause reflex contraction and dilatation of the vessels. He considered that they might have sympathetic innervation since they were supplied through splanchnic nerves. Woollard & Weddell (1935) considered that the lamellar corpuscles in the adventitia of limb blood vessels might be a starting point of a vascular reflex and that on standing up the afferent limb of the reflex would be excited by changes in the pressure of blood within the vessel. To test this possibility they blocked the femoral nerve with novocaine, so suppressing the afferent limb of the reflex. However, no difference in colour or temperature of the limb was observed on standing up and they concluded that the femoral artery was not a special region from which the vasomotor tonus of the lower extremity was regulated. Gammon & Bronk (1935), studying the discharge of impulses from Pacinian corpuscles in the mesentery of the cat, found that an elevation of intravascular pressure was an effective stimulus for the receptor and concluded that one of the functions of the Pacinian corpuscles in the mesentery was to signal the degree of distension of the mesenteric vessels. Gray & Malcolm (1950) also studied nerve impulses from mesenteric Pacinian corpuscles and found that they acted as a means of applying the mechanical stimulus to the axon and that there was no need to postulate a receptor cell or any other mechanism intermediate between the stimulus and the axon.

### MATERIAL AND METHODS

The observations reported are based on material from a hundred and fifty human subjects ranging in age from newborn babies to persons 93 years of age (Table 1).

In most cases the distal pad, both skin and subcutaneous tissue, from one or several fingers obtained at operation or at autopsy were studied and in a few instances, particularly in the case of infants and children, whole fingers were studied after the bone had been decalcified. For comparison a number of corpuscles from the cat's mesentery were also examined. The material was usually fixed in 10% commercial formalin, but other fixatives were also used in some instances. They included Bouin's solution, formol-bromide (Anderson, 1929), Fleming's solution (Cowdry, 1948) and absolute alcohol.

The specimens were embedded in paraffin wax and cut in serial sections perpendicular and parallel to the longitudinal axis of the finger. The thickness of the sections varied from 3 to  $12\mu$ . The staining methods of earlier investigators mentioned in the literature were repeated, including examination of unstained specimens. Examination of unstained specimens under polarized light was found

Age in years	Male	Female	Total
1st year of life	20	13	33
1–10	8	8	16
11-20	14	4	18
21-30	5	5	10
31-40	9	9	18
41-50	25	4	29
51-60	8	3	11
61-70	4	3	7
71-93	6	2	8
Total	99	51	150

Table 1. Distribution of the material by age and by sex

to be particularly helpful since it provides a reliable alternative method for the study of the myelin sheaths of the nerves and the arrangement and nature of the fibres. Elastic tissue was stained by Unna's orcein method, Weigert's elastic tissue stain and its modification by Hart, and by Gomori's aldehyde fuchsin method (Gomori, 1950). Stains for chondriome (Nassonov, 1923) were used on some adult material, but neither distinct chondriocontes nor mitochondria (Lawrentjew, 1926) were found in the inner bulb although some osmofile material could be detected near the unmyelinated part of the axon. Nerves were usually studied in frozen sections cut at  $20 \mu$ . Simplified Bielschowsky-Gross silver impregnation was used as a routine nerve staining technique (20% silver nitrate solution, 10 min.; three changes of 3% formalin solution in tap water, 15 min.; ammoniacal silver nitrate solution, 5 min.; two changes of 3% formalin solution, 5 min.; toning in approximately 0.05% gold chloride solution). For preparation of ammoniacal silver nitrate solution the first silver bath was used to which ammonia was added until the precipitate disappeared; then 50 % excess of ammonia was added to the bath. Some of the biopsy specimens intended for neurological studies were treated with hyalase for 20 min. prior to fixation in formalin (Weddell & Pallie, 1954). In paraffin sections myelin sheaths were stained by the Kultschitzky-Pal method. In frozen sections Anderson's modification of that method was used (Anderson, 1929). Myelin sheaths were also studied in specimens fixed with osmic acid and in unstained specimens by the use of optical polarization technique. The shape of the corpuscles and their vascular relationship was studied by means of wax plate reconstructions and graphic tracings.

Pacinian corpuscles were dissected apart by means of a micro-manipulator both in the fresh state and after maceration of the tissue in either 1% pepsin solution in 10% hydrochloric acid, or in trypsin solution (Medawar, 1941). All measurements referred to in this work were made from paraffin sections or from wax plate reconstructions. No corrections were made for shrinkage of the specimens either during fixation or embedding.

#### **OBSERVATIONS AND DISCUSSION**

### Distribution

Pacinian corpuscles in human digits were found in five positions: (1) the deep part of the palmar corium, (2) the palmar subcutaneous fat deep to the zone of sweat glands, (3) the sides of the middle and proximal phalanges adjacent to the periosteum, (4) between the flexor digitorum tendons and the palmar aspect of the middle and proximal phalanges and (5) at the attachments of some of the short digital muscles to the bases of proximal phalanges. In the case of the middle phalanx relatively few corpuscles were found in the midline area, instead they were concentrated in the subcutaneous tissue around the collateral digital nerves (nn. digitales palmares proprii) and the sides of the phalanx. None were found in the corium and subcutaneous tissue of the dorsal aspect of digits. A wax plate reconstruction of the radial half of a foetal index finger (204 mm. c.r. length) showed the following frequency of Pacinian corpuscles:

Distal phalanx	62 corpuscles
Middle phalanx	55 corpuscles
Proximal phalanx	61 corpuscles
Total (radial half of index finger)	178 corpuscles.

This study is mainly concerned with the structure and function of the first two groups (Pl. 1, fig. 1).

#### Microscopical appearance

Digital Pacinian corpuscles show considerable variations in shape and size even in one individual, but in their histological and neural structure they are more uniform than those in the mesentery where a range of 'transitional forms' are described along with the 'conventional types' by various authors (Ramström, 1908; Van de Velde, 1909; Dogiel, 1910; Sheehan, 1933*a*). The general shape of a digital lamellar corpuscle was found to be oval, sometimes slightly flattened or irregular, especially if packets of sweat glands were accommodated between them. The slightly thickened distal end is usually round while the proximal extremity tapers gradually towards the nerve fibre forming a stalk which is usually straight in a newborn child, but becomes increasingly sinuous or irregular as age advances. In the adult the sinuosity of the stalk is pronounced, and in old age it may constitute the major portion of the receptor so that a corpuscle may be cut across two or even three times in a single histological section (Pl. 1, P and P in fig. 2; cf. with text-fig. 1 and Pl. 3, fig. 23).

The average length of a corpuscle at birth ranges from 500 to  $700\mu$ ; the size increases gradually throughout life reaching 3-4 mm. in length, but in persons over 70 years of age the corpuscles show regressive changes, becoming smaller and irregular.

The growth of a corpuscle is controlled by two factors: (a) addition of new lamellae around the surface of the receptor and (b) retrograde growth of the inner bulb and its surrounding lamellae along the nerve fibre.

The two processes of growth are illustrated in Text-fig. 2 which shows a small corpuscle, the length of which is in relation to its breadth as 2:1. Surrounding the smaller corpuscle is the outline of a larger one of the same relative shape (as shown by the superimposed grid). The two corpuscles are so drawn that the amount of



Text-fig. 1. Drawing from a wax plate reconstruction showing superficial (right) and deep aspect (left) of two corial Pacinian corpuscles in relation to a large artery and a glomerular arteriovenous anastomosis (AN). Two veins (X and Y) draining the corpuscles join the outlets of the anastomosis. A large artery supplies the corpuscles and the anastomosis. N, nerve fibre entering the proximal end of the corpuscle. Figs. 2 and 3 (Pl. 1) and 36-40 (Pl. 4) are photomicrographs from this specimen. Distal pad of little finger. Female, 64 years.  $\times 42$ .

increase is uniform around the circumference and the distal extremity of the smaller corpuscle; this type of growth may occur by the development of new lamellae over the surface. The diagram now shows that proximal elongation has to be three times that of any other direction in order to maintain the original relation between length and breadth. Adult corpuscles usually become more elongated as the age advances, hence the ratio between retrograde and appositional growth must be more than **3:1.** As a result of retrograde growth the prenatal medullated axon is progressively incorporated within the receptor.

#### The outer bulb

The bulk of the corpuscle consists of an extensive outer bulb of specific structure and is devoid of nerves. It consists of a series of concentric lamellae separated from one another by inter-lamellar spaces containing a network of fibres, blood vessels and some free cells. The lamellae are less than one micron in thickness (Pl.1, figs. 8–10; Pl. 2, figs. 11–14) and consist of flattened cells arranged in a single continuous layer; they are supported by the fibres of the inter-lamellar spaces which are best demonstrated in specimens prepared with osmic acid (Pl. 1, figs. 5–7). As judged by their staining reaction these fibres appear to be of the collagen variety; specific elastic tissue stains fail to demonstrate any elastic elements (Pl. 2, figs. 21, 22). These histochemical findings can be confirmed by the use of polarized light



Text-fig. 2. Diagram showing the two types of growth as observed in digital Pacinian corpuscles: (a) apposition of lamellae around the surface and (b) retrograde growth of the inner bulb and the lamellae along the nerve. A ratio of 1:3 is required between appositional and retrograde growth to maintain a constant relationship between the length and breadth of the corpuscle. Any other ratio will change the shape of the receptor. As a result of retrograde growth, the prenatal medullated axon is progressively incorporated within the corpuscle.

since elastic fibres are not optically active unless under tension, whereas collagen fibres are positive uniaxial birefringent with respect to the long axis of the fibre (independent of the mounting medium). Fibres of the Pacinian corpuscles viewed through crossed polaroids show the properties of collagen material (Pl. 1, fig. 4). The dominant orientation of these fibres is circular, i.e., transverse to the major axis of the corpuscle (Pl. 1, T in fig. 4), but there is also a set of longitudinal fibres which, however, is much less distinct (Pl. 1, L in fig. 4). These fibres do not branch, but are more or less mingled with one another or grouped into minute bundles, which show a greater density over the surfaces of the lamellae, but otherwise appear to be evenly distributed in the inter-lamellar spaces in specimens that have not suffered from skrinkage. The arrangement and distribution of the fibres and their relationship to the lamellae are best demonstrated and compared if sections are cut in three perpendicular planes (Pl. 1, figs. 5–7). Early developing corpuscles (in foetuses of 80–130 mm. c.r. length) are cellular and do not contain fibres; at birth and in young children the fibres are few, but their quantity gradually increases during life.

The bodies of the cells constituting the lamellae are not easily demonstrated, but their nuclei can be shown by ordinary histological stains: most of these are flattened to such an extent that they appear as condensations of the lamellae in sections cut exactly perpendicularly to their surfaces (Pl. 1, fig. 10), while viewed from the surface the nuclei usually show an oval or elliptical shape, their long axes having no uniform orientation (Pl. 2, figs. 15, 16). Chromatin is evenly distributed throughout the nucleus; one, and occasionally two nucleoli are present, and in female specimens a mass of sex chromatin (Graham & Barr, 1952) next to the nuclear membrane can be recognized (Pl. 2, fig. 16, cf. with fig. 15). Most of the cells are confined to a single lamella (Pl. 3, fig. 31), but a certain number of them have cytoplasmic processes which cross the inter-lamellar spaces and form connexions between the lamellae. Such connexion is usually formed by a process which gains an attachment to the next lamella by a 'foot' (Pl. 1, A in figs. 9, 10; Pl. 2, A in fig. 11), but sometimes it joins a similar process of another cell (Pl. 1, fig. 8). Occasionally, the main portion of the cell body with its nucleus is found between the two lamellae which it connects (Pl. 1, B in fig. 9). The cytoplasmic process usually arises from that portion of the cell which is opposite to its nucleus (Pl. 1, A in fig. 9; Pl. 2, A in fig. 11), but occasionally it is asymmetrical (Pl. 1, A in fig. 10) and so sections of a certain orientation may show an inter-lamellar connexion without a nucleus related to it (Pl. 2, fig. 12). The outlines of the lamellar cells are demonstrated best when frozen sections or whole corpuscles are used and impregnated with silver (as employed when staining nerves); when lamellae after such treatment are isolated and flattened, the cell boundaries can be recognized as dark irregular cement-lines (Pl. 2, C in figs. 17, 18). Cell nuclei in digital Pacinian corpuscles usually occupy an eccentric or even a marginal position in the polyhedral cell body. It is interesting to note for comparison that cell nuclei in the lamellae of the cat's mesenteric corpuscles usually have a central position in the cell bodies (Pl. 4, fig. 35) and also that the area occupied by a single cell in the cat's mesenteric corpuscle is approximately twice as large as that in the human digital corpuscle (Pl. 4, fig. 35, cf. with Pl. 2, fig. 17, both photographs are reproduced at the same magnification). Some of the lamella cells show dark irregular patches (Pl. 2, A in fig. 18) which are apparently the attachment or 'foot' areas of cells from neighbouring lamellae (Pl. 2; cf. A in fig. 18 with A in fig. 11). The cells within a lamella are firmly cemented together since application of a micro-manipulator on an isolated lamella fails to produce any separation or cleavage lines along the junctions, even if some maceration has been done prior to the micro-dissection. No apertures in the lamellae were found which could provide communications between the interlamellar spaces as suggested by Dogiel (1910). Supported by the collagen fibres the lamellae provide non-elastic membranes completely separating one inter-lamellar space from the next. This histological finding is in conformity with that of Gray & Sato (1955), who found that permeability of the lamellae was very low compared with the fluid between them.

A lamella may constitute a complete layer around the surface of the corpuscle or may unite with a neighbouring one. In well-prepared transverse sections the continuity of each of them can usually be traced. In longitudinal sections, however, irregularities are frequently observed: two adjacent lamellae may fuse into one layer, especially towards the stalk of the receptor with the result that the diameter of the corpuscle is gradually reduced.

The origin of postnatal lamellae may be studied at the periphery of the Pacinian corpuscle where they are formed from the surrounding adventitia, which contains loose connective tissue with collagen and elastic fibres (Pl. 2, fig. 21), and typical fibrocytes (Pl. 2, fig. 19). Elastic fibres show no concentration nor specialized orientation around the corpuscle, hence no elastic capsule is found comparable to that of Meissner's corpuscle (Cauna, 1956a). The most peripheral lamellae of the corpuscle follow one another in very close sequence, but they contain collagen fibres like those of the deeper lamellae; their cells, however, show the typical appearance of fibrocytes, except that they are flattened in the lamellar plane and their processes are usually thicker and straighter than those of the free adventitial fibrocytes (Pl. 2, fig. 20; cf. with fig. 19). Presence of collagen fibres in Pacinian corpuscles and the development of new lamellae from the adventitial tissue is an indication that the lamellar cells are modified connective tissue cells.

Inter-lamellar spaces frequently show a type of cell ('wandering cell' of Key & Retzius) along with the blood vessels and some clear fluid. This cell usually has a deeply staining elongated or kidney-shaped nucleus surrounded by a cytoplasm with faint basophil granulation (Pl. 2, B in fig. 11 and figs. 13, 14). The cell body may be almost round (Pl. 2, fig. 11), elongated (Pl. 2, fig. 13) or thread-like (Pl. 2, fig. 14); it is frequently attached to the inner or outer surface of a lamella, but even then it can be easily distinguished from the lamellar cells by the conspicuous nucleus and well-stained cytoplasm: it seems to belong to defence cells.

## The inner bulb and nerve supply of the Pacinian corpuscle

The inner bulb or the central core is surrounded by the innermost zone of the lamellae (Pl. 3, figs. 23, 29) and contains the axon, its branches and terminals together with some supporting cells. In most cases the corpuscle is borne upon a single thick medullated nerve fibre; as an exception two medullated axons may supply it (Pl. 3, figs. 23–25). The nerve may proceed undivided and terminate by a spindle-shaped enlargement or end bulb at the distal extremity of the central core; but usually it gives origin to several branches of equal or nearly equal size (Pl. 3, fig. 29), which also terminate by end bulbs, from the periphery of which a zone of neurofibrils may spread around the ending for a few microns and then gradually fade without a distinct termination (Pl. 3, fig. 30). This appearance led Boeke (1926) to suggest that the neurofibrillar system of a nerve ending was in continuity with the texture of the surrounding tissues. The present study does not support Boeke's view; it is suggested instead that the fading neurofibrils may represent a process whereby the outworn terminals are gradually lost at the periphery of the ending and replaced by the growth of the terminal nerve fibre.

No fine medullated or non-medullated fibres were found entering the digital Pacinian corpuscles, but sometimes very fine fibres originating from the principal axon or its branches (Pl. 3, fig. 28) may easily appear as belonging to a different system of nerves if their point of origin cannot be determined. These fine fibres usually have an irregular winding course, undergo considerable ramification and form free endings within the inner bulb, so resembling the pericorpuscular network or Timofeew's apparatus described by Sala (1899) and Sokolow (1899) in methylene blue preparations.

At birth and in foetal corpuscles the myelin sheath is lost as the nerve enters the corpuscle, but later in life it extends inside the receptor for some distance (Pl. 3, fig. 26) and may contain typical nodes of Ranvier (Pl. 3, fig. 27). This is the result of progressive incorporation of the medullated axon within the corpuscle by retrograde growth of the lamellae along the nerve (Text-fig. 2). The older the individual and the longer the corpuscle, the more extensive is the intra-corpuscular medullated segment. In old persons the myelin sheath can be traced as far as the middle part of the inner bulb or even beyond it (Pl. 3, fig. 23), although the myelin becomes less regular and thinner in the distal portion. The neurilemma sheath accompanies the medullated axon inside the corpuscle, but it becomes increasingly irregular and blends with the cells which surround the terminal nerve fibres and endings. The cytoplasm of these surrounding cells can be recognized in stained specimens, but no boundaries are visible (Pl. 3, fig. 29); cell nuclei, however, show deeply staining chromatin and are similar in appearance to those of lemmocytes or Schwann cells from which they appear to be derived. It is significant that the inner bulb of the human digital Pacinian corpuscles differs considerably from that of the mesenteric corpuscles of the cat, in which between the proximal medullated segment and the distal part containing the terminals, a long intermediate segment can be seen. This intermediate segment contains an undivided non-medullated axon surrounded by semicircular cells arranged in symmetrical pairs (Pl. 4, fig. 43) as described by Schumacher (1911) and demonstrated by electron microscopy by Quilliam (1956). No such semicircular cells can be observed in digital corpuscles of man.

Nerve supply of Pacinian corpuscles differs essentially from that of the superficial receptors of the digital skin—Meissner's corpuscles, Merkel's cells and the papillary nerve endings—which receive their supply from the deep corial plexus where the axons derived from the branches of the collateral digital nerves undergo repeated ramification and spread over areas of several square millimetres. Consequently the nerves carrying impulses from the superficial receptors are heavily shared party lines (Cauna, 1956b). Pacinian corpuscles, on the other hand, lie deep to the corial plexus and receive their nerve supply directly from the collateral digital nerves (nn. digitales palmares proprii) or their branches which contain undivided axons, and although two adjacent corpuscles may sometimes share a nerve, the axons carrying impulses from the digital Pacinian corpuscles are private lines.

## Blood vessels

Corial and subcutaneous Pacinian corpuscles are found in close relationship to large blood vessels and to glomerular arterio-venous anastomoses (Text-fig. 1; Pl. 1, figs. 2, 3; Pl. 4, fig. 42). By their position they are comparable with the corpuscles found in the adventitia of major branches of the aortic system.

Adjacent arteries send small thick-walled twigs to the corpuscles; but their point

of entrance does not coincide with that of the nerve or veins and is usually within the middle portion of the receptor. The arteries divide in the periphery of the outer bulb producing a number of thin-walled vessels which ramify within the interlamellar spaces (Pl. 3, fig. 31); they show a complete endothelial lining, but otherwise are supported by the lamellae. If empty, they are of capillary size, but when full they may expand to up to  $40\mu$  in diameter resembling sinuses (Pl. 3, fig. 32), which are drained by veins also running in between the lamellae. No blood vessels were found within the inner bulb, but frequently they penetrate very near to it (Pl. 3, fig. 31), and cases are found where only one or two lamellae separate them from the nerve (Pl. 3, fig. 33). If, however, such a vessel proceeds in a distal direction beyond the nerve, it may take up an axial position in relation to the lamellae (Pl. 3, fig. 34; cf. with fig. 33 and Text-fig. 3) producing the impression that the inner bulb is vascular.





Text-fig. 4. Portion of a glomerular arterio-venous anastomosis and a terminal part of a Pacinian vein to orientate figures 36-40 (Pl. 4). The tracing is to scale with the photomicrographs.  $\times$  140.

The collecting veins of Pacinian corpuscles are thin-walled at first, they run towards the proximal end of the receptor, and in adult individuals their walls attain a considerable amount of elastic fibres before leaving the corpuscle (Pl. 2, fig. 22). This may be the result of incorporation of an extra-corpuscular part of the vein into the outer bulb by growth of the receptor as it is in the case of the medullated nerve. The veins leave the corpuscle diversely either at its proximal extremity or from the convexity of the S-shaped bend, but sometimes at some irregular position (Text-fig. 1). An extra-corpuscular Pacinian vein is characterized by the thickness of its wall and abundance of elastic fibres. The terminations of these veins were traced from four corial and three subcutaneous corpuscles by means of wax plate reconstructions, and the results were checked by graphic reconstructions; in all cases the veins joined the outlets of the neighbouring glomerular arterio-venous anastomoses (Text-fig. 1 and Pl. 4, figs. 37, 42). In two cases the veins were in communication with similar thick-walled vessels draining a packet of sweat glands.

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The termination of two Pacinian veins (X and Y in Text-fig. 1) into the outlets of a glomerular arterio-venous anastomosis is shown in Figs. 36-40. Fig. 36 shows the shorter vein (X) ending, and the longer vein (Y) approaching the anastomosis. The termination of the longer vein (Y) is shown in Figure 37 (cf. with Text-fig. 4) in which the arterial and the venous parts (A and V) of the anastomosis are still separated from one another. The transition of the thick-walled artery into the vein is seen in Fig. 38 (AN) and the continuity of the anastomosis with the respective arterial and venous parts is shown in Figs. 39 and 40 (cf. with Text-fig. 4).

# FUNCTIONAL SIGNIFICANCE OF THE ANATOMICAL FINDINGS

The receptor part of the corpuscle of the inner bulb is surrounded by a series of non-elastic lamellae which contain fluid in their spaces; this fluid cannot escape from the corpuscle. In addition, the inter-lamellar spaces contain blood vessels which can be filled or emptied according to changes in arterial supply and venous drainage of the receptor. The arteries of the corpuscles are derived from the big vessels proximal to the arterio-venous anastomoses and therefore the activity of an anastomosis cannot influence the supply of the corpuscle. The veins, however, join the outlets of the anastomoses and therefore the drainage of the corpuscle is dependent upon the state of activity of this anastomosis; when it is closed, the blood from the Pacinian corpuscles can flow freely to the network of the cutaneous veins, but when the anastomosis opens and the arterial blood fills its outlets, the pressure may stop, or even tend to reverse, the blood flow in the Pacinian veins. Since the corpuscle cannot expand, the increased pressure within the outer bulb will be transmitted to the receptors of the inner bulb. In this way the anatomical structure of the Pacinian corpuscle and the pattern of its blood vessels may provide a mechanism for signalling changes in local blood supply due to the activity of the arterio-venous anastomoses. The extensive non-nervous outer bulb and the presence of blood vessels within it is consistent with such a function.

Pacinian corpuscles may provide a starting point of a vascular reflex along with other receptors of the skin, but the action of the anastomosis is regulated by its own nerve supply (Pl. 4, fig. 41), and it is reasonable to suggest that the thicker single fibres might be concerned with a sensory function whereas the fine fibres, usually arranged in bundles, might control its action.

External pressure over the finger pads can also be transmitted to the inner bulb because the corpuscles are compressed between the skin and the skeleton of the finger. Vascular and mechanical stimulations have one factor in common, viz., that in both cases the local capillary circulation of the tissues is reduced. However, the two types of stimuli differ in an essential way: the external pressure can only be applied to the corpuscles through a screen of tactile receptors, whereas the vascular stimulation is independent of superficial nerve endings.

Experiments on animals have shown that the Pacinian corpuscles respond to pressure stimuli (Adrian & Umrath, 1929; Gray & Malcolm, 1950), but these experiments cannot answer the question as to whether such stimuli result in a subjective sensation. Experiments by Ramström (1908) on human peritoneal corpuscles show that they do not produce any sensation, and this finding is supported by anatomical considerations: digital skin is well provided with receptors of mechanical stimuli (Cauna, 1954), so the Pacinian corpuscles appear to be superfluous for such a function in the fingers; certain viscera also contain Pacinian corpuscles in large numbers, yet these organs have a limited sensation, but at the same time possess a highly calibrated blood supply which could be regulated by reflexes originating in the corpuscles.

#### SUMMARY

1. Human digital Pacinian corpuscles were studied in a hundred and fifty individuals between birth and 93 years of age by the use of cytological and nerve-staining methods, micro-dissection, wax-plate reconstructions and optical polarization.

2. The corpuscles were found in the deep part of the palmar corium, palmar subcutaneous tissue, at the sides of the middle and proximal phalanges adjacent to the periosteum, deep to the long flexor tendons of fingers and at the insertions of the short digital muscles.

3. Size, shape and structure of the corpuscles undergo certain changes from birth to old age. Each lamella of the non-nervous outer bulb consists of a single continuous layer of flattened cells and is supported by collagen fibres of the inter-lamellar spaces. A number of lamellar cells form cytoplasmic communications across the inter-lamellar spaces. New lamellae are formed from the adventitial tissue surrounding the corpuscles.

4. A corpuscle is supplied by a thick medullated axon occupying the central core or the inner bulb. Branches of the axon terminate by end bulbs with no intercommunications. Fine fibres sometimes form a network around the principal nerve from which they are derived—a pericorpuscular network (Timofeew's apparatus) derived from independent nerves was not observed. Before birth, the myelin sheath ends on reaching the receptor, but later in life it can be traced inside it for some distance because the medullated axon is progressively incorporated within the corpuscle by retrograde growth of the inner bulb and the lamellae along the nerve. The neurilemma sheath of the nerve is continuous with the cells constituting the inner bulb.

5. Digital Pacinian corpuscles are closely related to large arteries from which they are supplied. Thick-walled veins draining the corpuscles join the outlets of the adjacent glomerular arterio-venous anastomoses. This arrangement makes the drainage of the corpuscle dependent upon the state of activity of the anastomosis. When it opens, the Pacinian veins are blocked and the pressure inside the corpuscle is increased and transmitted to the receptors of the inner bulb so providing a mechanism for signalling changes in local blood supply due to the activity of the arteriovenous anastomoses.

We should like to acknowledge the help and encouragement given by Professor J. Short. Our thanks are also due to Mr C. J. Duncan and the staff of the photography department for their aid with the photographic work.

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#### EXPLANATION OF PLATES

All illustrations with the exception of figs. 35 and 43 are photomicrographs of human digital skin or subcutis taken from the palmar aspect of fingers or thumbs. Figs. 35 and 43 are photomicrographs of mesenteric Pacinian corpuscles of the cat. A 1.8 mm. oil immersion objective was used for figures reproduced at magnifications  $\times 1000$  or  $\times 1200$ .

#### PLATES 1 AND 2

- Fig. 1. Section across the pad of the index finger showing a corial Pacinian corpuscle deep to the reticular layer of the corium and groups of subcutaneous corpuscles deep to the zone of sweat glands. Stillborn child, male, weight 6 lb. Frozen section, simplified Bielschowsky-Gross silver impregnation method.  $20 \mu$ .  $\times 40$ .
- Figs. 2, 3. Transverse sections of two corial Pacinian corpuscles showing their usual relationship to large arteries and a glomerular arterio-venous anastomosis (cf. Text-fig. 1). P and P in fig. 2 are parts of one corpuscle. A large artery (A in fig. 2) is dividing into two branches (R and L); the right branch (R) ends in a glomerular arterio-venous anastomosis (AV in fig. 3). Distal pad of little finger. Female, 64 years. Picro-Mallory stain.  $12\mu$ .  $\times$  77.
- Fig. 4. Tangential section of a Pacinian corpuscle showing birefringent fibres with transverse (T) and longitudinal (L) orientation. Distal pad of ring finger. Male, 43 years. Unstained section, mounted in DPX and photographed through crossed polaroids (planes are parallel to the sides of the photograph).  $10\mu$ .  $\times 120$ .
- Figs. 5–7. Lamellae and inter-lamellar fibres of a subcutaneous Pacinian corpuscle cut in three planes perpendicular to one another. Fig. 5. Lamellae cut tangentially and obliquely, parallel to the major axis of the corpuscle. Fig. 6. Lamellae cut transversely, across the major axis of the corpuscle. Fig. 7. Lamellae cut longitudinally, parallel to the axis of the corpuscle. Distal pad of ring finger. Male, 43 years. Osmic acid (Kolatschew-Nassonov).  $7\mu$ . ×1200.
- Figs. 8-16. Portions of the outer bulb showing cells of lamellae and of inter-lamellar spaces. Figs. 8-15 are obtained from the distal pad of little finger of a *male*, aged 20 years. Fig. 16 is obtained from the distal pad of middle finger of a *female*, aged 32 years. Haematoxylin and eosin.  $10\mu$ .  $\times 1200$ . Fig. 8. Two lamellar cells connected across the inter-lamellar space. Fig. 9. A, a cytoplasmic process of a lamellar cell gains attachment to the opposite lamella by a foot; B, a lamellar cell placed between two lamellae which it connects. Fig. 10. An asymmetric process of a lamellar cell attached to the opposite lamella by a foot. Fig. 11. A, a cytoplasmic process attached to the next lamella by a foot; B, an inter-lamellar wandering

cell attached to the inner aspect of a lamella. Fig. 12. A connexion between two lamellae without apparent participation of cells. Fig. 13. Free spindle-shaped inter-lamellar wandering cell. Fig. 14. Free thread-like inter-lamellar wandering cell. Figs. 15, 16. Nuclei of male and female lamellar cells viewed from the surfaces of lamellae. A mass of sex chromatin next to the nuclear membrane can be recognized in the female nuclei (arrows).

- Figs. 17, 18. Lamellae of Pacinian corpuscles impregnated with silver nitrate, dissected and flattened to show their polyhedral cells. C, 'cement lines' of the cells; A, attachment or 'foot' area of a cell belonging to a neighbouring lamella (cf. with A in figs. 9, 10, 11). Distal pad of little finger. Male, 20 years. Simplified Bielschowsky-Gross silver impregnation method. Frozen section. Fig. 17: ×600; fig. 18: ×1000.
- Fig. 19. Two fibrocytes from the adventitial tissue surrounding the periphery of a Pacinian corpuscle. Distal pad of little finger. Male, 20 years. Simplified Bielschowsky-Gross silver method. Frozen section. ×1000.
- Fig. 20. Two cells from an outer lamella of a Pacinian corpuscle recognizable as fibrocytes. Distal pad of little finger. Male, 20 years. Simplified Bielschowsky–Gross silver impregnation method. Frozen section. ×1000.
- Fig. 21. A section through a portion of a Pacinian corpuscle (P) and the surrounding subcutaneous tissue. The section was stained for elastic tissue (black) by Gomori's aldehyde fuchsin method and photographed through crossed polaroids to show the birefringent collagen fibres (white). The planes of the polaroids correspond to the sides of the photograph, but the angle was reduced to  $87^{\circ}$  in order to obtain light background for stained elastic tissues. No elastic fibres are visible within the corpuscle nor immediately around it in the form of a capsule. Distal pad of middle finger. Female, 21 years.  $10\mu$ . Mounted in DPX.  $\times 120$ .
- Fig. 22. Transverse section through the peripheral part of a Pacinian corpuscle stained for elastic fibres. The corpuscle and the two deeper veins are devoid of elastic fibres, but the collecting vein (V) which is about to leave the corpuscle has attained an elastic adventitial network. Distal pad of little finger. Female, 64 years. Gomori's aldehyde fuchsin stain.  $12\mu$ .  $\times 600$ .

#### PLATE 3

- Fig. 23. Transverse section through the proximal and middle portions of a Pacinian corpuscle with two medullated nerve fibres extending as far as the middle part of the corpuscle. Distal pad of index finger. Female, 85 years. Unstained frozen section mounted in water mounting medium and photographed through crossed polaroids (planes are parallel to the sides of the photograph).  $40\mu$ .  $\times 100$ .
- Figs. 24, 25. Fields of figure 23 showing a higher magnification of the medullated fibres.  $\times 600$ .
- Fig. 26. Longitudinal section of a corial Pacinian corpuscle showing a medullated fibre in its proximal part. N, node of Ranvier (cf. with fig. 27). Distal pad of index finger. Male, 49 years. Anderson's modification of Kultschitzky–Pal myelin stain. 20μ. ×140.
- Fig. 27. A field of fig. 26 showing a higher magnification of a portion of the intra-corpuscular medullated fibre with the node of Ranvier (N). × 600.
- Fig. 28. Oblique section of the inner bulb showing three thick nerve fibres (arrows) and a fine fibre (F) arising from one of the thick nerves. Distal pad of middle finger. Male child, 2 days. Frozen section. Simplified Bielschowsky–Gross silver impregnation method.  $20 \mu$ . × 600.
- Fig. 29. Transverse section of the inner bulb of a Pacinian corpuscle showing four nerve fibres (arrows) of various thickness surrounded by a cytoplasmic substance and flattened cell nuclei with deeply staining chromatin. Distal pad of little finger. Male, 20 years. Paraffin section stained for nerves by a simplified Bielschowsky-Gross silver impregnation method, counter-stained with Harris haematoxylin.  $10\mu$ .  $\times 1200$ .
- Fig. 30. Longitudinal section of the distal part of the inner bulb of a Pacinian corpuscle showing nerve ending by a spindle-shaped enlargement or end bulb from which some neurofibrils extend into the surrounding tissue. The shadow in the lower left corner is another end bulb out of focus. Distal pad of index finger. Female child, 14 months. Frozen section. Simplified Bielschowsky-Gross silver impregnation method.  $20 \mu$ . × 1200.
- Fig. 31. Transverse section of a subcutaneous Pacinian corpuscle showing blood vessels between the lamellae of the outer bulb. IN, inner bulb. Distal pad of index finger. Stillborn male child, birth weight 6 lb. Frozen section. Simplified Bielschowsky–Gross silver impregnation method.  $20 \mu$ . × 600.

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- Fig. 32. A blood vessel in the outer bulb of a Pacinian corpuscle. The endothelial lining of the vessel is supported by the lamellae. IN, inner bulb. Distal pad of ring finger. Female, 93 years. Weigert's iron haematoxylin and Van Gieson stains.  $8\mu$ .  $\times 600$ .
- Figs. 33, 34. Transverse sections of the axial part of a Pacinian corpuscle (cf. with Text-fig. 3). Fig. 33 shows a blood vessel (V) separated from the inner bulb (IN) by two lamellae only. Fig. 34 is a section distal to the inner bulb showing a blood vessel (V) occupying an axial position to the surrounding lamellae. Distal pad of little finger. Male, 20 years. Mason's triple stain (fig. 33) and silver stain for nerves (fig. 34).  $10\mu$ . × 600.

#### PLATE 4

- Fig. 35. Surface view of lamellar cells of a mesenteric Pacinian corpuscle of the cat. The nuclei usually occupy a central position in the large cell bodies (cf. with fig. 17 which shows lamellar cells of human digital corpuscles at the same magnification). Adult male cat. Simplified Bielschowsky-Gross silver impregnation method. Frozen section. ×600.
- Figs. 36-40. Selected serial sections of a subcutaneous arterio-venous anastomosis showing the termination of two Pacinian veins (cf. with Text-fig. 1). P, Pacinian corpuscle. X, Y, Pacinian veins. A and V, arterial and venous segments of the anastomosis; AN, anastomosis. The planes of the sections are shown in Text-fig. 4. Distal pad of little finger. Female, 64 years. Picro-Mallory stain,  $12\mu$ . ×140.
- Fig. 41. Section of a glomerular arterio-venous anastomosis showing its nerve supply. T, thick single fibre; F, fine nerve fibres. Distal pad of ring finger. Male, 35 years. Frozen section. Simplified Bielschowsky–Gross silver impregnation method. Hyalase treatment.  $20\mu$ .  $\times 600$ .
- Fig. 42. Section of a subcutaneous Pacinian corpuscle (P) showing blood vessels in its outer bulb and veins (V) connecting the corpuscle with an arterio-venous anastomosis (AN). Distal pad of little finger. Female child, 8 weeks. Haematoxylin and eosin.  $10\mu$ . ×140.
- Fig. 43. Transverse section through the axial part (middle segment) of a mesenteric Pacinian corpuscle of the cat showing that the inner bulb consists of semicircular cells arranged in pairs (cf. with figs. 29 and 33 which show corresponding parts of human digital corpuscles). Adult male cat. Harris' haematoxylin and eosin.  $8\mu$ .  $\times 600$ .



CAUNA AND MANNAN—STRUCTURE OF HUMAN DIGITAL PACINIAN CORPUSCIES



CAUNA and MANNAN—Structure of human digital Pacinian corpuscles



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