

ELECTRON MICROSCOPY OF THE PACINIAN CORPUSCLE*

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PLATES 109 TO 116

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INTRODUCTION

The presence of Pacinian corpuscles in the fingers of man was first noted in 1741 by Lehmann (16), but it was not until almost exactly a century later that Pacini (21, 22) gave an account of their histological structure.

The unusual morphology and comparatively large size of this sensory ending attracted the attention of many nineteenth century microscopists including Henle and Kölliker (12), Todd and Bowman (39), Herbst (13), Krause (14), Grandry (9), Rauber (29), and Schwalbe (34). Despite this, in the early years of the twentieth century, important additions to the literature were made by Ramström (28), Michailow (19), and particularly Schumacher (33). More recently Lee (15), Glees, Mohiuddin, and Smith (8), and Sampaolo (30) have studied the structure of this end organ. In modern times, too, physiologists have shown considerable interest in it as a particularly satisfactory sensory ending for electrophysiological experimentation. These include Adrian and Umrath (1), Gammon and Bronk (6), Gernandt and Zotterman (7), Alvarez-Buylla and Ramirez de Arellano (2), Scott (36), and Gray and Sato (10, 11). Weddell, Palmer, and Pallie (40) recently have reviewed the Pacinian corpuscle in relation to other nerve endings.

The recent study of the Pacinian corpuscle with conventional microscopy by Quilliam and Sato (27) was an effort to provide histological data that would prove useful in a functional interpretation. The present investigation was an outgrowth of that work, since it became apparent that light microscopy could not be expected to yield much further information about the inner core region of the corpuscle. For this purpose the greater resolution of the electron microscope seemed appropriate.

Perhaps the most surprising finding of the present work is that the core region of the Pacinian corpuscle is bilaterally organized, rather than being concentrically symmetrical as in the region of the more peripheral lamellae. In addition, confident statements now can be made about such hitherto debatable points as the unitary nature of the nerve supply and the limited pene-

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tration of vascular capillaries into the corpuscle. The central nerve fiber shows characteristic specializations that have not been previously recognized. Furthermore, a relatively cellular growth zone exists between the core region and the peripheral lamellae. This adds lamellae to the latter. Its inner cells also send cytoplasmic extensions centripetally to form the bulk of the inner core. Thus, it is apparent that the Pacinian corpuscle has a morphological complexity beyond previous realization.

Materials and Methods

Pacinian corpuscles were dissected as quickly as possible from the mesentery of the small intestine of adult cats and newborn kittens. If the isolation of a particular corpuscle was not completed within a two-minute period, it was discarded. Satisfactory specimens were transferred immediately to an ice cold solution of 2 per cent osmium tetroxide buffered in the manner of Palade (23 *b*), and were fixed for one-half hour.

There was a major difficulty in obtaining satisfactory fixation of the core region of corpuscles from adult cats. This was attributed to the size and layered arrangement of the corpuscle. It proved quite possible, however, to strip off the outermost lamellae of the larger corpuscles and thus minimize the delay of fixative action. This was done with especially fine forceps, ground under a dissecting microscope. If the stripping could not be accomplished almost immediately, the specimen was rejected. In this way, fairly good fixation of some corpuscles from adult cats was obtained. Corpuscles of newborn kittens did not require this manipulation for good preservation.

After fixation, the tissues were washed briefly in distilled water and dehydrated within a one-half hour period. After embedding in butyl methacrylate, ultrathin sections were cut on a Porter-Blum microtome. In general the techniques of handling the tissue conformed with current procedures as outlined by Porter and Blum (26).

OBSERVATIONS

The relatively low power electron micrographs of Figs. 1 and 3 indicate clearly that there are three major zones to be found in the Pacinian corpuscle. The inner zone or core, which extends through most of the length of the corpuscle, occupies much of the figure, and includes the centrally placed nerve fiber. Around the core is a cellular layer which we find to be a growth zone in differentiating corpuscles. This layer will be referred to subsequently as the intermediate growth zone. Peripheral to this are the many concentrically arranged lamellae of the outer zone. Only a few of the innermost of these lamellae show on the micrographs of Figs. 1 and 3. These are conspicuously present, even to the light microscopist, and often number well over 30. It will be convenient to consider the detailed morphology of each of these zones separately and in the above order.

Inner Core.—The core of the Pacinian corpuscle consists of closely packed cytoplasmic lamellae. These are bilaterally arranged so that there are two opposing groups, one on either side of the central nerve fiber, separated by longitudinally oriented clefts. They are concentrically arranged one above the other. In transverse section they appear as two graduated series of semi-annuli.

The side walls of the longitudinal clefts are composed of the unevenly stacked ends of these lamellae. The core lamellae of four different corpuscles have been counted and all contained approximately 60 units. These relations show to advantage in Fig. 3 and at higher magnification in Figs. 4 and 5.

At moderate magnification it is apparent that scattered mitochondria can be found in the core lamellae. Their internal cristae often are well preserved and thus give certain identification (Palade (23 *a*)). Thus, these lamellae are cytoplasmic extensions of cells and do not represent extracellular material.

For some time we were puzzled where the perikarya¹ of the inner core lamellae might be. Thick cytoplasmic masses of considerable size, sometimes containing nuclei, were to be found in the outermost regions of the central core. Yet clearly there were not enough nuclei within the core region to account for the large number of lamellae, nor were they to be found at all in the deeper regions. However, portions of cytoplasmic arms usually were present in the longitudinal clefts. They were thick in comparison to the lamellae, and were sometimes branched. It could often be seen that they were continuous with particular lamellae on one or both sides of the cleft. With further study it became apparent that these cytoplasmic arms extended from perikarya that were located either at the junction of the intermediate growth zone and the core, or were at least near the latter. Some of these relations show in Figs. 4 and 5. Thus there are cells in the outer portions of the core region which have major processes penetrating into the clefts, and these processes then branch laterally to form the lamellae of the core as terminal expansions of their cytoplasm.

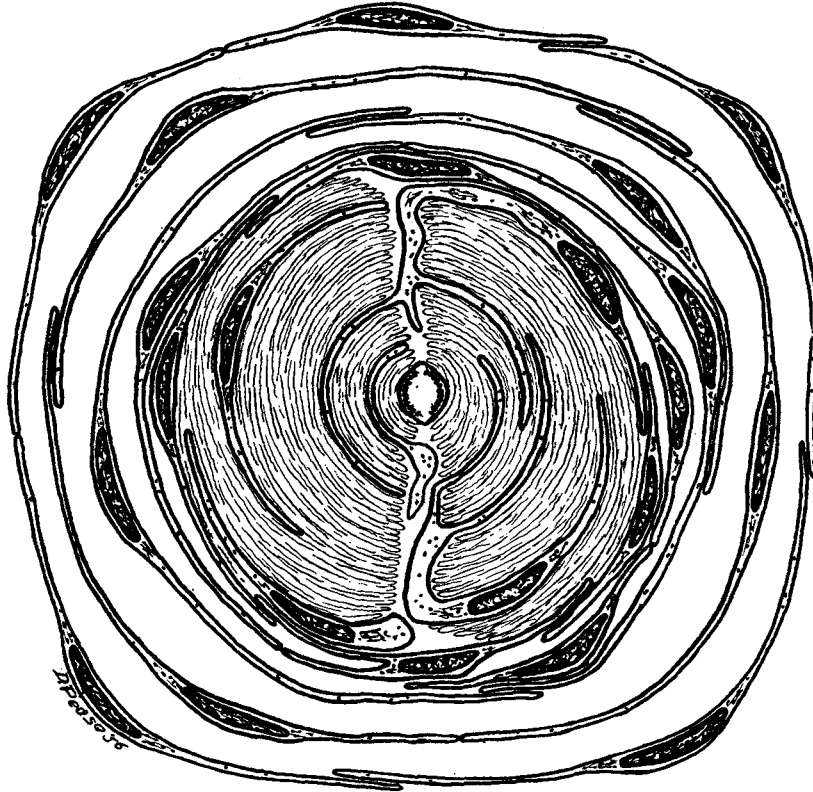
From longitudinal sections it is apparent that the cytoplasmic arms extending down into the clefts are essentially cylindrical. It is only after they become core lamellae that they form flattened sheets.

One cytoplasmic arm ultimately forms only a small number of lamellae. Up to four branches have been seen in a particular section, each giving rise to a lamella. Adjacent lamellae never arise from the same arm. These relations are schematically indicated in the drawing, Text-fig. 1. Without elaborate three-dimensional reconstructions one cannot be certain that one perikaryon does not give rise to several arms. However, considering the total length of the Pacinian corpuscle and the large number of lamellae, it is reasonable to suppose that many cells contribute to the core.

A special effort was made to study relations in the region where the nerve fiber enters the corpuscle. The axon, after losing its myelin sheath, nonetheless retains its Schwann cell sheath for a short distance. Although the most proximal projections of the inner core lamellae reach this level, there is com-

¹ The term "perikaryon" will be used in this article to designate a cytoplasmic body, to distinguish the body from its processes. We are using this word in its etymological sense, without prejudice as to the nature of the cell involved. We do not mean to imply a "nervous" connotation.

plete discontinuity between the Schwann sheath and the lamellae, and connective tissue spaces separate the two. As long as there is a myelin sheath, the surrounding connective tissue is only slightly differentiated. In the vicin-



TEXT-FIG. 1. The central region of a Pacinian corpuscle is schematically presented in section to show the relations of cells of the intermediate growth zone to the lamellae of the inner core and also to the concentric lamellae of the peripheral zone. It is particularly important to appreciate that the core region is bilaterally organized. Connective tissue plates divide the closely stacked lamellae into two groups. The core lamellae are cytoplasmic continuations of cells whose perikarya are either in or at least close to the intermediate growth zone. Major cytoplasmic arms from these perikarya extend into the clefts of the core and from there branch laterally to form lamellae which interdigitate with those of other cells. In immature corpuscles there is no sharp transition between the lamellae of the peripheral zone and the intermediate growth zone. In adult corpuscles, however, there are but few cells left in the intermediate growth zone.

ity of the junction between Schwann sheath and lamellae there are unspecialized cells that are probably fibroblasts, or perhaps histiocytes. Capillaries penetrate the corpuscle this far in the connective tissue spaces, but no further,

and do not actually traverse the interlamellar spaces at all. Since even the most proximal lamellae show a bilateral arrangement with respect to the two clefts, it is apparent that each cleft is an extension of the connective tissue space surrounding the entering nerve fiber. The clefts thus constitute a likely route for the exchange of metabolites.

Schumacher, as long ago as 1911 (33), recognized that the core region was bilaterally organized. He believed that the core lamellae were cytoplasmic, for he showed nuclei in some of these, but light microscopy was inadequate for visualizing further detail. The features of the core which he was unable to see were the multiplicity of the lamellae and their elaborate relations to parent perikarya. He observed correctly that hilar capillaries penetrated as far distally as the myelinated sheath of the entering fiber, and we can do no more than confirm his finding.

Photomicrographs and drawings widely used in teaching texts for demonstrating the structure of the Pacinian corpuscle sometimes appear to represent sections passing either too far distally or proximally to demonstrate the core. Such are to be seen in Schafer (31), Nonidez and Windle (20), and Maximow and Bloom (18). Thus these figures appear deceptively simple, although not all corpuscles may show the complexity of those from the cat mesentery.

Nerve Fiber.—The terminal portion of the nerve fiber is specialized in several noteworthy ways. As it enters the core it loses first its myelin sheath completely, and then, within a few micra, its Schwann sheath as well. Further distally the innermost core lamellae make direct contact with its naked surface (Fig. 6). The terminus is expanded so that it has approximately twice the cross-sectional area of the myelinated fiber.

The most important specialization of the nerve terminal, however, is probably the great concentration of mitochondria found in it. In the adult corpuscle, particularly, the mitochondria are notably larger than those of the main nerve fiber. Just below the surface of the unmyelinated fiber they are present in such crowded abundance that they form a palisade with their long axes radially oriented. A suggestion of these features may be seen at low magnification in Fig. 2. This is the only figure reproduced of an adult corpuscle where this pattern is fully differentiated. In the juvenile corpuscles (Fig. 6), although there are notably large numbers of mitochondria, and their size is considerable, they do not show the complete differentiation or radial arrangement of the adult. In other respects the axoplasm of the terminal nerve fiber is without particular specialization except that in cross-section the terminal nerve fiber is not ordinarily circular but is somewhat flattened. The slightly longer axis corresponds to the plane of the clefts between the core lamellae. It is doubtful, though, if any special significance should be attached to this, for the shape of the nerve is presumably modified by the bilaterally organized environment in which it finds itself. Occasionally, too, small blebs or short pedicels of nerve cytoplasm have been seen extending into the clefts. Since

they are not a regular feature of the nerve terminus, it is unlikely that they should be emphasized and may easily, in fact, have appeared with injury at the time of fixation.

In some, but by no means all, micrographs of terminal nerve fibers tiny vesicles may be seen approximately 50 m μ in diameter. When present they tend to be aggregated near the surface of the fiber and in the vicinity of the clefts. A few are visible in this position in Fig. 6. Their size and electron density make them comparable with the "synaptic vesicles" of Palade (24), Palay (25), de Robertis and Bennett (4), and Luft (17). In the Pacinian corpuscle, however, they are morphologically indistinguishable from vacuoles in the perinuclear zone of lamellar cells which might better be considered Golgi vacuoles. These can be seen to advantage in Fig. 10. It may also be noted that Schultz, Berkowitz, and Pease (32) found these in places other than nerve terminals in the lamprey spinal cord. Since their distribution is so variable, and includes even the dendrite of the Pacinian corpuscle, it is doubtful that they should be regarded as specifically concerned with synaptic transmission.

It is to be emphasized that the nerve fiber typically is single, although aberrant forms may be seen occasionally. Its terminus is simple and unarborized. Its extreme tip has not been identified, but we have sectioned at successive levels in this neighborhood, and at no time have we seen any bifurcation or more complicated division. Certainly 80 per cent of the terminal part of the fiber is normally unbranched.

Intermediate Growth Zone.—In the Pacinian corpuscle of kittens there is a prominent cellular zone between the central core region and the outer zone of concentric lamellae, and in any given cross-section, a considerable number of nuclei normally are visible here (Figs. 1, 3, and 7). This is a zone of growth, and eventually most of its cells become incorporated either into the core or into the outer zone of concentric lamellae. As a result, in the fully developed Pacinian corpuscle the growth zone, as such, is no longer an obvious feature. Thus in Fig. 2 only a few perikarya are to be seen in the transition region between the bilaterally organized lamellae of the core and the concentrically arranged ones of the periphery.

The growth zone has no sharply defined boundaries, even in immature corpuscles. There are all intergrades of cell types between those definitely incorporated in the core region and cells incorporated in lamellae of the outer zone. The outer circumferential lamellae form, and apparently lift away, from this region as can be seen in Fig. 7.

An additional reason for believing that this intermediate cellular zone represents a region of growth, is that mitotic figures occasionally may be found here in immature material. Such a cell is shown in Fig. 8. The nuclear membrane had disappeared from this cell before fixation, and the individual

chromosomes had condensed, and appear as small islands of relatively dense material. This represents the typical pattern of mitotic chromosomal structure as seen by electron microscopy in other tissues after buffered, osmic acid fixation. The particular cell in Fig. 8 is in late prophase.

The Peripheral Zone.—The peripheral zone consists mainly of the concentrically arranged lamellae, well known to the light microscopist. In the mature corpuscles of the cat mesentery, there are ordinarily 30 or more such lamellae. The more superficial of these are comparatively widely spaced one from another, while the inner ones tend to lie somewhat closer together. Each lamella consists of a number of cells whose peripheral cytoplasm is greatly attenuated. Neighboring cells ordinarily overlap each other slightly, so that in any one lamella there is complete cellular continuity. No gap in the structure of a lamella has ever been seen.

The cells of a lamella are extremely flattened as Figs. 9 to 12 indicate. Their average thickness is of the order of 0.2μ . Since there is a possibility of fixation and shrinkage artifacts, it is deemed prudent not to emphasize minimal thicknesses, but in Fig. 12 it can be seen as no more than 0.03μ . The perinuclear cytoplasm is scanty except at the lateral edges of the nuclear discs. Most of the organelles of the cell are found here. Ordinarily the endoplasmic reticulum is moderately prominent and usually appears as cisternae (Fig. 10). Golgi vacuoles and membranes may be found in this region, and there is a sprinkling of mitochondria. Scattered mitochondria are also found in the very attenuated cytoplasm at remote distances from nuclei (Fig. 11).

The interlamellar spaces show only slight electron density, yet usually a positive density can be demonstrated when these regions are compared with unoccupied methacrylate around the specimen. Thus it may be supposed that a small concentration of amorphous material is present. At times a finely granular deposit can be seen in these spaces, or even a reticulum. This suggests that a residuum of an aqueous organic colloid is being observed.

Collagenous fibrils are conspicuous in the interlamellar spaces. Most of the collagen lies close to the outer side of each lamella (Figs. 9 to 12), but a less marked condensation also exists along the inner surface of each lamella. Occasional fibrils of collagen are found in the intervening interlamellar spaces.

There is a striking increase in the quantity of collagen in mature corpuscles when compared with those from newborn kittens. Thus collagen must continue to be deposited after lamellae are formed.

The extralamellar lacework of fibrils was observed by Schwartz (35) in the only other published electron microscopic study of the Pacinian corpuscle, but since this work antedates the development of currently acceptable methods of preservation and preparation, it is not surprising that his micrographs show nothing but fibrous strata. He was unable to observe the characteristic periodicity of collagen and doubted therefore that the fibrils were in reality

collagen. However, there is no question that these fibrils observed here are collagen for we have seen the typical periodic structure.

Sections made tangential to the surface of peripheral lamellae show the collagenous mats viewed essentially in the horizontal plane. The fiber direction in relation to the corpuscle as a whole can be determined without difficulty, as in Fig. 13. It is quite clear that most of the fibers are oriented circularly, and thus at right angles to the long axes of the lamellae.

Traces of fibrils and also of amorphous material have been seen in the growth zone and core region. The arrangement of the fibrils has not yet been fully established, but a tendency for circular orientation is evident between the core lamellae of adult material. In these regions the fibrous feltwork is embedded in the amorphous material. Elastic plates or fibers have not been seen in any part of the corpuscle, thus confirming the work of Cauna (3).

Sometimes small irregularities in the lamellar arrangement of the outer zone may be found. Not too infrequently a lamella bifurcates. Also an occasional cell apparently does not differentiate properly and may be left in an interlamellar space. Under these circumstances, the undifferentiated cell may be more or less flattened, apparently having made an abortive attempt to form a lamella. In other cases such cells are globular and look much like lymphocytes, and thus may have been blood elements which wandered into the growth zone and were incorporated into a developing interlamellar space.

At the extreme periphery of a Pacinian corpuscle, the last half dozen or so lamellae are closely packed together with only narrow interlamellar spaces intervening between them. These lamellae immediately underlie a condensation of connective tissue which constitutes the external capsule of the corpuscle. This may be seen in Fig. 14. Although capillaries are found external to the corpuscle, none has been observed internally except those accompanying the myelinated portion of the nerve fiber as already indicated.

DISCUSSION

The Pacinian corpuscle offers an unusual opportunity for quantitatively evaluating the relationship between a nerve fiber and its vascular supply. Since it is clear that capillaries do not ordinarily penetrate beyond the region where the axon loses its myelin, it is apparent that the terminal portion of the nerve fiber is often more than 300 μ away from the nearest capillary. This is the radius of a good sized adult corpuscle (Winklemann and Osment (42)). It seems possible that some metabolic exchange is by way of the axoplasm of the nerve fiber itself (Weiss and Hiscoe (41)). It also seems likely that the clefts in the core region might serve as a metabolic exchange route as well, communicating on the one hand with the extracellular connective tissue spaces outside of the corpuscle, and on the other, bringing nutritive materials into close approximation to the nerve fiber itself. This pathway

could serve the many cells of the intermediate growth zone also and thus be a most important feature of the Pacinian corpuscle from a metabolic point of view. The presence of these clefts perhaps explains or at least clarifies the problem of how the nerve can be maintained and remain so active. Without such an arrangement the many peripheral lamellae would constitute a most formidable barrier to diffusion processes if all metabolites had to penetrate through them (Gray and Sato (10, 11)).

It is interesting to speculate whether the cells which give rise to the lamellae should be regarded as highly specialized fibrocytes fundamentally of mesodermal origin, or whether they might be specialized Schwann cells originally of neural crest derivation. Two factors lend favor to the former view. It is clear that the lamellar cells are associated with collagen which is usually accepted as being a connective tissue component. In two instances the Schwann cell sheath has been followed slightly beyond the point where the myelin terminated, and it was present as a continuous sheath directly applied to the axon. Coincident with this area were the tips of the deepest and most proximal core lamellae. They were not in direct contact with the Schwann cells or nerve fibers but rather were separated by narrow connective tissue spaces. Even in this zone where just a few core lamellae were beginning to make their appearance, it was quite apparent that their bilateral organization was fully established. Thus there was no indication of continuity between the Schwann sheath and core lamellae. Instead there was every morphological reason for emphasizing discontinuity and suggesting a separate origin.

The bilateral organizational pattern in the core is so greatly different from that of the peripheral zone of concentric lamellae that it is surprising that both are apparently derived from the same cell type. Cytoplasmic organelles are the same in both regions. Mitochondria appear identical. The endoplasmic reticulum is cisternal in character and moderately represented in both places. The cytoplasm contains only a few scattered granules. In the intermediate growth zone itself, transitional cells specializing in both directions can be seen easily, constituting a continuous spectrum of morphological change.

A particularly interesting problem is the manner in which the lamellae of the outer zone are elevated away from the intermediate growth area. There is some reason to believe that osmotic forces are involved importantly in this. The corpuscles as a whole appear to possess considerable turgor pressure. This was particularly evident to us as we prepared corpuscles by stripping off the outer lamellae with sharp forceps under a dissecting microscope. As the living lamellae were punctured, it could be seen easily that they collapsed as a minute amount of fluid escaped. The lamellae were apparently held apart entirely by the fluid pressure between them. It seems likely that this hydrostatic pressure is maintained by colloidal material in the interlamellar fluid which would give it a relatively high osmotic value. Since these colloids pre-

sumably cannot escape after interlamellar compartments are sealed off, osmotic filling would elevate lamellae. The collagenous fibers arranged circularly over the outer surface of each lamella no doubt would tend to limit this expansion. Similarly, the connective tissue sheath on the surface of the corpuscle might provide a final limitation to corpuscular dilatation.

The Pacinian corpuscle is generally presumed to be a pressure receptor. Certainly an action potential may be evoked from it by a surprisingly minute mechanical stimulus (Gernandt and Zotterman (7) and Scott (36, 37)). The arrangement of the non-nervous tissue, establishing separate fluid compartments, suggests that externally applied pressure would be transmitted uniformly to the whole surface of the unmyelinated nerve terminus. It is difficult to see how such hydrostatic pressure in itself could be the factor responsible for stimulating the nerve fiber, for the corpuscle as a whole cannot change shape greatly. Possibly the hilar zone represents a weak region which would allow some herniation, and longitudinal displacement might then apply traction to the core region and nerve fiber.

SUMMARY

The Pacinian corpuscle has a framework of cytoplasmic lamellae arranged concentrically in the outer zone, and bilaterally in the core. Between these is an intermediate growth zone.

The inner core shows an unexpected complexity in that its component lamellae are arranged in two symmetrical groups of nested cytoplasmic sheets. Longitudinal tissue spaces form clefts separating the two groups. The perikarya of the core lamellae lie in or near the intermediate growth zone, and send arms into the clefts. The arms then branch and terminate as lamellae which interdigitate with those of neighboring cells.

The single nerve fiber loses its myelin sheath just before it reaches the inner core but retains its Schwann cell cytoplasmic covering for a short additional distance. The Schwann sheath is not continuous with the lamellae of the inner core. Inside the core the fiber contains a striking circumferential palisade of radially disposed mitochondria. The fiber does not arborize.

Vascular capillaries penetrate the hilar region of the corpuscle only as far as the myelinated sheath of the nerve, and they have not been seen elsewhere in the corpuscle. There is direct continuity between the clefts of the core and tissue spaces in the vicinity of the capillaries. It is likely that this provides a route whereby metabolites reach the active nerve ending, as well as the cells of the growth zone.

The outer zone consists of at least 30 flattened concentric cytoplasmic lamellae separated from one another by relatively wide fluid-filled spaces. Collagenous fibrils are present, particularly on the outer surface of lamellae, and tend to be oriented circularly.

The girdle of proliferating cells constituting the growth zone, which is prominent in corpuscles from young animals, is the layer from which the outer lamellae are derived. Osmotic forces probably elevate the lamellae, and maintain turgor pressure.

BIBLIOGRAPHY

1. Adrian, E. D., and Umrath, K., *J. Physiol.*, 1929, **68**, 139.
2. Alvarez-Buylla, A., and Ramirez de Arellano, J., *Am. J. Physiol.*, 1953, **172**, 237.
3. Cauna, N., *Anat. Rec.*, 1956, **124**, 77.
4. De Robertis, E. D. P., and Bennett, H. S., *J. Biophysic. and Biochem. Cytol.*, 1955, **1**, 47.
5. Diamond, J., Gray, J. A. B., and Sato, M., *J. Physiol.*, 1956, **133**, 54.
6. Gammon, G. D., and Bronk, D. W., *Proc. Soc. Exp. Biol. and Med.*, 1934, **31**, 788.
7. Gernandt, B., and Zotterman, Y., *Acta Physiol. Scand.*, 1946, **12**, 56.
8. Glees, P., Mohiuddin, A., and Smith, A. G., *Acta Anat.*, 1949, **7**, 213.
9. Grandry, M., *J. anat. et physiol.*, 1869, **6**, 390.
10. Gray, J. A. B., and Sato, M., *J. Physiol.*, 1953, **122**, 610.
11. Gray, J. A. B., and Sato, M., *J. Physiol.*, 1955, **129**, 594.
12. Henle, F. G. J., and Kölliker, A., Über die Pacinischen Körperchen an den Nerven des Menschen und der Säugethiere, Zurich, Meyer and Zeller, 1844.
13. Herbst, G., Die Pacinischen Körper und ihre Bedeutung, Göttingen, Bandenhoek und Ruprecht, 1848.
14. Krause, W., Die Terminalen Körperchen der einfach sensibeln Nerven, Hannover, Hahn'sche Hofbuchhandlung, 1860.
15. Lee, F. C., *J. Comp. Neurol.*, 1936, **64**, 497.
16. Lehmann, J. G., Dissertatio inauguralis medica de consensu partium corporis humani occasione spasmi singularis in manu eiusque digitis ex hernia observati; exposito simul nervosum brachialium et cruralium coalitu peculiari atque papillarum nervearum in digitis dispositione, Vittemberg, 1741.
17. Luft, J. H., *Anat. Rec.*, 1955, **121**, 440.
18. Maximow, A. A., and Bloom, W., A Textbook of Histology, Philadelphia and London, W. B. Saunders Co., (6th edition), 1952.
19. Michailow, S., *Folia Neurobiol.*, 1909, **2**, 603.
20. Nonidez, J. E., and Windle, F. W., Textbook of Histology, New York, McGraw-Hill Book Co., (2nd edition), 1953.
21. Pacini, F., Letter to Società Medico-Fisica di Firenze, quoted in *Brit. and Foreign Med. Rev.*, 1845, **19**, 78.
22. Pacini, F., Nuovi organi scoperti nel corpo umano, Pistoja, Ciro, 1840.
- 23a. Palade, G. E., *Anat. Rec.*, 1952, **114**, 427.
- 23b. Palade, G. E., *J. Exp. Med.*, 1952, **95**, 285.
24. Palade, G. E., *Anat. Rec.*, 1954, **118**, 335.
25. Palay, S. L., *Anat. Rec.*, 1954, **118**, 336.
26. Porter, K. R., and Blum, J., *Anat. Rec.*, 1953, **117**, 685.
27. Quilliam, T. A., and Sato, M., *J. Physiol.*, 1955, **129**, 167.
28. Ramström, M., *Anat. Hefte.*, 1908, **36**, 311.

29. Rauber, A., Untersuchungen über das Vorkommen und die Bedeutung der Vater'schen Körper, München, Verlag von Caesar Fritsch, 1867.
30. Sampaolo, C. L., *Bol. Soc. Ital. biol. sper.*, 1955, **31**, 1620.
31. Schafer, S., Essentials of Histology, (H. M. Carleton, and R. H. D. Short, editors), London, Longmans Green & Co., 16th edition, 1954.
32. Schultz, R., Berkowitz, E. C., and Pease, D. C., *J. Morphol.*, 1956, **98**, 251.
33. Schumacher, S. von, *Arch. mikrosk. anat.*, 1911, **77**, 157.
34. Schwalbe, G., Lehrbuch der Anatomie der Sinnesorgane Erlangen, Verlag von Eduard Besold, **2**, 2nd edition, pt. 3, 1887.
35. Schwarz, W., *Z. Zellforsch.*, 1951, **36**, 436.
36. Scott, D. Jr., *Fed. Proc.*, 1949, **8**, 142.
37. Scott, D. Jr., *Fed. Proc.*, 1951, **10**, 123.
38. Takashi, M., Sakai, I., and Usizima, H., *Anat. Rec.*, 1955, **122**, 17.
39. Todd, R. B., and Bowman, W., The Physiological Anatomy and Physiology of Man, London, John W. Parker, 1845.
40. Weddell, G., Palmer, E., and Pallie, W., *Biol. Rev.*, 1955, **30**, 159.
41. Weiss, P., and Hiscoe, H. B., *J. Exp. Zool.*, 1948, **107**, 315.
42. Winklemann, R. K., and Osment, L. S., *Arch. Dermatol. and Syphilol.*, 1956, **73**, 116.

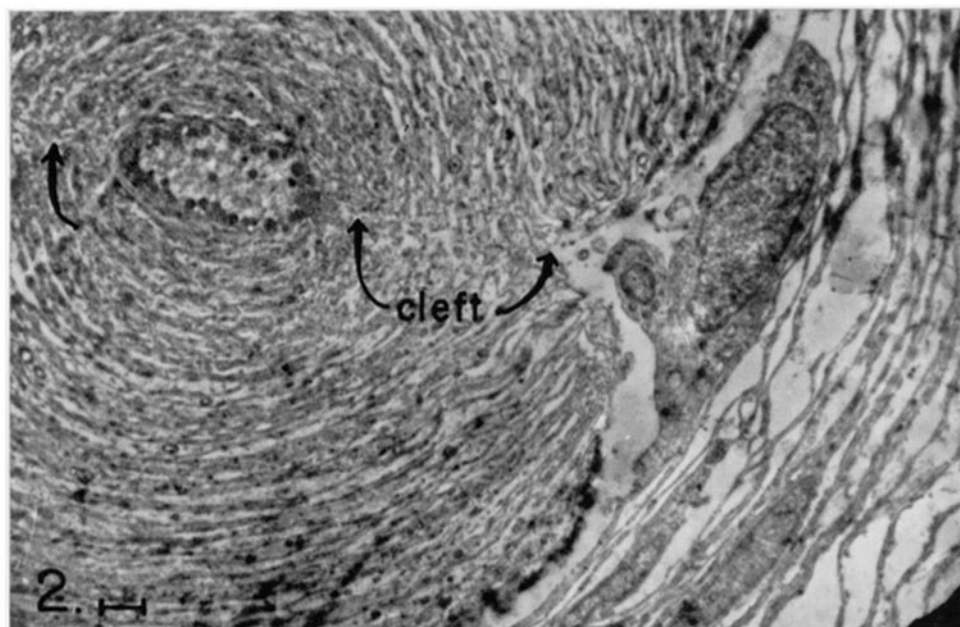
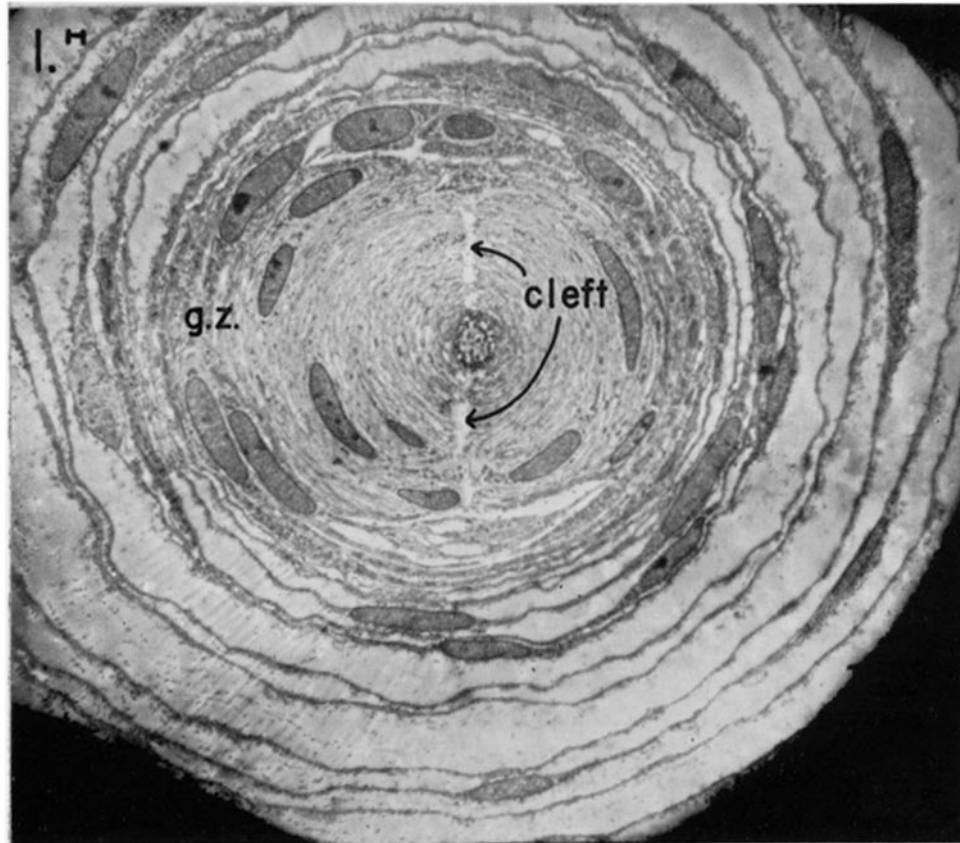
EXPLANATION OF PLATES

PLATE 109

FIG. 1. An electron micrograph of a transverse section through the central region of a Pacinian corpuscle from a kitten. In the center is the nerve fiber with many mitochondria. Two groups of closely packed lamellae surround this. The groups are separated by an obvious cleft, which is oriented vertically in the micrograph. Passing from the core region, one reaches a zone containing many cell bodies. This we have termed the intermediate growth zone (*g.z.*). This blends somewhat imperceptibly with the peripheral zone of concentric lamellae, only the innermost of which are visible in this picture. $\times 2,000$.

Micron marks accompany this and subsequent figures.

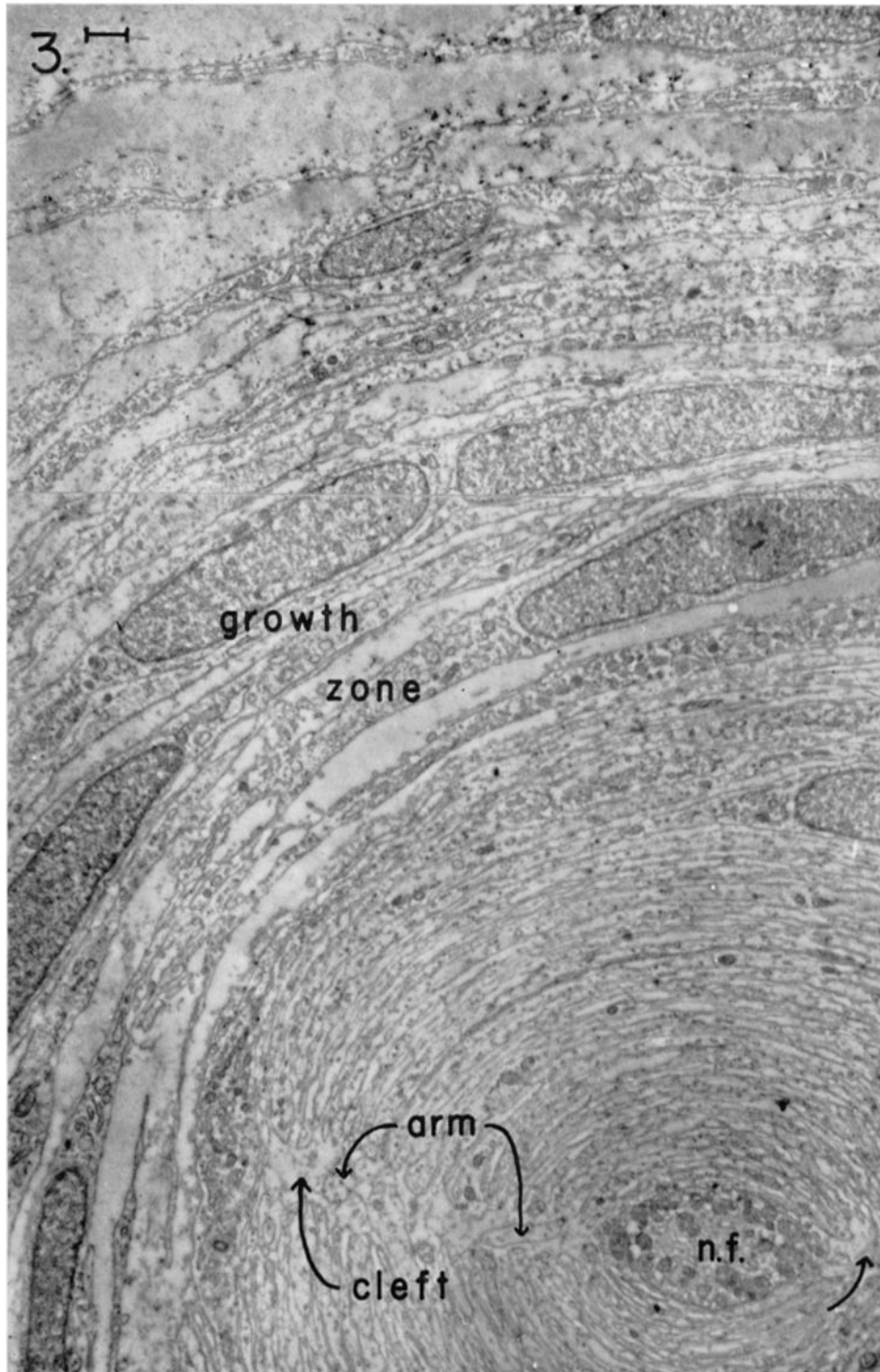
FIG. 2. A low power view of the core region of a corpuscle removed from an adult cat. This differs from corpuscles of juvenile animals in that the mitochondria of the nerve fiber are more definitely arrayed in a palisade just underlying the surface. There are also but few cells left in the intermediate growth zone. The cleft (arrows) is definitely present but is less obvious. This is partly because the cytoplasmic arms extending into this region are more attenuated in the adult than in the young, and the cleft is filled with more or less circular profiles of these. $\times 5,600$.



(Pease and Quilliam: Electron microscopy of Pacinian corpuscle)

PLATE 110

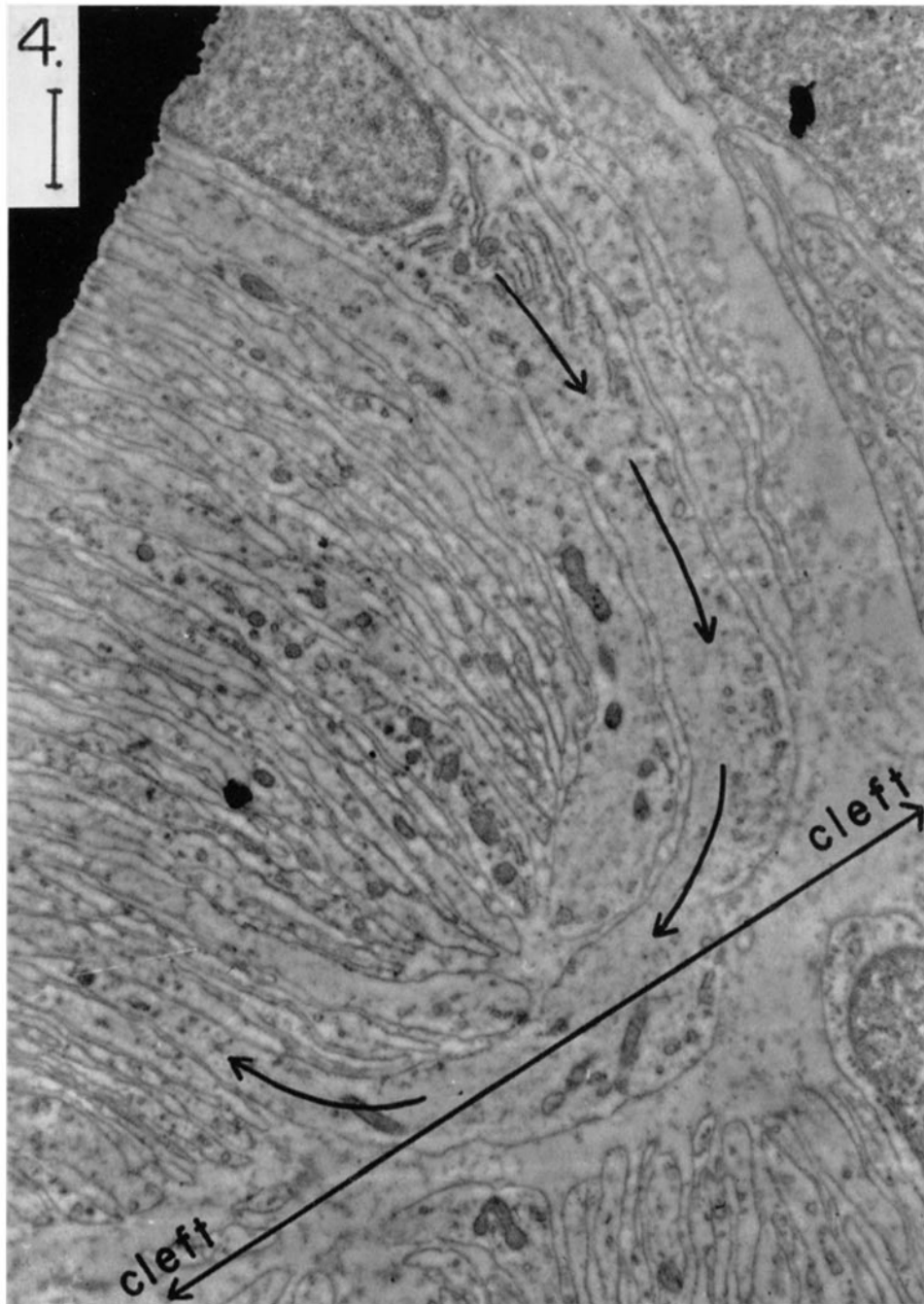
FIG. 3. The central region of a Pacinian corpuscle of a kitten at relatively low magnification. In the lower right hand corner may be seen the nerve fiber (*n.f.*) with its contained mitochondria. To the left is the connective tissue cleft with sectioned profiles of cytoplasmic arms (*arm*). A small portion of cleft also shows in the right corner indicated by an arrow. Note that no perikarya are to be seen deep in the core region. Nuclei are present in some numbers, however, in the growth zone. The outer cells of the growth zone are forming definitive circumferential laminae, and there is a complete spectrum of transition from relatively unspecialized cells of the growth zone to elevated circumferential lamallae. $\times 5,700$.



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PLATE 111

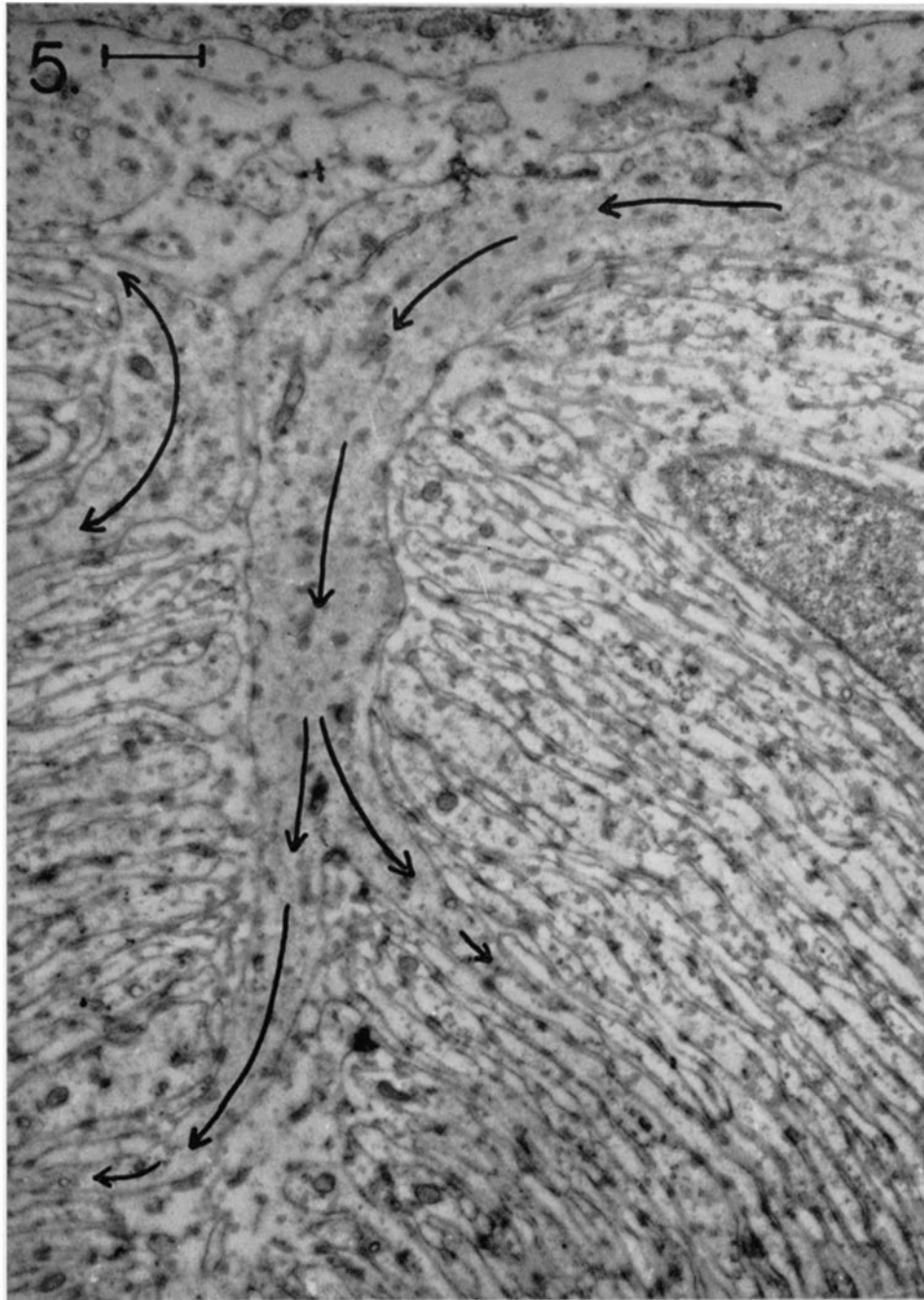
FIG. 4. A transverse section of the outer part of the core of a kitten's corpuscle to indicate the relationship between perikaryon, cleft, and core lamellae. The cell in the uppermost part of the figure lies just inside the growth zone. Its cytoplasm can be followed as a massive arm extending down into the cleft (arrows). Deep in the core the cytoplasmic arm can be seen to terminate as an interdigitating core lamella (final arrow). At this higher magnification, it can also be noted that many core lamellae show mitochondria as well as other cytoplasmic organelles. Compare with text-figure. $\times 13,000$.



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PLATE 112

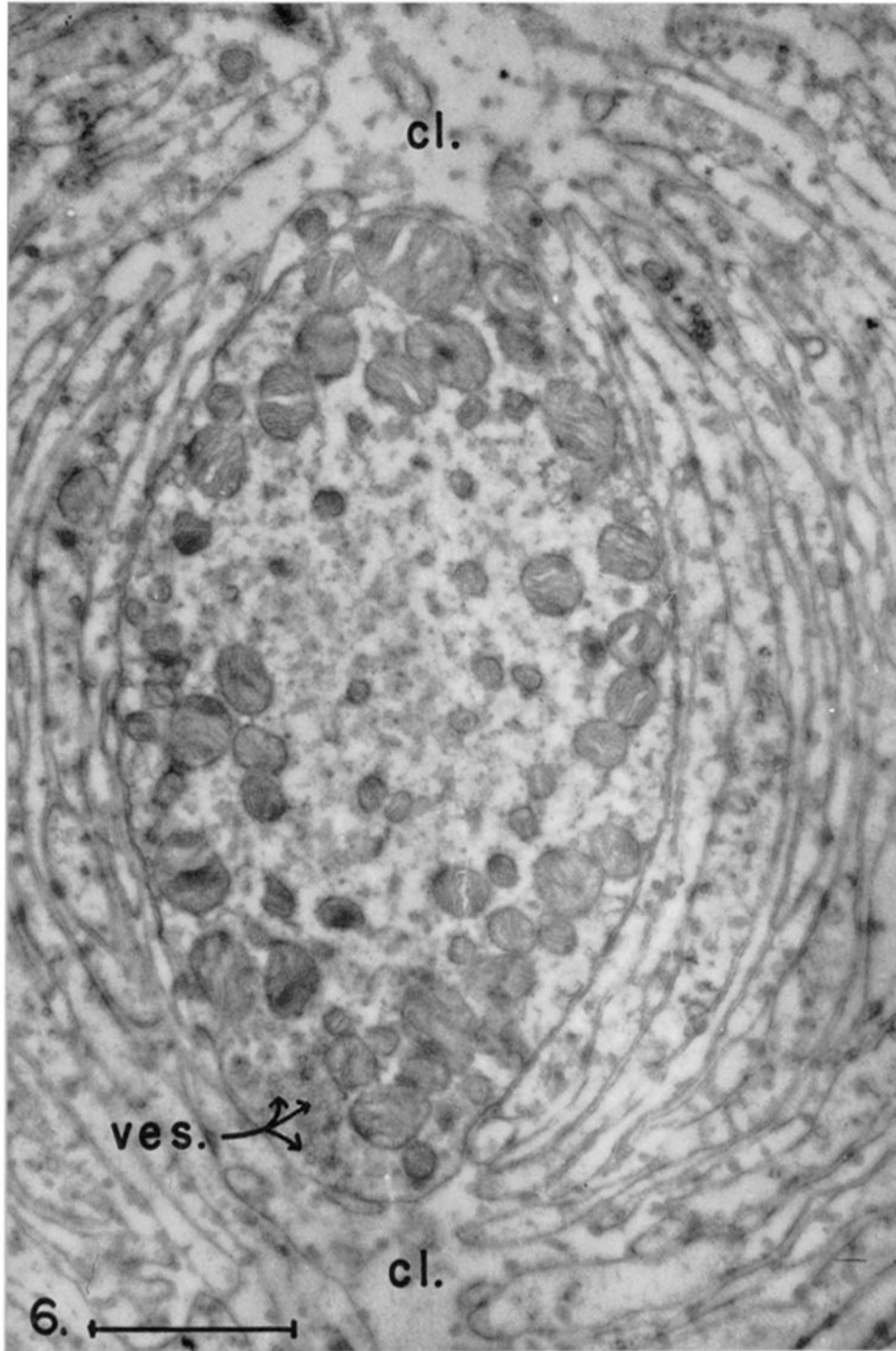
FIG. 5. A transverse section near the surface of the core region of a kitten's corpuscle showing a massive cytoplasmic arm extending deeply into the cleft of the core from the region of the growth zone. Deep in the cleft the arm subdivides and forms lamellae on both sides of the cleft as indicated by the arrows. In the upper left of the figure a portion of an adjacent arm is visible with divisions into two lamellae on the same side of the cleft as indicated by the double headed arrow. $\times 14,000$.



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PLATE 113

FIG. 6. The terminal nerve filament of a Pacinian corpuscle of a kitten in transverse section. It is flattened so that the long axis is in the plane of the cleft (*cl.*). The many rather large mitochondria are a conspicuous feature in this micrograph. In the adult particularly, they form a definite palisade just below the surface of the nerve fiber. Note also within the nerve numerous small vesicles (*ves.*) which are discussed in the text. Details of the innermost core lamellae may also be studied. Note that the innermost ones are applied directly to the nerve surface, and each succeeding one is directly applied to the one before it. $\times 30,000$.

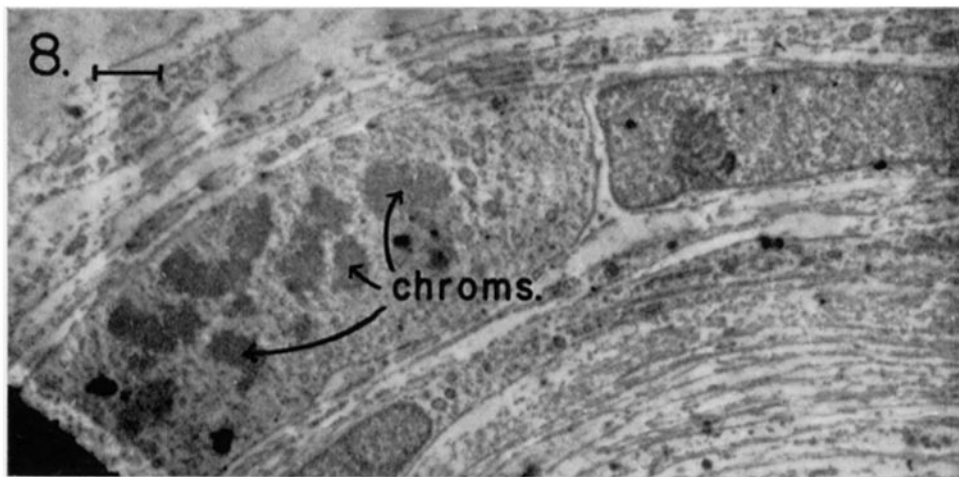
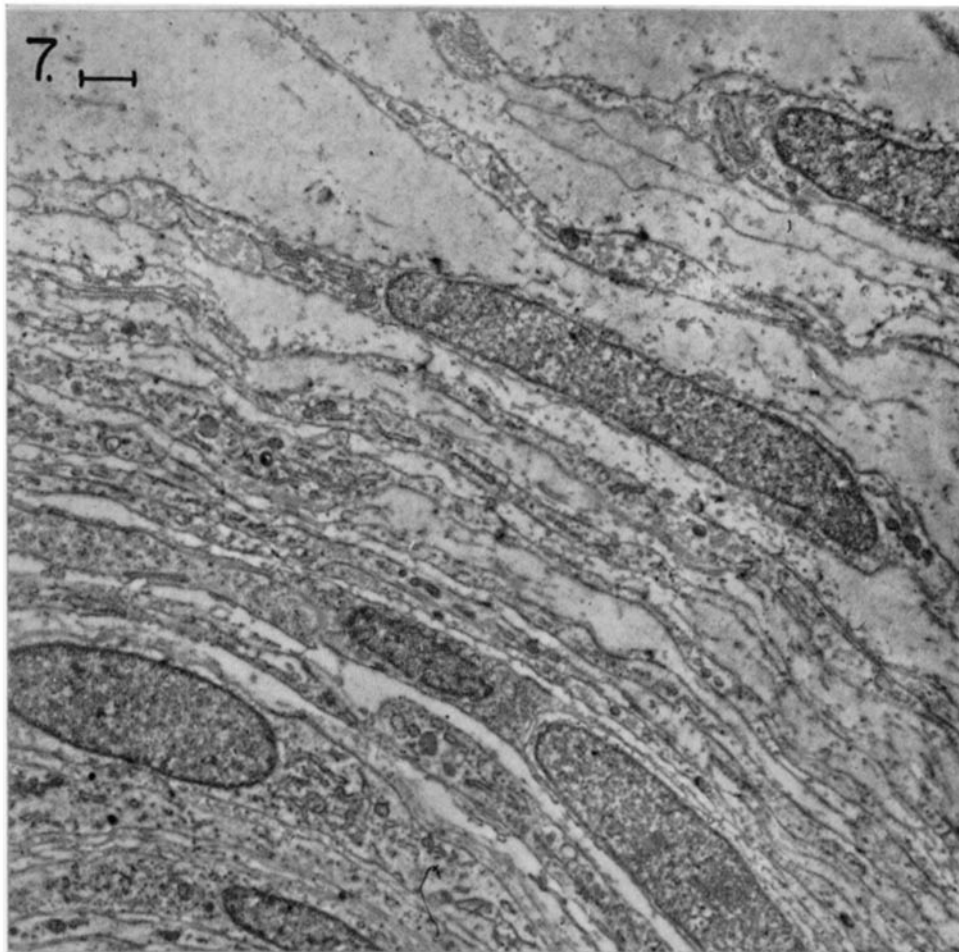


(Pease and Quilliam: Electron microscopy of Pacinian corpuscle)

PLATE 114

FIG. 7. A transverse section through the transitional region between the growth zone and the peripheral circumferential lamellae in a juvenile corpuscle. Various stages in the specialization of cells to form circumferential lamellae can be observed. Only the outermost lamellae are fully elevated. $\times 6,800$.

FIG. 8. A cell in the intermediate growth zone showing a mitotic figure. Prometaphase chromosomes (*chroms.*) have an appearance typical of osmic acid fixation. This is from a corpuscle removed from a kitten. $\times 8,600$.



(Pease and Quilliam: Electron microscopy of Pacinian corpuscle)

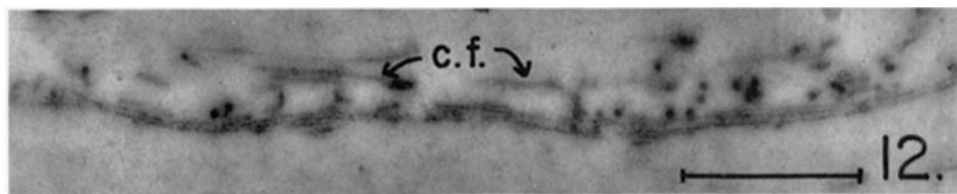
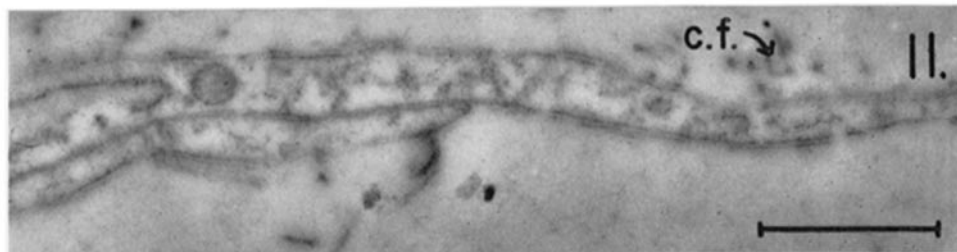
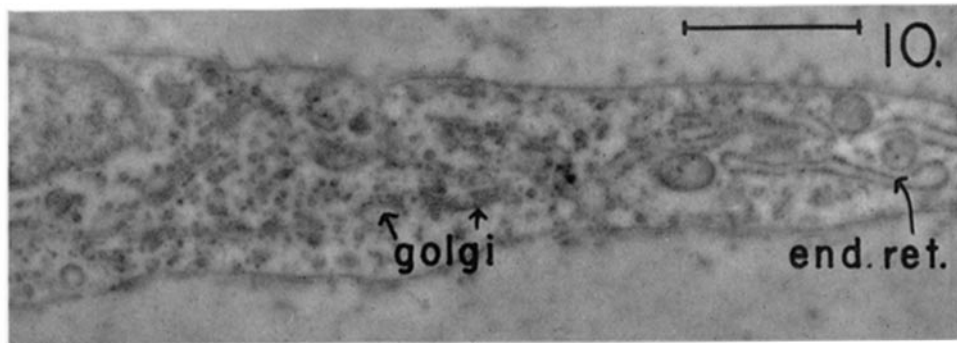
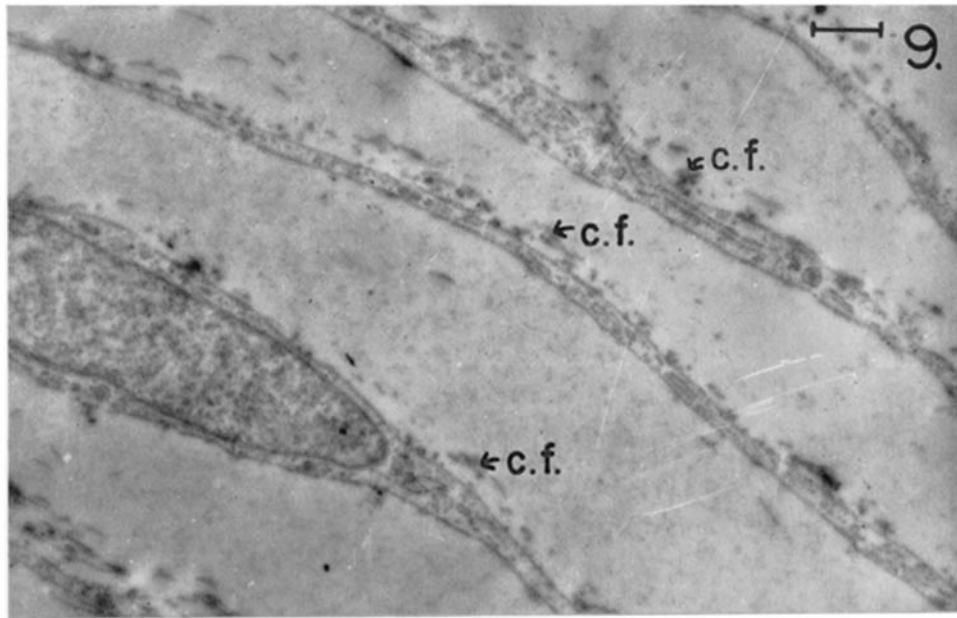
PLATE 115

FIG. 9. A transverse section through several circumferential lamellae of the peripheral zone. Note that the lamellae consist of continuous cytoplasmic sheets containing typical organelles. Collagenous fibers (*c.f.*) are cut more or less obliquely. Notice that they are mainly to be seen on one side of each lamella. This corresponds to the peripheral side. There is often a faint flocculent precipitate more or less visible in the interlamellar spaces. $\times 9,200$.

FIG. 10. A high resolution micrograph of a portion of the perikaryon. A bit of the nucleus shows to the left. Golgi membranes and vacuoles are indicated. Several mitochondria may be seen. Some cisterns of the endoplasmic reticulum (*end. ret.*) are visible. $\times 23,600$.

FIG. 11. A zone of overlap of peripheral lamellae between two cells. Although overlapping cells are common, some cells butt simply against one another as indicated in the schematic diagram of the test figure. $\times 23,600$.

FIG. 12. The cytoplasmic sheets of the peripheral lamellae can become extremely attenuated as may be seen here. In places, this cytoplasm is no more than 300 Angstrom units thick. $\times 23,600$.

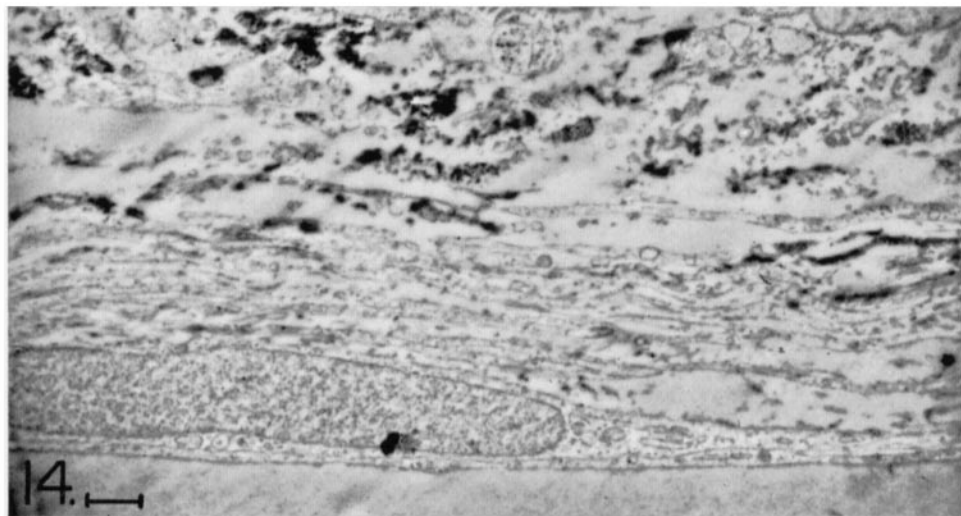
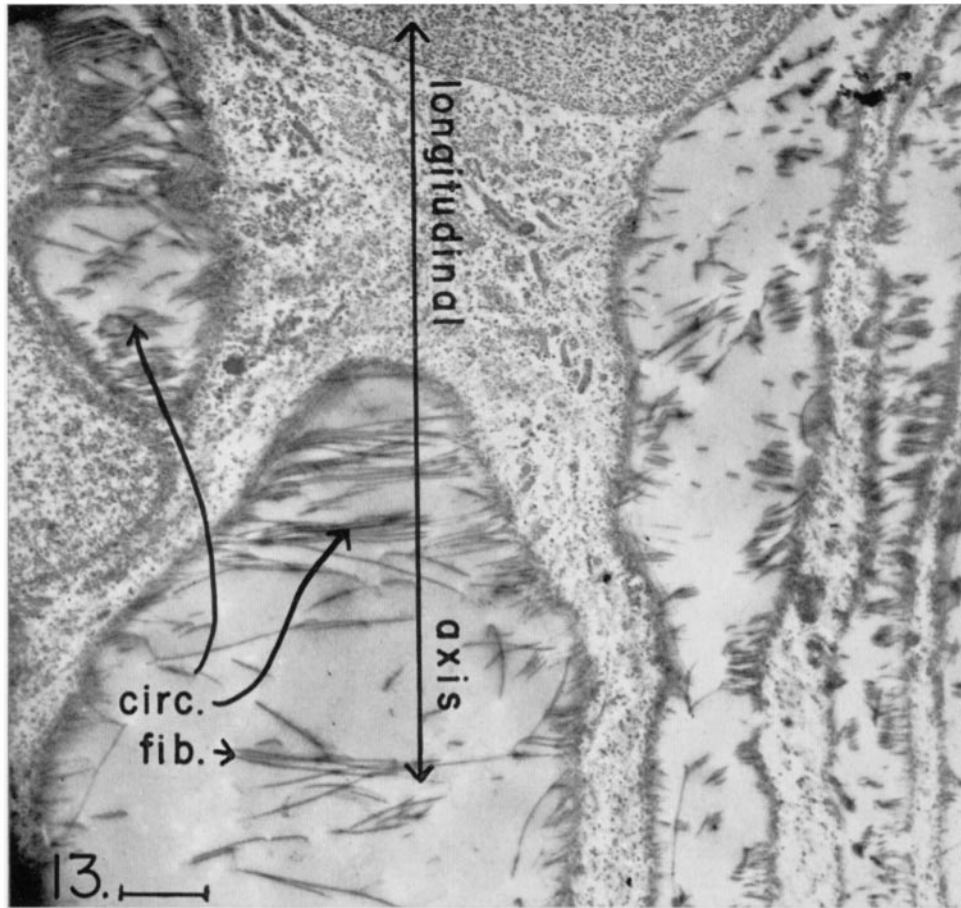


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PLATE 116

FIG. 13. The plane of this section was tangential to the surface of one lamella from an adult Pacinian corpuscle. The direction of the long axis of the corpuscle is indicated by the arrow. Many collagenous fibers are to be seen often lying in the plane of the section. Most of these are oriented at right angles to the longitudinal axis and thus represent circular fibers (*circ. fib.*) in relation to the corpuscle as a whole. To the right are portions of two adjacent lamellae with their collagenous fibers sectioned rather obliquely. $\times 11,500$.

FIG. 14. A transverse section through the capsular and most peripheral region of a kitten Pacinian corpuscle. It may be seen that there is a tendency for the peripheral lamellae to be more or less packed together close to the surface of the corpuscle. Outside of this zone, and slightly blending with it, fibroblasts, dense masses of collagen, capillaries, and occasional nerve fibers are to be found. These constitute a typical capsular arrangement. $\times 7,100$.



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