The Fine Structure of the Adepidermal Reticulum in the Basal Membrane of the Skin of the Newt, *Triturus**

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PLATES 12 TO 16

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ABSTRACT

The unique reticulum in the basal membrane of the adult newt's skin consists of a series of nodular swellings from which there radiate fibers. Electron micrographic studies showed that the nodules consist of layers of fibrillae arranged approximately and irregularly at right angles to one another. Some are packed to form a capsule; still others extend into the internodular zone to form the radiating fibers. The fibrils are banded and are revealed best after fixation with potassium permanganate. The reticulum is compared with that of the larval newt and the frog tadpole. The epidermal side of the reticulum is bounded by a membrane separated from the plasma wall of the epidermal cell by a clear space. These we have termed *adepidermal membrane* and *space*, and have compared them with similar structures in larvae.

Using histochemical and classical histological techniques, Singer and Andrews (1) demonstrated a unique adepidermal reticulum in the basal membrane of the skin of the newt (*Triturus viridescens*). It consisted of a series of nodules from which there radiated fibrillae in a plane tangential to the epidermis. The nodules and the internodular fibrillae were demonstrated best with ammoniacal silver; they also were visualized with acid dyes, particularly aniline blue. Histochemical tests failed to reveal nuclear substance in the nodules; and the conclusion was drawn that the nodule was the center of origin of the fibrillae and consisted itself of fibrillae or of an amorphous material. The adepidermal reticulum was observed in the skin of the adult and the red land stage form but not in that of the larva. The present study was undertaken to elucidate the fine structure of the nodule and internodular reticulum.

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The basal membrane is ordinarily defined as the thin zone between the epidermis and dermis of the vertebrate skin consisting of a delicate meshwork of reticular fibers imbedded in a homogeneous ground substance. It varies in structure and abundance from species to species and even in different life stages of the same species. From light microscopic studies Rosin (2) reported an orderly fibrous arrangement for the basal membrane of the amphibian larva consisting of fibers arranged at right angles to one another (orthogonal). Porter (3) and Weiss and Ferris (4, 5), using the electron microscope, showed that the larval basal membrane contained layers of fibrillae alternating at right angles to each other. In the case of the adult frog (see electron micrographs published by Ottoson *et al.* (6)) a much less regular fibrillar array is apparent in the basal membrane but somewhat similar to that of mammalian skin (7, 20). In some of our unpublished studies, we have also observed a relatively unoriented pattern in the skin of the adult frog.

Methods and Materials

Initially we fixed the skin of the newts in 1 per cent buffered osmium tetroxide at pH 7.4 according to

Palade (8). We found later, however, that potassium permanganate demonstrated better the fibrillae of the basal membrane. The main bulk of our material was, therefore, fixed in either 0.6 per cent $KMnO_4$ according to Luft (9) or in a 1.2 per cent unbuffered solution of $KMnO_4$ at pH 7.0–7.2. Small pieces of arm or belly skin, taken from anaesthetized adult newts, were fixed for ½ to 20 hours at 0°–2°C., dehydrated, and then embedded in butyl-methacrylate at 60°C. The blocks were sectioned with a Porter-Blum microtome, and viewed with either an RCA EMU2 or EMU3 electron microscope.

OBSERVATIONS

In transverse section at low power the gross structure of the basal membrane was essentially that described by Singer and Andrews (1). There were periodic swellings, or nodules, which alternated with thinner internodular regions and which were spaced about one to several basal epidermal cells apart. A nodule in cross-section was approximately 7 μ thick and 10 μ long, whereas the internodular band was roughly 1 μ thick. For more quantitative detail on the gross anatomy of this structure see Singer and Andrews (1).

At higher magnification the nodules were seen to consist of bundles of fibrillae surrounded by a clear ground substance. The bundles were arranged in somewhat irregular layers. Within each layer the fibrillae were parallel but those of successive layers differed in their direction. Successive layers often tended to be arranged at right angles so that the direction repeated in alternating fashion. A gross orthogonal pattern has been described for the basal membrane of amphibian larvae by Rosin (2) with the light microscope, and its fine structure elaborated by Porter (3) and Weiss and Ferris (4, 5) with the electron microscope. However, in the adult newt the orthogonal pattern, if it is such, was generally distorted. The distortion was most prominent near the margins of the nodule at the region of transition to the internodular zone. Moreover, there was marked variation in size and organization of the layers from one nodule to the next. Near the surface of the nodule the layers often had the rounded contour of the circumference and the layers and fibrillae were more densely packed, forming in this way a capsule (Figs. 2 to 5). The difference in packing of the fibrils and layers may not be real but due to a differential effect of the fixing fluid, methacrylate embedding, or tissue spreading. It may, however, suggest that the ground substance is more abundant in the center of the nodule. The contour of the nodule on its epidermal side is somewhat flattened whereas it is rounded on the dermal side.

Fibrillae were also observed in the internodular region of the basal membrane but they could not always be demonstrated; instead an amorphous, dark, undifferentiated band was sometimes visualized. When evident, the fibrillae of the internodular zone could be traced from the nodule itself. Fibrils which were oriented parallel to the plane of section from alternate layers in the nodule, could be seen to converge as they entered the internodular region. Thus, there was evidence that the fibrillae were continuous through nodule and internodule. But unlike the nodule, the internodule did not consist of layers of fibrils arranged at angles to one another, for the fibrils of the internodule ran predominantly in one direction. Here and there a bundle of fibrils dipped down into the dermis.

The details of fibril structure was studied best in the nodule. The individual fibril appeared in cross-section as a cylinder approximately 250 to 350 A in diameter with a less dense central core. In longitudinal view the fibril often showed a regular banded structure. One major and one minor band were distinctly seen. Occasionally another faint secondary band could be distinguished interposed between them. The major bands were spaced roughly from 350 to 450 A apart. The periodicity was measured primarily in tissue fixed with $KMnO_4$ since the bands were more distinctly seen there. We did, however, make a few measurements on tissue fixed with OsO_4 and found the measured period to fall within the range quoted above. The periodicity of these fibrils compares favorably with that reported in the literature for similar fibrils in the basal membrane of amphibians and mammals (3, 7). The nature of these fibrils could not be ascertained. It is of interest that their measured period is less than that of collagen (10–13, 21). Whether this is due to tissue shrinkage or to some real difference in the nature or developmental stage of the fibrils is unanswered.[1]

When two or three fibrils were adjacent, their banding tended to coincide so precisely that those of one were aligned with those of the next (Figs. 6 and 7). Such a fibrillar alignment has been re-

[1] Note Added in Proof: Keith Porter and George Pappas have pointed out in a recent paper (*J. Biophysic. and Biochem. Cytol.*, January, 1959, 161) that methacrylate embedding does indeed induce shrinkage in collagen fibers, thus shortening the 640 A spacing.

ported before (5, 10), and its possible significance has been discussed (11).

The fibrils of the dermal regions had approximately the same periodicity, ranging between 350 and 500 A. The bands of these fibrils were much more distinct. Here we saw one dense major and minor band, and two faint additional bands which were quite consistently distinguishable, one on either side of the minor band. The dermal fibrils were generally thicker than those of the basal membrane, being approximately 400 to 550 A in diameter, with some as thick as 800 A. The fact that the reticular fibers of the basal membrane had the same periodicity as the dermal fibers even though they were not of the same diameter is consistent with other reports in the literature (7, 12, 13).

The basal membrane was always distinctly delimited on the epidermal side by a continuous membrane approximately 200 to 350 A thick, which in turn was separated from the epidermis by a space of low density, roughly 200 to 400 A wide. A similar structure has been described for frog and mammalian skin (6, 7, 20). This membrane and space must be distinguished from the fibrillar basal membrane and several suggestions for the most suitable nomenclature have appeared in the literature (6, 7). We propose calling them the *adepidermal membrane* and the *adepidermal space.* Our reasons for introducing these new terms will be given in the discussion. No epidermal or dermal filaments were ever seen to cross these structures and in this way to connect the basal epidermal cells with the basal membrane. The continuity of the adepidermal membrane was unbroken at the level of the intercellular space between adjacent epidermal cells. The membrane was wider and less dense than the plasma membrane and here and there had a somewhat granular or striated appearance. It lay roughly parallel to the basal epidermal cells, but was unaltered at the region where short invaginations of the plasma membrane extended into the basal cytoplasm of these cells (Fig. 9). Such infoldings have been described before (14, 15), and it has been suggested that they may be the site of formation of vesicles which are continuously being pinched off the plasma membrane to move into the cytoplasm, thus providing a mechanism for active transport. If that be so, the method by which substances traverse the adepidermal membrane must be quite different since no such infoldings are observed there.

The basal membrane was not separated so distinctly from the dermis. Usually a cell, presumably a fibroblast, pressed close against the basal membrane. The cytoplasm of such fibroblasts had a cisternal type of endoplasmic reticulum. Similar fibroblasts could occasionally be seen deeper in the dermis, where bundles of fibrils were intimately approximated to the cell parallel to its long axis; and sometimes they seemed to disrupt and obscure the outer cytoplasm and to be embedded close to the nucleus. These fibrillae in contact with the cytoplasm exhibited the characteristic banded structure and their diameter varied roughly from 250 to 500 A. The relation of the fibrils to the fibroblasts was similar to that already described by Wasserman *et al.* (16, 17) and Jackson (18) (Fig. 8).

DISCUSSION

The basal membrane in the skin of the adult newt differs in certain ways from that of the larva and, yet, in other ways it resembles the larval arrangement. As for the differences, the membrane of the adult consists of periodic swellings in which there is a great concentration of fibrillae, and of thinner internodular regions which contain only a single layer of fibrillae radiating from the swellings. In the larval newts, however (Fig. 12), as well as in the larval salamander and tadpole (3–5; see Fig. 10) the basal membrane is relatively uniform in thickness and everywhere consists of many layers of fibrils. In the adult newt the reticulum consists of the unit-nodule plus radiating internodular fibrillae; but in the larvae no unit of any sort is found and the fibrillae appear to be continuous within the membrane.

Another important difference in the skin of larval and adult amphibians is in the structure of the "membrane" and "space," which separates the epidermis from the basal membrane. We have elected to designate these structures as "adepidermal membrane" and "adepidermal space" respectively. In the adult the adepidermal space is structureless and contains, presumably, a fluid or gel (Figs. 1, 3, 9). In the skin of the premetamorphic newt, however, we have observed distinct granules in the space (Fig. 12); they are numerous, close to one another and arranged in single file within the space. Adepidermal granules were recognized in larval forms by Porter (see Fig. 7 in Montagna, 19) and by Weiss and Ferris (4, 5) who suggested that some causal relation may exist between the spacing of the granules and the development of the fibrillar pattern and fabric of the basal membrane (5).

We noticed differences in the caliber of the fibrils in the various forms we studied (compare fibrillar sizes and magnifications in Figs. 10 to 12). The finest fibrils were observed in the larval newt, roughly of the order of 200 A; and the largest in the tadpole, up to 500 A; those of the adult newt were intermediate, approximately 300 A.

Although the differences between the amphibian larvae and the adult newt are striking, there are notable similarities (Figs. 10 to 12). In the basal membrane of the larval salamander and tadpole alternating layers of fibrils at right angles to each other have been reported (3–5). We have also studied the ultrastructure of the tadpole's skin (*Rana clamitans*) and have made initial observations on the skin of the larval newt, *Triturus viridescens*, before metamorphosis (Figs. 10 and 12). Our results agree with previous reports for the tadpole and show that in the newts this larval pattern is also adhered to. The orthogonal arrangement is continuous with only occasional interruptions in the pattern (Fig. 10). In the case of the basal membrane of the adult newts, the fibrils within the nodules are arranged in layers resembling a distorted orthogonal pattern with each layer itself consisting of a stack of fibrils. The distortion is greatest in the capsular portion of the nodule where the fibrillae are arranged circumferentially. If the nodules were not separated by the internodular region and instead were pressed close against one another without an intervening capsule, then the reticulum would resemble closely that of the larva.

A second similarity between the basal membrane of the adult newt and that of the larva is that the fibrillae of both adult and larva are uniform in diameter within each group, and have a characteristic banded structure. And, finally, relations of the reticulum with the epidermal cells on one side and the dermis on the other are similar. These resemblances suggest a similarity in the developmental forces which operate in the formation of the reticulum of the basal membrane. However, in the adult there are influences which tend to distort the orthogonal pattern and create the periodic swellings, the capsules, and the intervening radiate fabric. The nature of these influences and, indeed, the mechanism of formation of the adult reticulum is not known. It is possible to imagine that the nodules are laid down by individual cellular elements. The cells may be periodically spaced and produce the nodules with its radiating fibers. However, the nodules, when first elaborated, are probably quite close to one another and only secondly are separated. In the case of the immediately postmetamorphic or land stage of the newt the nodules are separated by a smaller interval (1). At first there may be a pronounced pattern of alternating fibrillar layers such as in the larva and the layers may be continuous from one nodule to the next by virtue of the relative absence of an internodular zone. As the animal grows, the formation of additional nodules may not proceed as rapidly as the increase in area of the skin. The nodules under such a circumstance would be pulled apart. Assuming that the fibrillae between the internodules are adherent and do not completely separate or, indeed, are continuous from one nodule to the next, they would be placed under tension in the plane of the epidermis and the tension would be transmitted to the nodules which would be pulled radially in the same plane. Perhaps the effect would be as though to draw the strings of a purse. The ordered orthogonal pattern of the nodules would be disturbed by the radial tension and by any associated twisting. Perhaps the distribution of forces on the surface of the nodule is such to draw together the surface fibrils to form a capsule. These speculations may explain how the similarities and differences between the larval and adult basal membrane arise. They do not explain the mechanism of initial formation of the fibrillae.

How the reticulum is formed is not known and the sections of larval and adult skin which we have studied have offered no definitive answer. There are various theories of the formation of the basal membrane which have been reviewed in a previous work (1) and need not be repeated here. In that work silver-stained sections of regeneration skin were observed under the light microscope and the appearance and disposition of the early reticulum and epidermal cells suggested that the reticulum may be a product of the basal epidermal cells. In the present study we have not been able to resolve the problem, one way or the other, for the lack of appropriate stages and because of technical difficulties. The only signs of cellular participation in fibril formation were seen in areas below the already formed membrane. Fibroblasts were observed in intimate association with fibrillae as though the fibrils were being formed in the outer cytoplasmic layers, a relation which has already been reported. Weiss and Ferris (5) favor the theory that fibroblasts give rise to the fibrillae and that the epidermis functions in the orientation of the fibrillae.

Another structure of interest in the skin of the newt was the thin unbroken membrane separated by a small uniform space from the overlying epidermal cells. We propose to call it *adepidermal membrane* rather than *basement membrane* as suggested by Ottoson and others (6, 20) or *dermal membrane* by Selby (7). Ottoson *et al.* (6) suggested the term "basement membrane" since this is the nomenclature commonly used by electron microscopists in referring to similar submicroscopic membranes in a variety of different organs (22–24). Yet even here uniformity is not achieved and Yamada, for instance, refers to the membrane underlying the epithelium in the gall bladder of the mouse simply as a limiting membrane (25). Selby (7) in suggesting the term "dermal membrane" recognized the prior claim of histology to the term "basement membrane." We agree that the term basement or basal membrane or its other synonyms is too heavily committed in the histological literature of the last 75 years to the distinct zone under the epidermis of the vertebrate skin which is distinguished with the light microscope. Yet we feel that the term *dermal membrane* is inadequate because the *adepidermal membrane* lies between the basal membrane and the epidermis, and since the basal membrane itself is classically not considered a part of the dermis the term does not correctly describe the position of the membrane relative to the basal reticulum. We feel that the term *adepidermal membrane*, or indeed the more general term *adepithelial membrane*, is rightly descriptive of the membrane in question without conflicting with any historically established usage.

Finally, it is of interest to remark further upon the staining of the nodules in ordinary histological preparations (1). With a triacid stain, such as Mallory's azan, the center of the nodule stained with the red component azocarmine and the periphery with aniline blue. The differential staining was attributed (1) to a difference in physical state of the center and periphery of the nodule causing an accumulation and precipitation of the red particulate component of the stain in the center and a binding of the molecularly dispersed dye in the capsule; the idea that a qualitative chemical difference such as the presence of nuclear material in the center of the nodule could account for the dye distribution was rejected after histochemical analysis of the nodule. Studies with the electron microscope show a difference in packing of the fibrillae of capsule and nodular center which can account for the difference of staining; they also show that the nodule is not a cellular structure, but part of the extracellular matrix.

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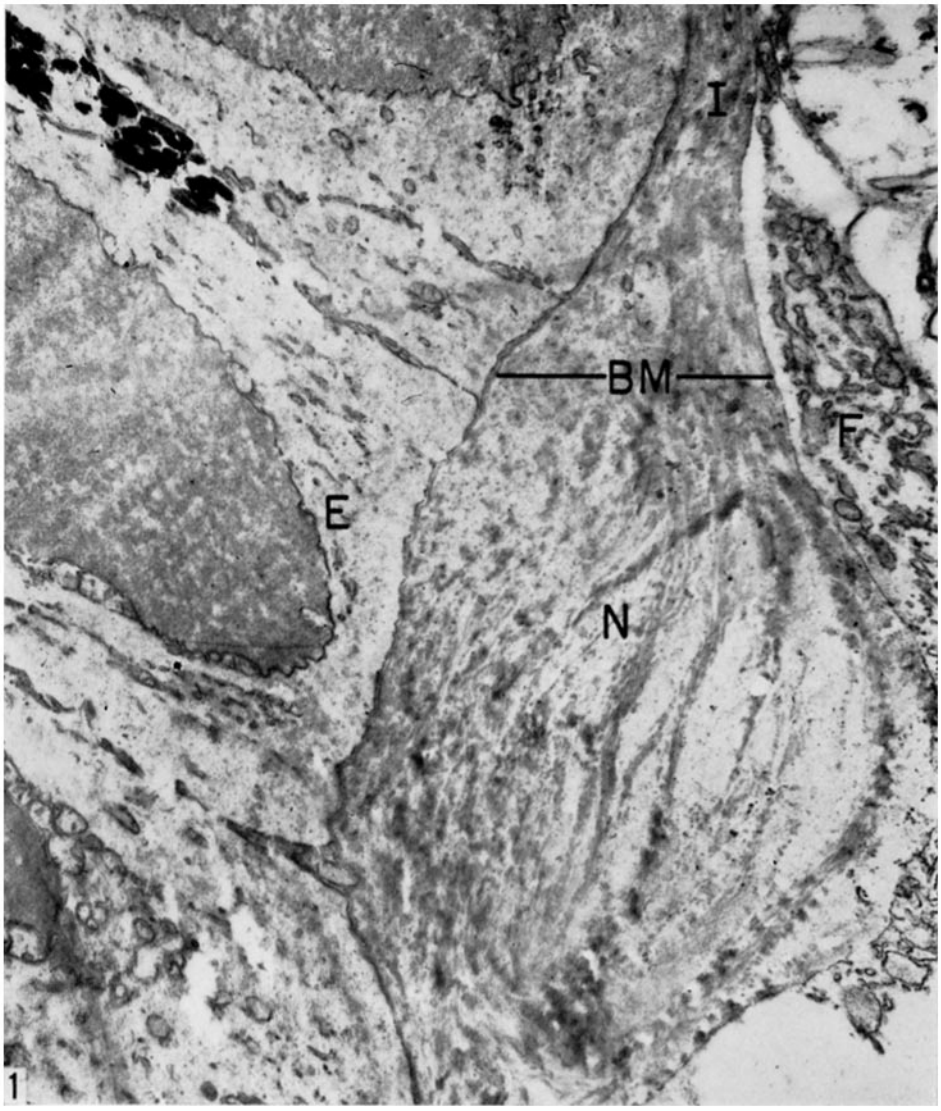
Explanation of Plates

Plate 12

FIG. 1. Cross-section of arm skin from an adult newt (*Triturus viridescens*) fixed in 1.2 per cent $KMnO_4$ for 5 hours. The epidermal cells (*E*) are separated from the fibrillar basal membrane (*BM*) by the adepidermal space and membrane respectively. The nodular (*N*) and internodular (*I*) region of the basal membrane can be seen. A fibroblast (*F*) lies close to the basal membrane on the dermal side. × 9,000.

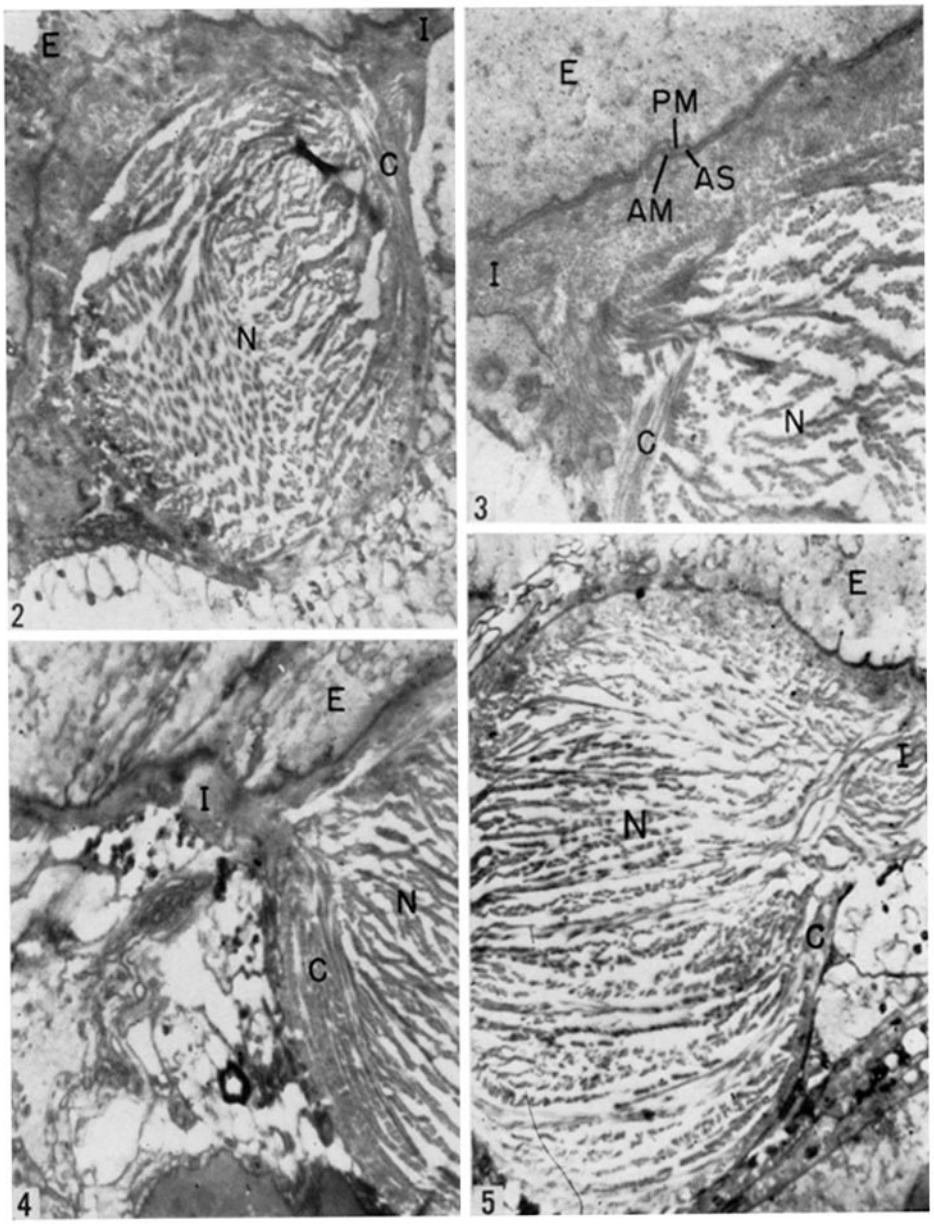


(Salpeter and Singer: Adepidermal reticulum of newt)

PLATE 13

FIGS. 2 to 5. Four different nodules of the basal membrane of the arm skin of adult *Triturus* showing the various fibrillar arrangements encountered. The skin was fixed in 1.2 per cent $KMnO_4$ for 20 hours. Note the formation of a capsule (*C*) by the fibrils at the circumference of the nodules (*N*), as seen best in Fig. 4. The orthogonal arrangement of fibrils is clearly preserved in Fig. 5 and somewhat distorted in Fig. 2. The relation of the adepidermal membrane (*AM*) to the adepidermal space (*AS*) and to the plasma membrane (*PM*) of the epidermal cell (*E*) is demonstrated in Fig. 3. Note the infoldings of the plasma membrane. *I*, internodule.

Magnifications: Fig. 2, × 8,000; Fig. 3, × 18,000; Fig. 4, × 7,500; Fig. 5, × 7,500.

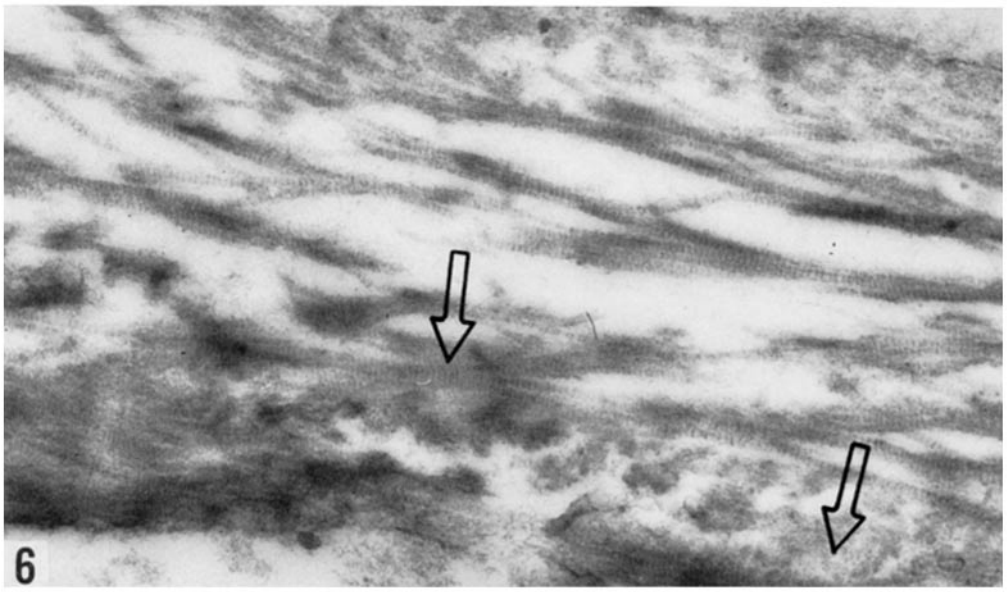


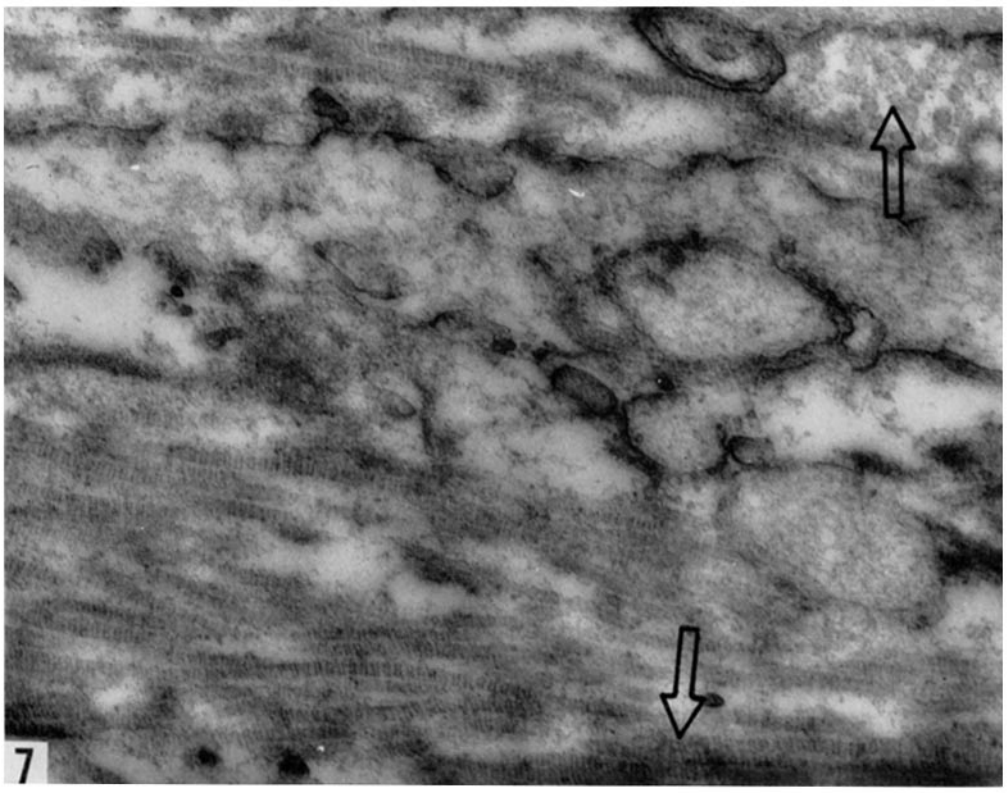
(Salpeter and Singer: Adepidermal reticulum of newt)

PLATE 14

FIG. 6. Fibrils of the internodular region of the basal membrane of the arm skin of the adult newt fixed in 1.2 per cent $KMnO_4$ for 20 hours. Most fibrils appear in longitudinal view, but a region where they are cut across is shown by the lower arrow. Note the distinct banding of the fibrils with a clear major and minor band. Upper arrow points to instance of lateral alignment of like bands of adjacent fibrils. × 40,000.

FIG. 7. Dermal fibrils of the arm skin of the adult newt fixed in 1.2 per cent $KMnO_4$ for 20 hours. The diameter of these fibrils (upper arrow) is approximately twice that of those in the basal membrane (compare Fig. 6, lower arrow). Although the banding is more distinct in the dermal fibers than in the basal membrane the periodicity is about the same. Lower arrow points to an area of lateral alignment of bands. × 40,000.



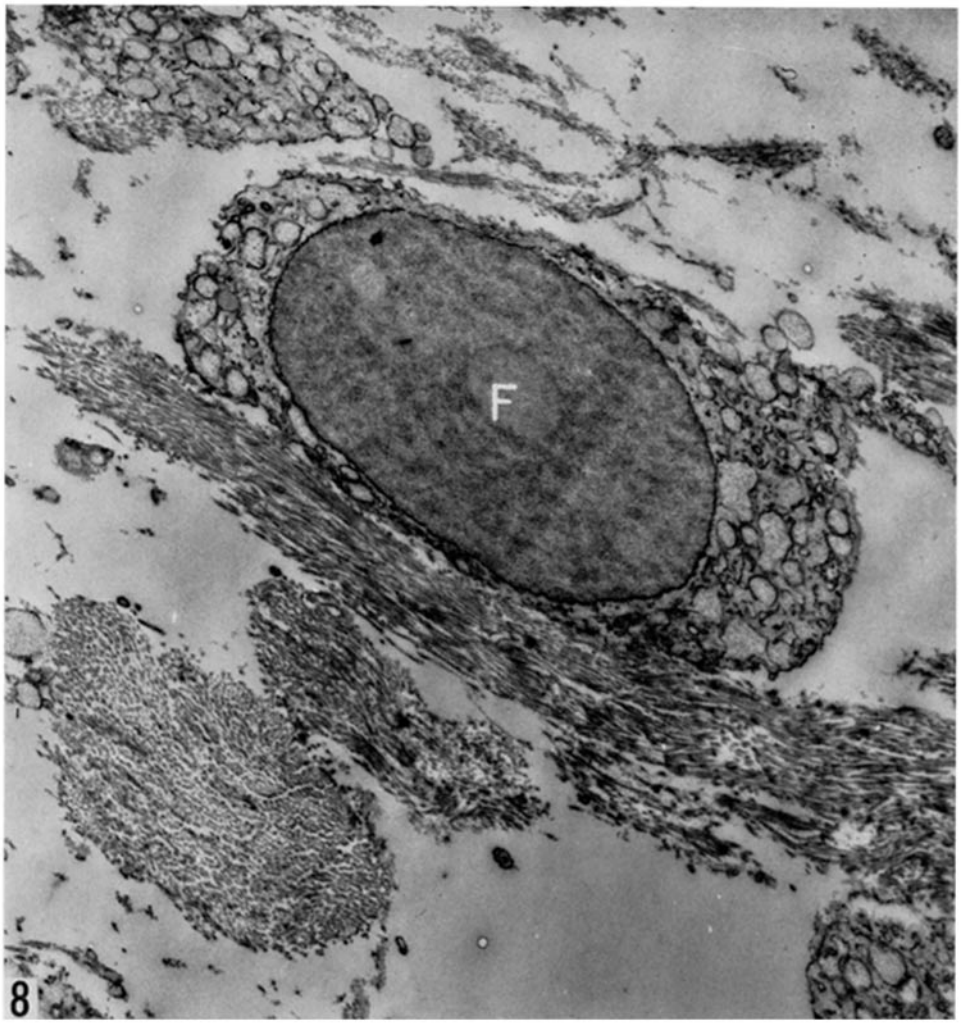


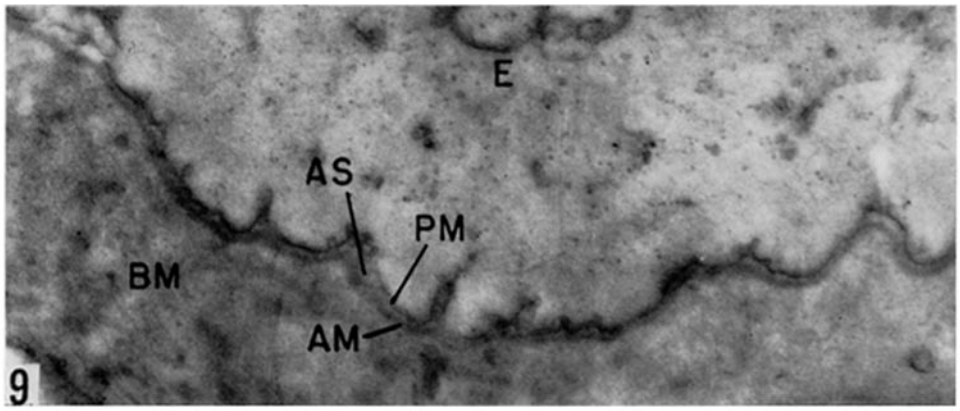
(Salpeter and Singer: Adepidermal reticulum of newt)

PLATE 15

FIG. 8. Fibroblast (*F*) in dermis of arm skin of adult *Triturus* fixed for 20 hours in 1.2 per cent $KMnO_4$. Note the intimate relation of fibrillae to the cytoplasm. × 7,000.

FIG. 9. Shows relation between plasma membrane (*PM*) of basal epidermal cell (*E*) and the adepidermal membrane (*AM*). Here and there the plasma membrane invaginates into the basal cytoplasm of the epidermal cell; small vesicles appear to form and perhaps to pinch off from the invagination (see also Fig. 3). The adepidermal space (*AS*) distinctly separates the plasma membrane from the thicker, straighter adepidermal membrane. *BM*, basal membrane. × 30,000.



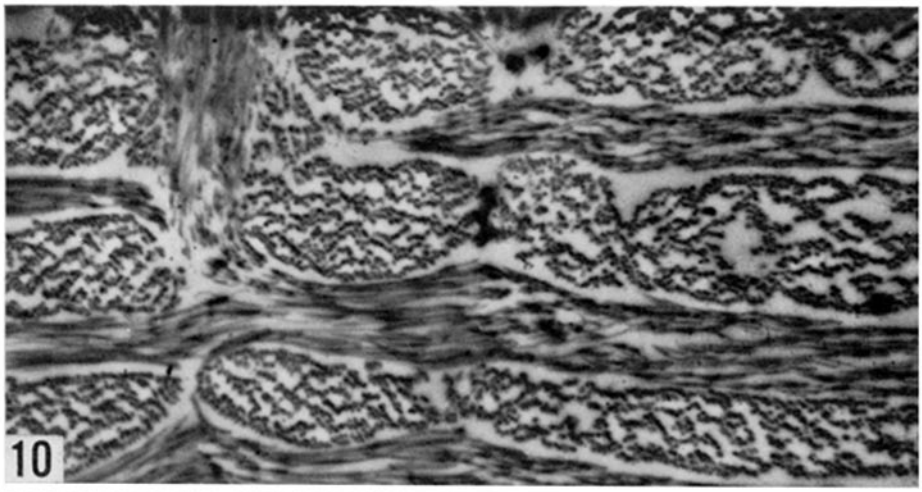


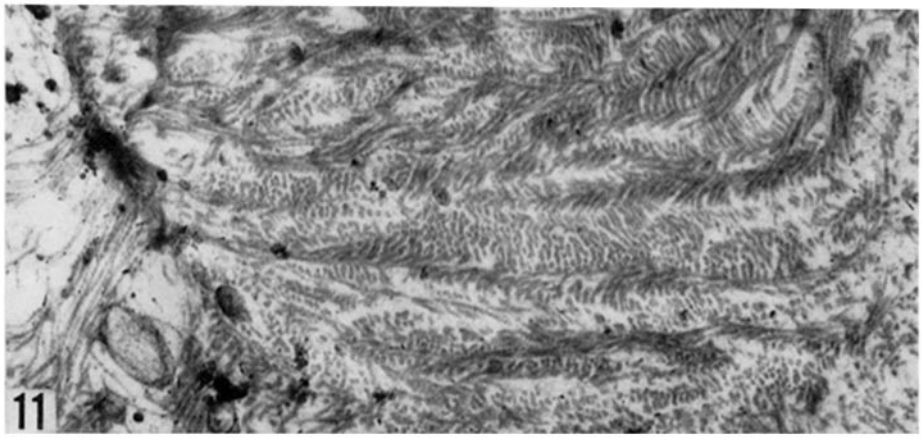
(Salpeter and Singer: Adepidermal reticulum of newt)

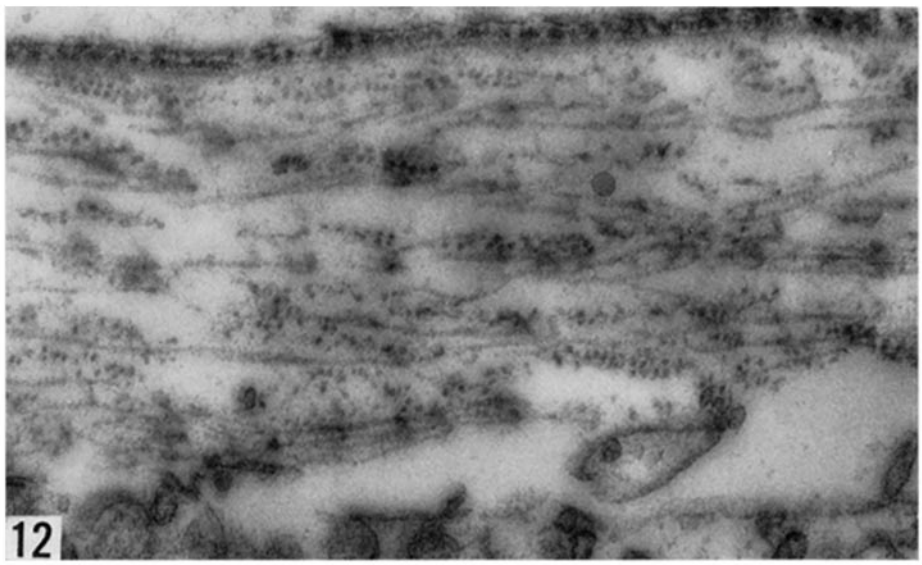
PLATE 16

FIGS. 10 to 12. Cross-sections through the basal membrane of the tadpole, the adult newt, and the larval newt, respectively. Note the alternating arrangement of fibrillar layers in each case but most striking in the tadpole (10), and least so in the larval newt. In the larval newt (12) the plasma and adepidermal membranes can be seen above, and between them the granules. Fixative, $KMnO_4$.

Magnifications: Fig. 10, × 9,000; Fig. 11, × 18,000; Fig. 12, × 40,000.







(Salpeter and Singer: Adepidermal reticulum of newt)