INTRANUCLEAR AND CYTOPLASMIC ANNULATE LAMELLAE IN TUNICATE OOCYTES

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ABSTRACT

Electron microscope studies were made on various tunicate oocytes at different stages of growth and development. Both the inner and outer lamellae of the perforated nuclear envelope demonstrate considerable blebbing activity. The blebs of the inner lamella detach into the nucleoplasm where they undergo a special type of fusion process resulting in the formation of numerous, usually single, differentiated annulate lamellae of various lengths. The blebbing of the outer layer of the nuclear envelope contributes to the vesicular and granular endoplasmic reticulum characteristically present in the ooplasm and perhaps to the differentiation of cytoplasmic annulate lamellae as well. Cytoplasmic stacks of annulate lamellae frequently have ribosomes associated with them. In addition, granular accumulations are sometimes observed around or between the annuli. The morphological evidence suggests that, at least in many cases, the annuli in the annulate lamellae are patent.

INTRODUCTION

The term annulate lamellae was first used by Swift (1956) to describe groups of parallel lamellae which are often, but not always, arranged in stacks in the cytoplasm (Kessel, 1963 b). The membranes contain periodically arranged annuli comparable in fine structure to the annuli in the nuclear envelope. Each lamella typically consists of two parallel membranes separated by a cisternal space approximately 20 to 40 m\(\mu\), and since the ends of the lamellae are often fused each unit appears as a flattened sac or vesicle.

Annulate lamellae have been observed of late in the cytoplasm of a considerable variety of cell types, a feature which would tend to suggest that these structures perhaps have a more important role in the activity of cells possessing them than was formerly supposed. Annulate lamellae are commonly found in the cytoplasm of both invertebrate and vertebrate germ cells (Afzelius, 1957; Palade, 1955; Swift, 1956; Rebhun, 1956, 1961; Ruthmann, 1958; King and Devine, 1958; Pasteels, Castiaux, and Vandermursche, 1958; Merriam, 1959; Okada and Waddington, 1959; Kane, 1960; Wischnitzer, 1960; Barer et al., 1960; Gross et al., 1960; Kaye et al., 1961; Mahowald, 1962, 1963; Balinsky and Devis, 1963; Kessel, 1963a,b). However, the lamellae have also been observed in somatic cells (Swift, 1956; Ross, 1962; Harrison, 1962) as well as in tumor or cancer cells of various kinds (Schulz, 1957; Wessel and Bernhard, 1957; Binggeli, 1959). Thus far, it appears that annulate lamellae are most prominent or best developed in the cytoplasm of young cells actively engaged in growth and differentiation. The annulate lamellae possess certain structural characteristics of both the nuclear envelope and the granular endoplasmic reticulum. However, they so closely resemble the nuclear envelope in structure that it appears in some cells as if pieces of the nuclear envelope were placed in stacked,
parallel array in the cytoplasm (Kessel, 1963 b, 1964 b). In some cells, ribosomes may be associated with the surface of the annulate lamellae (Kessel, 1964 b). Recently, information has been provided regarding the morphogenesis of the annulate lamellae in the oocyte of Necturus (Kessel, 1963). No direct evidence appears to be yet available regarding the function of annulate lamellae, although suggestions have been made (Swift, 1956).

The presence of annulate lamellae within the nucleus is rare, having been reported thus far in only a few cells (Merriam, 1959; Hsu, 1963; Kessel, 1964 a). Indeed, the presence of any type of membrane system within the nucleus is unusual. This report dealing with various tunicate oocytes records the presence of intranuclear annulate lamellae, provides information regarding the mechanisms whereby such intranuclear membrane structures arise, and describes the system of cytoplasmic annulate lamellae also present.

MATERIALS AND METHODS

The tunicates used in this study, Ciona, Molgula, and Styela sp., were obtained from both the Woods Hole, Massachusetts region and the Pacific Bio-Marine Company of Venice, California. Portions of the ovary containing oocytes of different sizes and in different stages of development were fixed in either a 1 or 2 per cent solution of veronal-acetate buffered osmium tetroxide (Palade, 1952) at pH 7.5 or 8.0. The osmium tetroxide was prepared using both distilled water and artificial sea water. The tissues were fixed for periods of 1 to 2 hours at 4°C. Subsequent to rapid dehydration in a series of cold ethanols and treatment with propylene oxide, the oocytes were embedded in Epon 812 (Luft, 1961). Sections displaying silver or gold interference colors were obtained with a Porter-Blum ultramicrotome equipped with glass knives. The sections were mounted on coated or uncoated grids and stained with a saturated aqueous or alcoholic solution of uranyl acetate or with lead acetate (Watson, 1958) and examined in an RCA EMU-3D.

OBSERVATIONS

I. The Nuclear Envelope

The oocyte nuclear envelope consists of two distinct osmiophilic membranes, the inner and outer membranes, which are approximately 70 A wide and separated by a less dense perinuclear space usually 150 to 300 A in width. At frequent and regular intervals the inner and outer membranes join to form a pore region which, in profile view, has a diameter of approximately 800 A (Figs. 1 to 5). These structural features are essentially similar to those of the nuclear envelope in a large number of metazoa cells (Watson, 1955, 1959; Wischnitzer, 1958; Barnes and Davis, 1959).

In sections perpendicular to the nuclear surface a thin, dense structure frequently appears to traverse the region of the nuclear pore (Figs. 1, 3). The position of this structure and the density characteristics associated with it are variable. Such structures associated with the nuclear pores of other cells have been referred to as pore or annular diaphragms by some investigators (Afzelius, 1955; Hagnau and Bernhard, 1955; Watson, 1955). Still others have suggested that such structures do not represent a diaphragm covering the pore, but rather a configuration of the rim of an open pore visible because of specific planes of section (Watson, 1959; Barnes and Davis, 1959). Thus some controversy has been expressed as to whether the pores of the nuclear envelope are open or closed.

In the tunicate oocytes, the pore region sometimes appears to be traversed at the level of the nuclear membrane by two fine parallel membranes appearing less distinct and dense than the nuclear membrane (Fig. 3). In other cases, only one distinct band of variable density and position appears to traverse the pore (Figs. 1 to 3). More rarely, and in thinner sections, the pore shows no evidence of any traversing membrane whatsoever (Figs. 4, 5). Some degree of electron opacity appears associated with the pore region when viewed in perpendicular sections of the nuclear envelope (Figs. 4, 5). It is difficult, however, to determine exactly to what extent this is due to the presence of a material within the pore and how much may be due to the section level which passes through the very edge of the pore rim. The electron-opaque material is more favorably viewed in oblique or nearly tangential sections of the nuclear envelope (Fig. 2).

In oblique or nearly tangential sections of the nuclear envelope, the pores appear as ring-shaped structures or annuli (Fig. 2), having an outside diameter of approximately 1,000 A. A homogeneous matrix of moderate density is present within the annuli as well as between them (Fig. 2). The wall of the annulus in some cases appears to be composed of small, spherical structures approximately 150 A in diameter. They appear similar to structures referred to as subannuli.
in the nuclear pores of other cells (Wischnitzer, 1958; Merriam, 1959). Dense granules about 150 Å in diameter are also observed in the central region of many of the annuli.

Of some interest is the fact that a definite substructure appears associated with the membranes comprising the nuclear envelope in certain of the micrographs. In such cases, a variation in density is noted in the membranes due to the presence of a large number of small, closely packed, spherical units having the form of vesicles in perpendicular sections of the nuclear envelope (Fig. 5, arrows). These vesicle-like structures possess a diameter of about 50 to 60 Å and can be observed in both the inner and outer layers of the nuclear envelope.

II. Activity of the Inner and Outer Nuclear Membranes

Both the inner and outer nuclear membranes appear to engage in considerable activity during the course of oogenesis. This is reflected in a blebbing from both layers of the envelope. A large amount of blebbing takes place along the outer layer of the nuclear envelope especially during early stages of oogenesis (Figs. 6, 7). The blebs have ribosomes associated with their surfaces while still being a part of the outer membrane and enclosing space continuous with the perinuclear space. The outer nuclear membrane sometimes has ribosomes attached to its outer surface also. The size of the blebs is similar to that of a large number of rough-surfaced vesicles which are present in the ooplasm throughout oogenesis and appear to comprise a vesicular form of the granular endoplasmic reticulum (Figs. 6, 16).

The inner layer of the nuclear envelope is also capable of blebbing, but in this case the blebs are usually smaller than those associated with the outer layer of the nuclear envelope and they were not observed to be associated with ribosomes (Fig. 8). Individual intranuclear vesicles thus formed remain in close proximity to the nuclear envelope. The oocytes in which these intranuclear vesicles were observed are smaller than those in which differentiated intranuclear annulate lamellae occurred. This observation would tend to suggest that the intranuclear vesicles precede the intranuclear annulate lamellae in time in the developing oocyte.

The active vesiculation of both the inner and outer nuclear membranes in these and other oocytes (Kessel, 1963 a, b; 1964 a, b) indicates that the envelope must be in a highly dynamic state insofar as membrane synthesis and replacement are concerned and that undoubtedly active membrane flow is involved in this process (cf. Bennett, 1956).

III. Intranuclear Annulate Lamellae

Intranuclear membrane systems are of infrequent occurrence. In the tunicate oocytes, these membrane systems take the form of vesicles, lamellae, and, in the differentiated state, annulate lamellae. Recent studies on the oocyte of *Styela* have provided information regarding some of the stages involved in the morphogenesis of the intranuclear annulate lamellae (Kessel, 1964 a). Similar results have been obtained in the oocytes of *Molgula* and *Ciona*, and stages in the morphogenesis of intranuclear annulate lamellae in these cells are shown in Figs. 8 to 12. The raw material for the formation of annulate lamellae in the nucleus appears to be the individual vesicles derived from a blebbing of the inner nuclear membrane (Fig. 8). On the basis of the morphological variations observed in oocytes of different sizes, the following sequence is suggested. Two vesicles, in close proximity to each other, touch along a small portion of their surface (Fig. 9). The vesicles do not appear to completely fuse, but remain connected by a narrow channel (Fig. 10). An annulus is formed very soon in this region of partial fusion of two vesicles, resulting in the youngest possible stage of an annulate lamella (Fig. 11). Further growth of the intranuclear annulate lamella appears to occur by the partial fusion of vesicles at the ends of those already differentiated (Figs. 12, 13).

The intranuclear annulate lamellae usually occur singly rather than arranged in stacked, parallel array. Sometimes an individual lamella is oriented with its long axis parallel to the nuclear envelope while in other cases the long axis of the lamella is oriented at right angles to the nuclear envelope. In still other instances, the lamellae are curved (Fig. 12). In some cases, the intranuclear annulate lamellae are several microns in length.

In both perpendicular and oblique or nearly tangential sections, the structural characteristics of the intranuclear annulate lamellae appear essentially similar to those of the nuclear envelope. The manner in which intranuclear annulate lamellae appear to be constructed in the tunicate oocytes is very similar to the manner in which...
cytoplasmic annulate lamellae are formed in the *Necturus* oocyte (Kessel, 1963b).

**IV. Cytoplasmic Annulate Lamellae**

Cytoplasmic annulate lamellae are present in the ooplasm during oogenesis in all tunicates examined. They were observed in oocytes both before and after the appearance of yolk particles. The lamellae are characteristically arranged in stacked, parallel array, and the stacks are scattered in a seemingly non-preferential manner throughout the ooplasm (Figs. 14, 16, 17). Both the length of the individual lamellae and the number of lamellae comprising a single stack are exceedingly variable. Thus, the number of lamellae in a single stack may vary from two to as many as three dozen (Fig. 14). In each lamella, the annuli are separated by a distance of approximately 100 to 125 nm, varying to some degree with the plane of section with respect to the annulus. The annular regions in different lamellae comprising a stack tend to be aligned directly opposite each other (Figs. 14, 17). The lamellae often have ribosomes associated with them, being arranged along the outer surface of the lamellae as well as in the ooplasm between the lamellae. An aggregation of granular material may also be present between the stacked annulate lamellae (Fig. 14). Further, this granular material shows a rather specific orientation with respect to each annulus in the lamellae. The clusters of granular material have a diameter approximating that of the annulus, and typically are located in the ooplasm directly opposite annular regions of adjacent lamellae. In some cases, annulate lamellae occur without such associated granular material. Although no direct evidence is yet available, the granular clusters appear to be closely packed ribosomes.

The ends of individual lamellae often appear expanded into spherical or elongate vesicles which usually have ribosomes on the outer surface and appear structurally similar to isolated, rough-surfaced vesicles in the nearby ooplasm (Fig. 16). In addition, larger, vacuole-like expansions of the ends of the annulate lamellae are observed (Fig. 17). In some cases, two lamellae may be continuous with a single such vacuole-like structure (Fig. 17).

When the cytoplasmic annulate lamellae are sectioned nearly tangentially and a surface view of the annulus obtained, circular profiles or ring-shaped structures are observed similar to those in the nuclear envelope. In the majority of cases in which the lamellae are sectioned perpendicu-

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**Figure 1** Section perpendicular to the nuclear surface with the pores shown in side view at different levels of sectioning (arrows). A dense membrane appears to traverse the center of the pore region in some cases, while in others the level at which the membrane appears to traverse the pore is variable. Nucleus (N); cytoplasm (C). X 92,000.

**Figure 2** Nearly tangential section of the nucleus showing the ring-shaped or annular configuration of the pores in such a view. Note that the annuli appear embedded in a rather homogeneous matrix of moderate density. The central region of many of the annuli contains a dense structure (arrow). The rim or wall of the annulus in certain instances appears to be composed of several vesicular or perhaps tubular structures (arrows). X 92,000.

**Figure 3** Section perpendicular to the nuclear surface. The pores in such a view show considerable variation in structure which is attributed to the level at which the pore has been sectioned (arrows). Nucleus (N); cytoplasm (C), containing numerous ribosomes. X 65,000.

**Figure 4** At higher magnification it is possible to observe that the nuclear pore does not appear to have a membrane or diaphragm traversing it (NP). Slightly off-center sections of two other nuclear pores are present (arrows). Nucleus (N); cytoplasm (C). X 144,000.

**Figure 5** In this micrograph both the inner and outer membranes of the nuclear envelope appear to be composed of small vesicular or perhaps tubular units which are most clearly observed in the regions of the arrows. Two pores are located at NP. Nucleus (N); cytoplasm (C). X 175,000.
FIGURES 6 AND 7  These figures demonstrate the blebbing (B) characteristic of the outer nuclear membrane. Note that the blebs contain ribosomes associated with them, as do isolated, rough-surfaced vesicles in the cytoplasm (RV). Nucleus (N); intranuclear vesicles (INV); ribosomes (R); mitochondrion (M); nuclear envelope (NE). × 92,000.
larly so as to display the annulus in side view, dense membranes appear to traverse the annular regions (Figs. 14, 16, 17). However, under suitable conditions, it is also possible to observe profile views of an annulus in which no such dense membrane appears to be associated with the annulus (Figs. 15, 18, 19). There is thus some suggestion that what appears as a diaphragm or pore membrane in profile views of annulate lamellae may represent a section of the rim of an open pore, as was suggested also for the pores or annuli in the nuclear envelope.

V. Endoplasmic Reticulum

The endoplasmic reticulum is represented in the developing oocytes by numerous rough-surfaced vesicles scattered throughout the ooplasm. Their diameter varies depending upon the section level, but many range from 200 to 400 m. They were observed in oocytes of all sizes studied. In addition to the ribosomes which appear attached to the outer surface of the membranous vesicles, ribosome particles are also scattered throughout the ooplasm, where they usually occur singly rather than in rosettes or clusters (Fig. 16). That the vesicular endoplasmic reticulum appears to be derived for the most part from a blebbing of the outer nuclear membrane has already been mentioned. Few lamellar elements of the endoplasmic reticulum appear in the developing oocytes, but, when present, they are observed in the very small oocyte before any indication of yolk deposition.

The predominantly vesicular form of the endoplasmic reticulum in the tunicate oocyte is unlike the lamellar or reticular form typically present in many somatic cells (Porter, 1961; Fawcett, 1961; Palade, 1956) and the well developed system of endoplasmic reticulum present in the crayfish oocyte (Beams and Kessel, 1963).

DISCUSSION

A question of considerable interest that has arisen since the discovery of pores in the nuclear envelope is whether or not these areas represent actual physical contact between the nucleoplasm and cytoplasm or whether this contact is mediated by the presence of a thin membrane or diaphragm. While many of the electron micrographs of the nuclear envelope of tunicate oocytes show a structure across the pore which could be interpreted as a diaphragm, the variations in structure noted lend themselves more easily to an alternative explanation: namely, that the membranous structure often seen crossing the pore is not a diaphragm, but rather a portion of the nuclear membrane surrounding the pore which has been included in the plane in back or in front of the section and which by projection appears to lie across the pore. This conclusion is essentially that expressed by Barnes and Davis (1959) and by Watson (1959) for certain mammalian somatic cells, and by Marinos (1960) for plant cells. The fact that many of the sections examined were only slightly thinner than the diameter of the pore would make it relatively rare to obtain a section normal to the nuclear membrane which passes through the pore without enclosing portions of the pore margin.

The nuclear pores often contain an electron-opaque material when viewed with the electron microscope (Afzelius, 1955; Wischnitzer, 1958; Watson, 1955, 1959), and it has been suggested that such material might affect nucleocytoplasmic exchanges (Mirsky and Osawa, 1961). Experimental studies by Feldherr (1962, 1964) have indicated that the nuclear pores are not areas which permit free exchange between the nucleus and cytoplasm and that colloidal particles bind to the material within the pores. In this connection, the observations by Merriam (1961) on isolated nuclear envelopes of nearly ripe eggs of *Rana pipiens* are interesting. He observed that thin sections of isolated nuclear envelopes gave evidence of diffuse material within the "pores" as well as a more condensed diaphragm across their "waists." All material within the "pores" including the condensed diaphragm were found to be removed by trypsin digestion. Since both annular and diaphragm materials remain within the envelope when it is isolated, Merriam (1961) considered these components to be a part of the structure of the nuclear envelope, not merely evidence of material passing through the "pores." No evidence was obtained by Merriam (1961) for any ribonuclease-removable material in any part of the "pore" complex.

Because of similarities in structure of the nuclear envelope and the annulate lamellae, it is of interest to determine the nature of the annulus in the cytoplasmic lamellae. A question which arises in this connection is whether the dense membrane which appears to traverse the annuli in the annulate lamellae is actually a diaphragm or whether the annulus in this case is open. Diagrams by
Ross (1962) and Balinsky and Devis (1963) have shown the annular regions in lamellae to be traversed by a membrane. In fact, the term “pitted membranes” was employed by Balinsky and Devis (1963) in characterizing these structures. However, in this investigation annular regions in the lamellae were observed, although quite infrequently, in which a membrane did not appear to traverse an annulus. This observation would tend to suggest that the annular regions in at least some annulate lamellae are not closed by a membrane, but that the explanation for the appearance of such a structure in many of the sections may be similar to that given previously for the nuclear envelope.

The mechanics involved in the morphogenesis of an annulus by the partial fusion of two vesicles pose a difficult problem. Possible explanations would appear to depend on whether or not a diaphragm traverses the annulus in the annulate lamellae. If such a structure is present, then conceivably if only portions of two vesicles fuse, but do so very completely, a diaphragm-like structure might result. The contribution of membranes from two vesicles might also explain to some extent why the formed diaphragm appears to have a density greater than that of the units which formed it. However, the evidence seems to favor the view that the annuli in the annulate lamellae are open. If this be true, then the hole (pore) must be formed at the time that the vesicles fuse or shortly thereafter and in the area of partial fusion itself.

In some cells, ribosomes appear to be associated with annulate lamellae in the cytoplasm (Afzelius, 1957; Merriam, 1959; Kessel, 1964 b) while, in other instances, ribonucleoprotein particles have not been observed to be associated with them (Rebhun, 1956; Ruthmann, 1958). The presence of ribosomes associated with the annulate lamellae in tunicate oocytes might warrant the assumption that these lamellae represent a specialized form of the endoplasmic reticulum in addition to the many rough-surfaced vesicles present in the ooplasm. However, the structural differences between the granular endoplasmic reticulum and annulate lamellae may also suggest functional differences between the two systems which, in some cells, are observed to be continuous (Rebhun, 1961). Certainly, differences in the physical nature and viscosity of the materials associated with the annulate lamellae as compared to the vesicular endoplasmic reticulum are indicated.

In this connection, the results of Kane (1960)

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**FIGURE 8** The inner layer of the nuclear envelope in this micrograph is engaged in the process of forming a bleb (arrow) which will subsequently be released into the nucleoplasm (N). Cytoplasm (C). × 92,000.

**FIGURE 9** Vesicles so derived by the blebbing activity of the inner nuclear membrane and located in close proximity to each other undergo a rather special type of fusion process. An initial stage of such activity is shown here, and in this instance a partial fusion of two vesicles is indicated in the region of the arrow. Nucleus (N), cytoplasm (C). × 92,000.

**FIGURE 10** A slightly later stage in the partial fusion process of two vesicles to produce an annulus. The vesicles are connected by a narrow channel which is longer than that observed in Fig. 7 and represents the region of the forming annulus (FA). × 80,000.

**FIGURE 11** This shows the final stage in the morphogenesis of an annulus resulting from the partial fusion of two vesicles. This appears to be the youngest possible stage of an annulate lamella. The annulus is present at A. A matrix of moderate density already appears to surround the annulus and in this instance the rim of the annulus appears to be broken (arrow). × 80,000.

**FIGURE 12** A relatively long, differentiated annulate lamella appears curved in the nucleoplasm close to the nuclear envelope (NM). Annulate regions in the lamella are shown at different levels of sectioning and are in part recognizable by their density characteristics (IAL). The intranuclear annulate lamellae appear to increase in length by the partial fusion of vesicles at the ends of young annulate lamellae such as present in Fig. 9. Nucleus (N); cytoplasm (C). × 63,000.
FIGURE 13 A considerable number of annulate lamellae (IAL) are present in this nucleus (N). Vesicles appear attached to the ends of many of the lamellae, indicating further growth by increasing in length. The annular regions are recognized by their increased density as compared to the remainder of the lamellae. The annulate lamellae are present throughout the peripheral regions of the nucleus. Intranuclear vesicles (INV) are also present close to the nuclear envelope, which in this micrograph is sectioned so as to show the nuclear pores in surface view (ANE). Cytoplasm (C). × 32,000.
showed that, following the extraction of one-half of the cellular protein in the Arbacia egg, the annulate lamellae appeared unaffected while the endoplasmic reticulum was much more markedly affected. Pasteels et al. (1958), in studying the centrifuged fertilized egg of Paracentrotus, noted that most of the vesicular, rough-surfaced endoplasmic reticulum was present in zone 2 while the vitelline platelets were mainly localized in zone 3. In the spaces between the platelets in zone 3 were observed annulate lamellae, Golgi material, and a few rough-surfaced vesicles of the endoplasmic reticulum.

A dense material is often seen to be associated with the annulus in both the nuclear envelope and the annulate lamellae. Merriam (1959) has suggested that such material associated with the annulate lamellae in the oocyte of an echinoderm, Dendraster, may represent ribonucleoprotein in non-particulate form. Several observations are available to suggest that the annulus is a structure of considerable importance in physical and chemical activities of the cell. For example, recent studies by Feldherr (1962, 1964) tend to suggest a rather delicate, but effective mechanism controlling macromolecular exchanges between the nucleus and cytoplasm at the region of the nuclear annuli. The preferential orientation of granular material around the annuli of the annulate lamellae in tunicate oocytes also suggests that specific forces and activities may be selectively localized in these regions.

Although stages in the process have not yet been documented, it is suggested that the cytoplasmic systems of annulate lamellae may have their origin in a specialized type of fusion of numerous rough-surfaced vesicles derived from a blebbing of the outer nuclear envelope, as appears to be the case in oocytes of the echinoderm, Thyone (Kessel, 1964 b).

Although no direct evidence can as yet be provided, the intranuclear annulate lamellae may represent or reflect a specialized type of interaction between the nucleus and cytoplasm related to development and differentiation.

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Figure 14 This figure shows a stack of annulate lamellae in the ooplasm. The ends of the lamellae are often attached to rough-surfaced vesicles (arrows). The annuli in each lamella tend to be organized directly opposite those of adjacent lamellae. Ribosomes are located on the outer membranes of the lamellae as well as in the ooplasm between the lamellae. Note aggregation of granular material opposite each of the annuli (G). X 66,000.


**FIGURE 15** Two annulate lamellae located close to a yolk body (YB). Note that in the region of the arrows the annulus appears open and not traversed by a diaphragm. × 79,000.

**FIGURE 16** A stack of annulate lamellae in the ooplasm. The ends of the lamellae appear expanded into vesicles similar to isolated ones in the cytoplasm, both having ribosomes on their outer surface (arrows). Mitochondrion (M); ribosomes (R). × 53,000.
Figure 17 These annulate lamellae do not appear to have the granular accumulations opposite each of the annuli. The ends of several of the lamellae are continuous (arrows) with rough-surfaced vesicles or vacuoles (V). Ribosomes (R); mitochondrion (M). X 33,000.
FIGURES 18 AND 19  Comparatively thin sections of a portion of two stacks of annulate lamellae. In several instances (A), the annulus appears to be open with no pore or annular diaphragm present. In certain cases (arrows), the annular region appears to contain a band of varying density and thickness associated with it. This appears to be due in many cases to the plane of section including a portion of the pore rim. Fig. 18, X 66,000; Fig. 19, X 92,000. 