ELECTRON MICROSCOPE STUDY OF THE VITELLINE BODY OF SOME SPIDER OOCYTES

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PLATES 95 TO 98

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The vitelline body in spider oocytes was first seen by von Wittich (1845, cited by Bounoure (2)) and shortly afterwards by von Siebold (1848). It was described as a round body located near the nucleus. Balbiani some years later (1) proposed that a relationship exists between the vitellus formation and the developmental changes taking place in this body during the oocyte growth. In regard to its morphological constitution he advanced the hypothesis that it is formed by a condensation of material around the cell center.

It is generally admitted, according to Balbiani's concept, that vitellus (or yolk) formation is related in some way to the vitelline body, but little agreement can be found in the several descriptions concerning the morphology of the body itself.

The early accounts of the vitelline body describe it as consisting of a more or less thick layer of multiple, concentrically arranged lamellae surrounding a central core composed of granular or vesicular elements. It was also claimed that round or crescentic masses of granular or filamentous material, located near the oocyte nucleus, were vitelline bodies. Such variations were noted in different vertebrate as well as invertebrate oocytes (see Prenant (16), Wilson (27)).

Histochemical studies (25) made more recently have demonstrated the existence of ribonucleic acid in the vitelline body of some animal species. Also, polarized light studies have shown (12) that the lamellar layer has negative birefringence, and this optical behavior has been attributed to the mitochondria. Notice must be taken of the fact that mitochondria were considered the main constituent of the lamellae.

The structure of the central core was not clearly defined, except for the probable presence of the cell center.

Even though vitelline bodies are especially characteristic of oocytes, other paranuclear bodies existing in somatic or germinal cells have often been described as similar to them.

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It is the purpose of the present paper to contribute to the understanding of vitelline bodies by describing (*a*) components of the lamellar layer and of the central core; (*b*) the relationship of the elements found in the vitelline body with the vitellus (yolk) formation; (*c*) similarities and differences between vitelline bodies and other cytoplasmic structures existing in other cell types.

Materials and Methods

Specimens from the following spider families were used: Lycosidae, Thomisidae, Gonyleptidae, Sicaridae.[1]

The ovaries were removed from the living spider, placed in a drop of fixative, (osmium tetroxide 1 per cent buffered at pH 7.6 with veronal acetate (6)), and then freed from the attached serific glands under a low power binocular microscope.

The material was then transferred immediately to a tube containing the fixative and kept at 0°C. for 15 to 30 minutes. Following dehydration it was embedded as usual in *n*-butyl methacrylate. The sections were cut with a Porter-Blum microtome (15), mounted on parlodion-coated grids, and then examined with an RCA EMU electron microscope.

In order to localize the structures of greatest interest for electron microscopy, thick sections (about 0.5 μ) were taken from the same part of the block as the thin ones and examined under phase contrast. Thick sections from which the methacrylate had been removed with acetone were also stained with crystal violet (1 per cent water solution). The Feulgen and pyronine methods were used to detect nucleic acids. Fresh material was studied with the phase contrast microscope and with polarized light.

OBSERVATIONS

The present paper deals only with the structure of the vitelline body as seen in various stages of oocyte growth. The optical observations on fresh or fixed material were made as a basis for the better understanding of the electron microscope images and will be reported first.

Optical Observations

Vitelline nuclei were found in the oocytes of the Lycosidae or Thomisidae forms; the oocytes of Gonyleptidae and Sicaridae spiders do not have vitelline bodies but they were nonetheless studied in order to compare their cytoplasmic organization with that of the first mentioned species.

(*A*) *Phase Contrast Microscopy and Stain Techniques.*—As observed in nonfixed oocytes by phase contrast equipment, the vitelline bodies are seen to consist of a peripheral layer of concentric lamellae and a central core, much as described in early papers. The inner limit of the cortex is generally well defined, and there the lamellae are closely packed; the outer limit on the other hand is diffuse because the lamellae there are spread out in the cytoplasm.

[1] Suborder, Arachnoidea; family, Lycosidae; genus, *Lycosa*; species, *L. pampeana*.
Family, Sicaridae; genus, *Scytodes*; species, *S. thoracica*.
Family, Thomisidae; genus, *Thomisus*; species, undetermined.
Suborder, Opilionoidea; family, Gonyleptidae; Subfamily, Pachylinae; genus, Heteropachyloidellus; species, *H. robustus*.

In *Thomisus* oocytes two vitelline bodies may be found, one of which is located usually in the peripheral cytoplasm. The rest of the cytoplasm appears homogeneous in the young oocytes (*Lycosa*), and increasingly granular in the older ones. In every case the granules were found evenly distributed throughout the cytoplasm.

Phase contrast optical examination of thick sections shows the oocyte structure to better advantage than fresh material. Thus the distribution and morphological characteristics of the mitochondria can be recognized. They appear as long, slender filaments in all the developmental stages of oocyte growth. In the young oocytes (*Lycosa*) they form patches of varying sizes either in the central or in the cortical regions of the cell. During more advanced stages of growth on the other hand they are scattered in the cytoplasm, but occur in greater numbers in the cortical region where they form a seemingly continuous layer. They can be seen also in smaller amounts among the lamellae of the vitelline body cortex.

The pyronine method applied to thick sections stains deeply this lamellar cortex which suggests the existence of ribonucleic acid in this zone. Urbani (25) first pointed out the presence of pyronine-positive substances in the vitelline body in studies on *Antedon* and *Pholcus*. The same author noted further that vitelline nuclei of *Tegenaria* showed a positive reaction only in the outer zone of the lamellar layer. The Feulgen method does not stain any part of the vitelline body.

(*B*) *Polarized Light.*—Fresh oocytes, examined under the polarizing microscope, show a typical Maltese cross in the place of the vitelline body cortex, a fact known from the Parat and Jacquiert observations (12). When the first order red plate is interposed, the body cortex shows the colors that characterize two ordered structures, such as: Radially arranged negative index ellipsoids or circumferentially positive index ellipsoids. This indicates that the cortex has negative birefringence with respect to the body radius.

The interpretation of these observations in relation to those from electron microscopy will be discussed below.

Electron Microscope Study

The following description of the vitelline body is based on observations made especially on Lycosidae oocytes. First the fully developed vitelline bodies will be described. Then there will follow a brief mention of the developing vitelline bodies of young oocytes and some observations made on the oocytes of Thomisidae, Gonyleptidae, and Sicaridae. Finally brief reference will be made to vitellus formation.

Fully Developed Vitelline Bodies.—As learned from light microscope observations two parts can be distinguished in the vitelline body: (1) the vitelline body cortex and (2) the central core.

1. Vitelline Body Cortex.—

This was found to comprise the following elements (*a*) lamellar structures; (*b*) mitochondria; (*c*) Golgi elements.

(*a*) *Lamellar Components.*—The lamellae, described by optical microscopy, are the main components of the vitelline body cortex and prove to be similar to what is described in the current electron microscope literature as "the endoplasmic reticulum" (13, 14, 7–9). Each unit consists of two parallel membranes and an intervening space (a cisterna), altogether 250 to 300 A in width, with small particles attached to the outside surface. The electron micrographs in Figs. 4 and 5 (taken from half-grown oocytes which therefore have fully developed vitelline bodies) show these features of the structures as well as elements in between the cisternae profiles.

The appearance and distribution of the lamellae at low magnifications are similar to those described from optical observations. They are found loosely disposed at the periphery of the body cortex, and toward the outside the interlamellar spaces become increasingly large and the orientation of the lamellae departs further from the regular circumferential arrangement. Toward the inside, where they are in contact with the central core material, the lamellae are more closely arrayed. In some places single units penetrate the components of the central core. It cannot be decided from the micrographs obtained whether there is a closer relationship between the endoplasmic reticulum and the central core material than the natural morphological association noted.

As seen in Figs. 4 and 5 the cisternae are filled with a homogeneous substance which is slightly more dense than the surrounding matrix.

Basophilic structures described as composed of double walled lamellae with small granules attached and claimed to be vitelline nuclei, have been recently reported by Rebhun (17, 18).

(*b*) *Mitochondria.*—The electron micrographs showed mitochondria of the vitelline body cortex as long vesicular structures, about 0.2 μ in diameter, with few internal cristae. They are randomly distributed among the circumferentially arranged cisternae. Thin sections usually show them in circular or oblique profiles.

(*c*) *Golgi Elements.*—Small groups of closely packed thin tubules are found among the lamellae of the body cortex and similar groups also exist in other cytoplasmic zones. They have the same general appearance as that of elements recognized by several authors (4, 5, 18–21) as forming part of the Golgi component. Each group is usually composed of 3 to 6 tubules, 130 A in diameter, surrounded by small vesicles about 200 A in diameter. Many of these latter could be profiles of transversally sectioned tubules (Fig. 4). Significant structural differences between the Golgi elements from young or grown oocytes could not be found.

2. Central Core.—

The central core components found in the electron micrographs can be described in two separate groups. The first group consists of a special type of structure to be referred to as "capsulated bodies." In the second group less prominent elements will be included such as: free vesicles, clumps of vesicles, and multivesicular bodies.

Capsulated Bodies.—These are the predominant components of the central core. They are formed by two different parts: (*a*) a couple of central masses that will be termed "the geminated masses;" (*b*) a capsular layer.

(*a*) *Geminated Masses.*—These frequently appear as twin elements, about 0.5 μ in diameter, having round or oval shape (Figs. 2, 3, 6, and 7). They consist of a finely granular material intermixed with filaments of higher electron density (Fig. 7). In some cases a rounded-up condensation of the latter filaments is seen in the center of the masses (Figs. 3 and 7). Each mass is enveloped by a continuous double membrane the units of which are separated by a space of about 150 A. In some micrographs the membranes of the geminated masses are in apparent continuity with the capsular membrane, thus suggesting the possibility that these inner masses may originate from infoldings of the capsular membrane. The contiguous faces of these masses seem pressed together (Figs. 6 and 7). At this contact the four membranes are closer and the electron density increased in such a way that the individual membranes are difficult to resolve.

(*b*) *Capsular Layer.*—The geminated masses are surrounded by an outer layer of material of variable and low electron density, outlined by a folded single membrane. Small vesicles of 750 A in diameter were found inside this layer (Fig. 7). They should not be confused with the membrane infoldings which appear in the micrographs as circular or elongated profiles running throughout the capsular layer and which at some points come into contact with the membranes of the geminated masses. Pictures taken of tangential sections of the capsular membrane show very complicated images of the folds which could be interpreted as a different structure. They can be observed in Figs. 6 and 7.

(*c*) *Other Elements of the Central Core.*—Multivesicular bodies such as the ones found in rat oocytes by Sotelo and Porter (24) and noticed by Palade (11) in a basophil granulocyte of the rat spleen were found in the central core. They are composed of an enveloping membrane inside which a variable number of vesicles of about 400 A in diameter are more or less loosely disposed. In a recent paper Zetterqvist (29) described them in the columnar cells of the mouse jejunum.

Some vitelline bodies proved to have large masses of ill defined outline formed by closely packed vesicles of about 600 A in diameter. It could be determined that these masses correspond to dark patches often seen in the thick sections examined by phase contrast microscopy.

Large numbers of free vesicles can be easily observed in the accompanying pictures of the central core. They are found in the space left free by the other components. Their number seems to be greater at the peripheral region of the central core, near the central layers of endoplasmic reticulum (Figs. 3, 5, and 7).

Developing Vitelline Bodies of Young Oocytes.—Incompletely differentiated vitelline bodies of young oocytes are seen as groups of cytoplasmic organelles, assembled in a disorderly way. The profiles of the endoplasmic reticulum elements appear as single loops or sectors of circles. These are scattered throughout the cytoplasm or as part of the above-mentioned groups of cytoplasmic organelles. The concentric arrangements of lamellae are not yet formed (Fig. 1).

It has been noted that vitelline bodies are made up of mitochondria, Golgi elements, endoplasmic reticulum trabeculae, capsulated bodies, multivesicular bodies, and free small vesicles. In later stages these elements become organized, in such a way, that endoplasmic reticulum, mitochondria, and Golgi elements form the cortex, while the capsulated bodies, multivesicular bodies, and small vesicles form the central core.

One immature vitelline body is shown in Fig. 1; and another, partly developed and showing a few cortical lamellae, is illustrated in Fig. 3.

Comparative View between Oocytes with and without Vitelline Bodies.—In the half-grown oocytes of Thomisidae the endoplasmic reticulum does not seem to be arranged in the same regular manner as described for Lycosidae. The lamellae of the body cortex remain somewhat disordered and in addition free groups of lamellae are to be found throughout the cytoplasm. These are in some cases integrated into bundles of four to ten parallel cisternae, whereas in other cases, the cisternae are concentrically arranged forming bodies of circular or oval outline. The latter resemble the structures described by Rebhun in *Spissula solidissima* (18).

Multivesicular bodies of complicated structure were seen in Sicaridae or in Gonyleptidae oocytes. They are characterized by a variable number of enveloping membranes and high content of small vesicles. In some instances the enveloping membrane is discontinuous and the vesicles then lie free in the vicinity. It may be said that the spider oocytes having no organized vitelline nuclei, show scattered in their cytoplasm all the components (except for the capsulated bodies) of the vitelline nucleus.

Vitellus Formation.—Many of the oocytes examined were found to be in the phase of growth in which yolk makes its appearance. In no case was it observed that structures composing the vitelline body gave way to yolk formation. Thus, it may be stated that vitellus does not originate in morphological relationship with the components of the classically described "vitelline body." It is important to stress the point that the yolk granules may arise in many

sites of the cytoplasm independent of the known cellular structures. They were seen also within the limits of the vitelline body but the real origin of the yolk granules could not be determined.

DISCUSSION

The histochemical tests used here have described the existence of ribonucleic acid in the vitelline body. This had already been demonstrated in the oocytes of *Antedon*, *Pholcus*, and *Tegenaria* (25) and confirmed in the present investigation for Lycosidae oocytes. Palade (10) has correlated cytoplasmic basophilia with small particulates existing free in the cytoplasm or associated with the membranes of the endoplasmic reticulum and previous to this Dalton (3) related the lamellated pattern existing in the body of the chief cells of the stomach and in pancreas exocrine cells, with basophilia. The imperfectness of the methods used in this earlier study obviously prevented detection of the granular component associated with the lamellae. In the light of the findings of these authors and the parallel examination of fresh material, stained thick sections, and electron micrographs one may arrive at the following conclusions relative to the object of this study on spider oocytes: (*a*) the vitelline body cortex is formed mainly by cisternae of the endoplasmic reticulum; (*b*) the basophilia detected in the cortex by histochemical methods is related to the granular components of the endoplasmic reticulum; and (*c*) the endoplasmic reticulum preexists apparently with the same characteristics in the living animal.

Relative to the last point it is important to note that Parat and Jacquiert (12) using polarized light defined the strong birefringence of the body cortex, and in the course of our work it was found that the birefringence sign is negative with respect to the radius. It does not seem probable that the anisotropy of the vitelline body cortex can be due to a phospholipoprotein complex originating from hypertrophic mitochondria, as Parat and Jacquiert have proposed, for the electron micrographs do not show any morphological evidence of such a process. Instead the lamellated pattern of endoplasmic reticulum with the attached granules would account for the optical properties of the vitelline body cortex, although it is not possible to decide from the incomplete analysis carried out whether the birefringence derives from the circumferential arrangement of the membranes (form birefringence) or from the molecular pattern of the constituents of these layers (intrinsic birefringence). The circumferential parallel array of the lamellae and the surrounding media may be interpreted as a "composite body" in accordance with Weiner's theory (26). In this regard it might be mentioned that Sjöstrand (19) has described in exocrine pancreatic cells negative birefringence relative to a direction perpendicular to the cell surface and has related this optical property of pancreatic cells to the submicroscopic membranes found oriented parallel to the cell surface.

Some comment should be made on the often proposed relationship of the vitelline nuclei with yolk formation. The material studied for the present work showed that yolk may develop in cytoplasmic regions not closely related structurally to the vitelline body. The question could perhaps be answered by studying with the electron microscope the other structures claimed by optical researchers as being vitelline bodies but not showing their typical morphology.

The admitted presence by some cytologists of the cell center in the vitelline body brings up the question of the similarity of this structure with the idiosome of male germ cells. The considerable difference between the idiosome and the vitelline body is evident in the multiple character of the components of the vitelline central core as compared with the relatively simple morphology of the idiosomic centrosome, even taking into account the probable existence of diffuse centrosomes (22).

On the other hand, a certain similarity between the two structures exists in the fact that both have a peripheral layer containing mitochondria and Golgi elements. However, the present study shows that the major components of the vitelline body peripheral layer are cisternal elements of the endoplasmic reticulum. The meagre information existing on the subject makes it difficult to decide this point of relationship. Very little can also be said about the nature of the organized components encountered in the vitelline body central core. Their structure must be compared with many others existing in the oocyte cytoplasm of invertebrates and vertebrates. This study should be extended to stages of oocyte development more advanced than the ones reported in the present paper.

It must be recognized that the striking structures found in the central core (geminated masses) look like little cells (parasitic forms) having a thin cytoplasmic layer and a nucleus limited by a double membrane.

Since, however, no Feulgen-positive material exists in the central core (see above under A, Optical Observations) it seems very improbable that the geminated masses represent nuclei.

The fate of the yolk nucleus components during fertilization and the first stages of development is an interesting field to investigate. This involves the study of the whole organization of eggs which means that many collateral problems will arise.

SUMMARY

The structure of the vitelline nuclei of Lycosidae and Thomisidae was described as follows: Vitelline nuclei are constituted of two parts: (*a*) a peripheral layer (vitelline body cortex), and (*b*) a central core. The vitelline body cortex is demonstrated to be formed by many cisternae of the endoplasmic reticulum among which mitochondria and Golgi elements are intermingled. The central core is made up mainly of a special type of body described under the name of "capsulated body." Capsulated bodies comprise a capsular layer,

limited by a membrane, and two central masses called "geminated masses," each one limited by a double membrane. Irregular masses of closely packed vesicles are found in some cases among the capsulated bodies and free vesicles are present in large numbers.

The optical properties of the vitelline body cortex compared with the electron microscope findings lead us to the concept that this layer is a "composite body" according to Weiner's theory.

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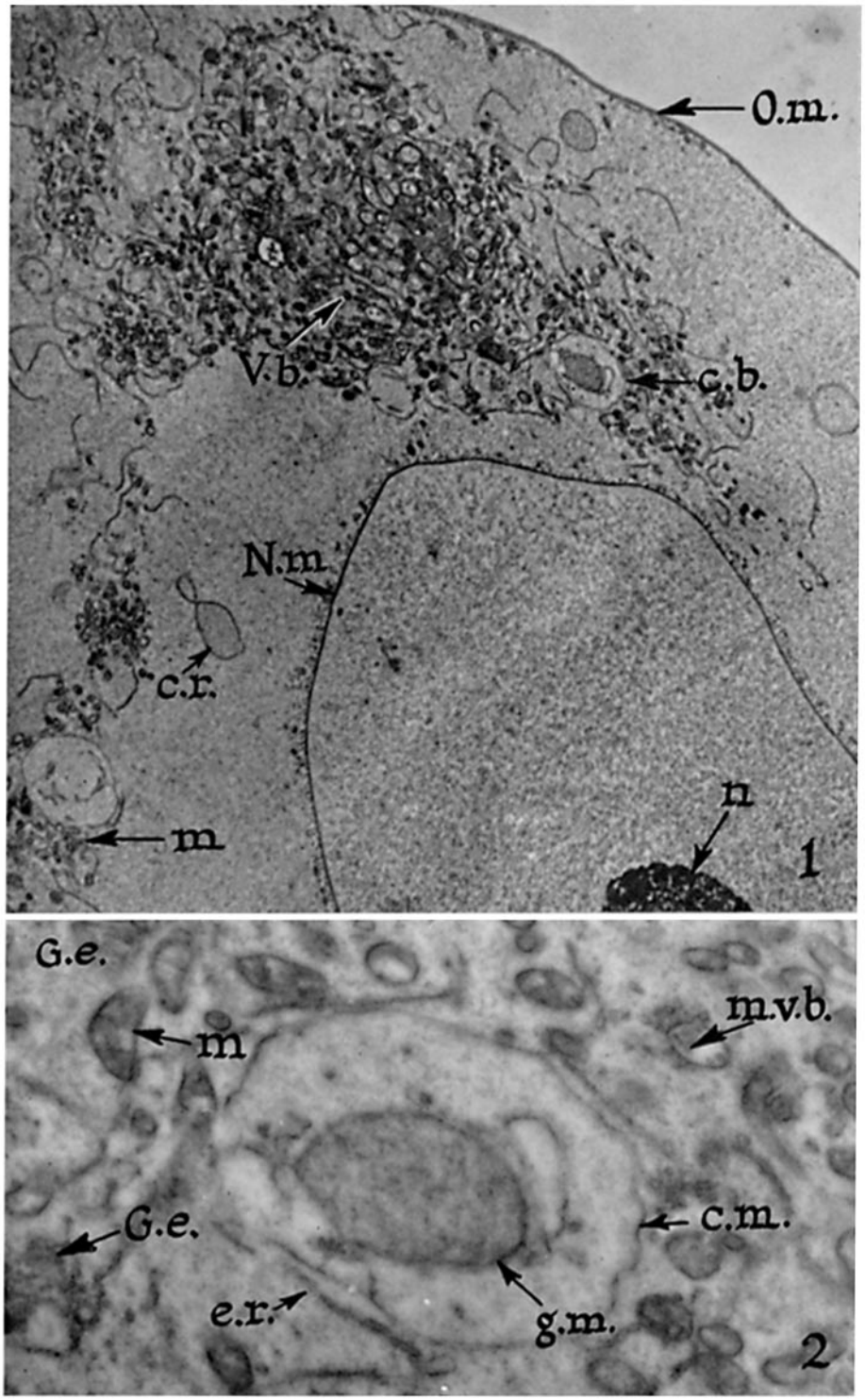
EXPLANATION OF PLATES

c.b., capsular body.
c.m., capsular membrane.
e.r., endoplasmic reticulum.
e.r.s., endoplasmic reticulum septae.
G.e., Golgi elements.
g.m., geminated masses.
i., infoldings of the capsular membrane.
j.d.m., joined double membrane of the geminated masses.
m., mitochondria.
m.v.b., multivesicular body.
n., nucleolus.
N.m., nuclear membrane.
O.m., oocyte membrane.
s.v., small vesicles.
V.b.c., vitelline body cortex.
V.b., vitelline body.
v., vesicles.

PLATE 95

FIG. 1. Low magnification electron micrograph of a young oocyte showing a forming vitelline body. The endoplasmic reticulum is still unorganized in this stage and besides the cisternae seen intermixed with the elements of the vitelline body, there are free cisternae (*c.r.*) scattered in the cytoplasm. Along the external side of the nuclear membrane there is a thin layer of granular material which in the thick sections was observed to stain with pyronine. *Lycosa*. × 4500.

FIG. 2. High magnification electron micrograph of the capsulated body (*c.b.*) shown in the right side of the preceding figure (near the nuclear membrane). The capsular membrane (*c.m.*) limits a wide space of low electron density in which there is a mass of high electron density limited by a double membrane. This mass corresponds to one of the geminated masses which will be shown in the following figures. Mitochondria (*m*) and Golgi elements (*G.e.*) can be seen in this figure. On the right side one multivesicular body (*m.v.b.*) is shown. *Lycosa*. × 23,000.

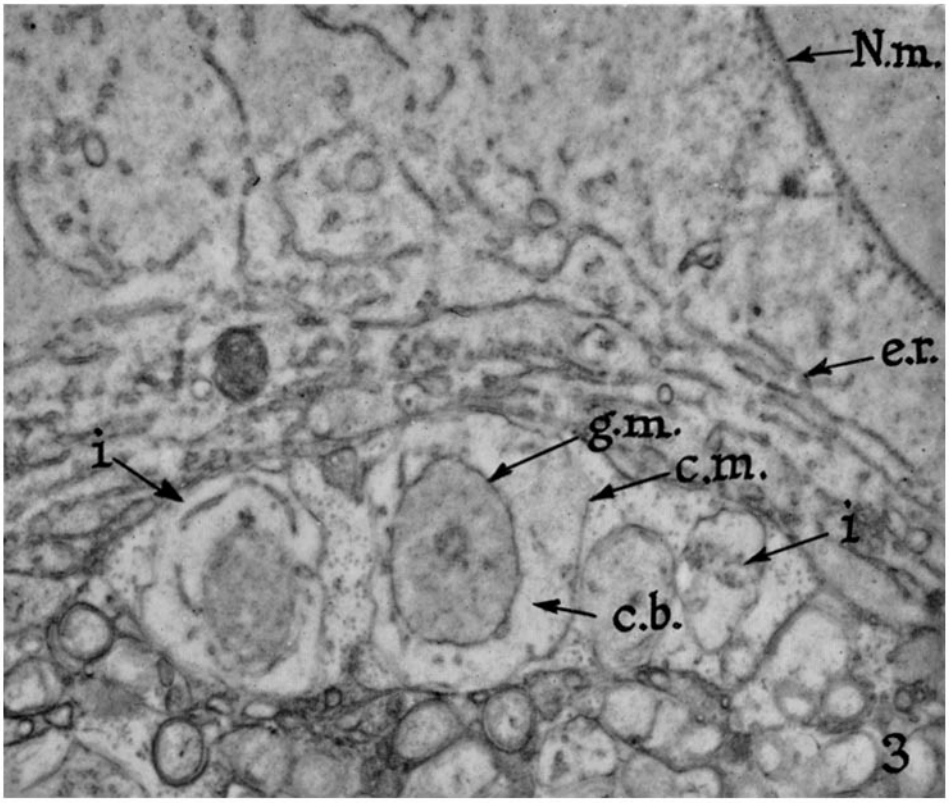


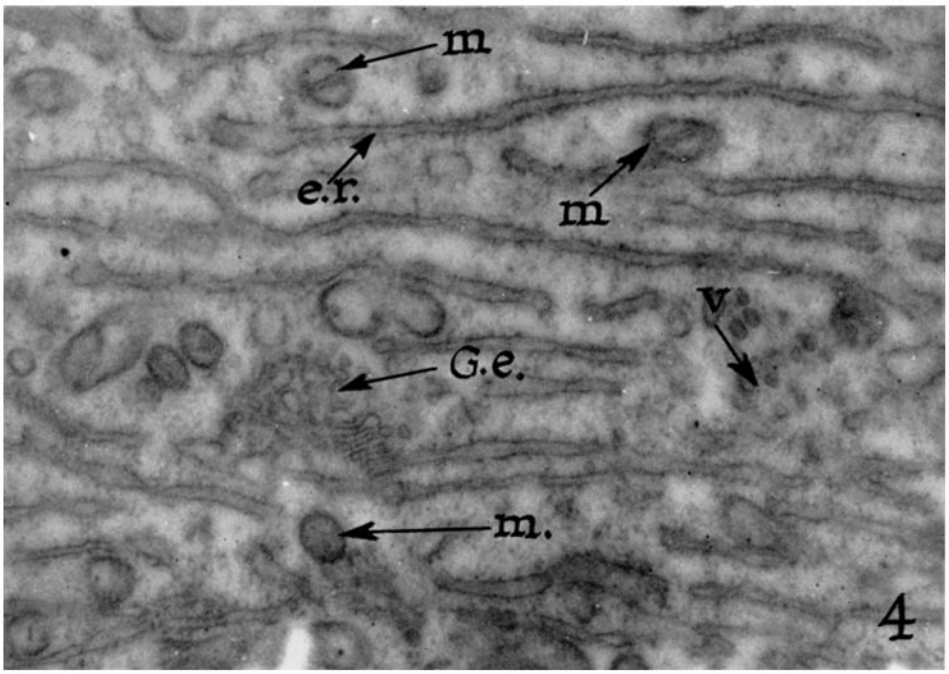
(Sotelo and Trujillo-Cenóz: Vitelline body of spider oocytes)

PLATE 96

FIG. 3. Electron micrograph of a vitelline body corresponding to a more advanced stage than the one shown in the preceding figures. *C.b.* shows a capsulated body with one of its geminated masses inside (*g.m.*). The vitelline body cortex is already organized but has only a few layers of endoplasmic reticulum (*e.r.*). The nuclear membrane (*N.m.*) shows the granules already mentioned in Fig. 1. The infoldings of the capsular membrane (*c.m.*) can be seen in (*i*). *Lycosa.* × 23,000.

FIG. 4. High magnification micrograph taken from the middle region of the cortex of a developed vitelline body. The endoplasmic reticulum cisternae (*e.r.*) are disposed in concentrically arranged lamellae among which some mitochondria (*m*) and Golgi elements (*G.e.*) can be found. Particulates similar to those described by Palade can be seen along the walls of the cisternae. *Lycosa.* × 70,000.

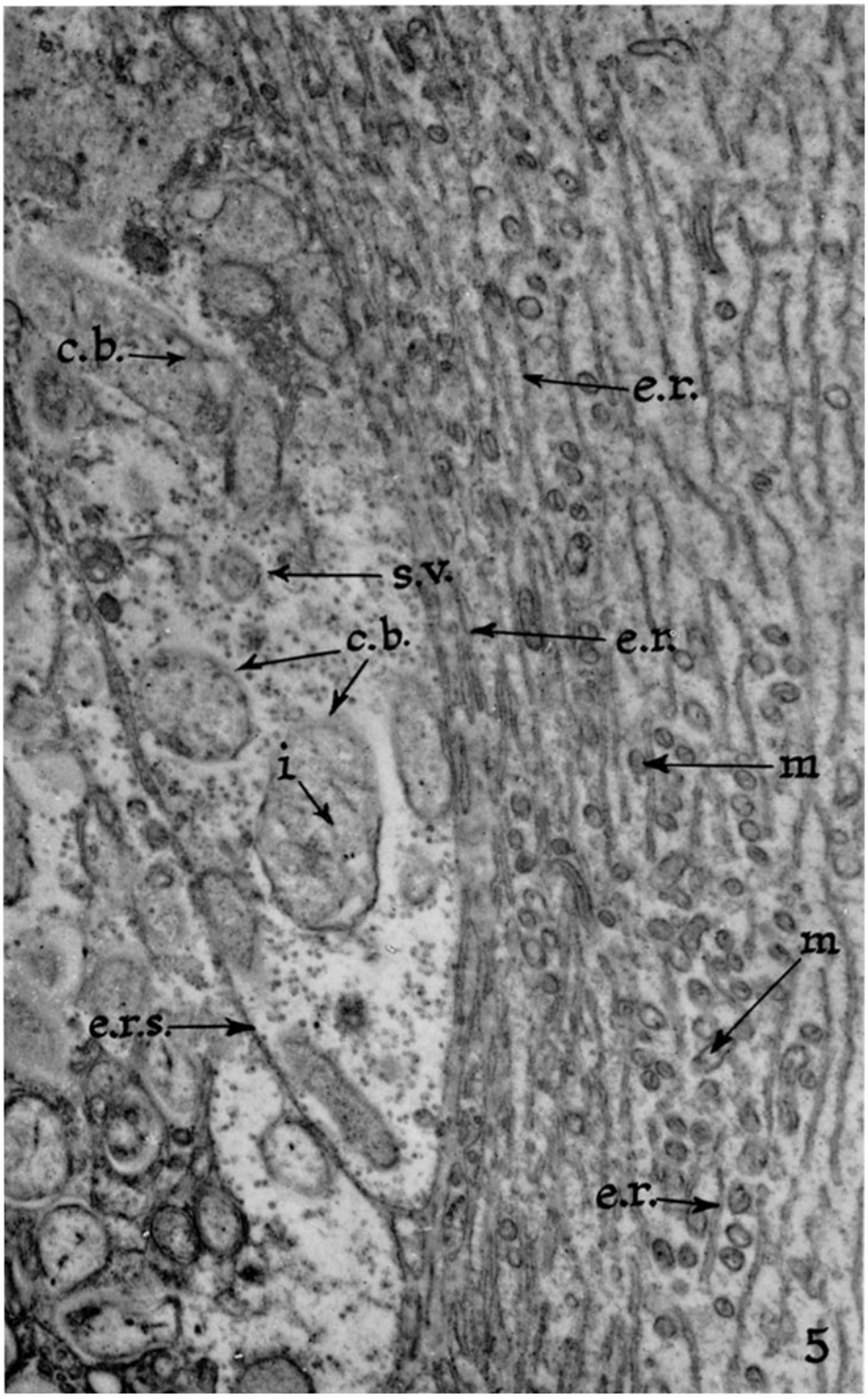




(Sotelo and Trujillo-Cenóz: Vitelline body of spider oocytes)

PLATE 97

FIG. 5. Electron micrograph of a fully developed vitelline body showing nearly all its components. The limit between the cortex and the central core shows one septum coming from a cisterna of the endoplasmic reticulum (*e.r.s.*). The space in between this septum and the cortex is occupied by capsulated bodies (*c.b.*) and large amounts of small vesicles (*s.v.*). The background of the central core seems to be constituted of a semiliquid structureless substance having very low electron density. Granules such as the one observed among the endoplasmic reticulum lamellae cannot be found in this region. (*m*) mitochondria, (*i*) infolding of the capsular membrane of the capsulated bodies. *Lycosa*. × 35,000.

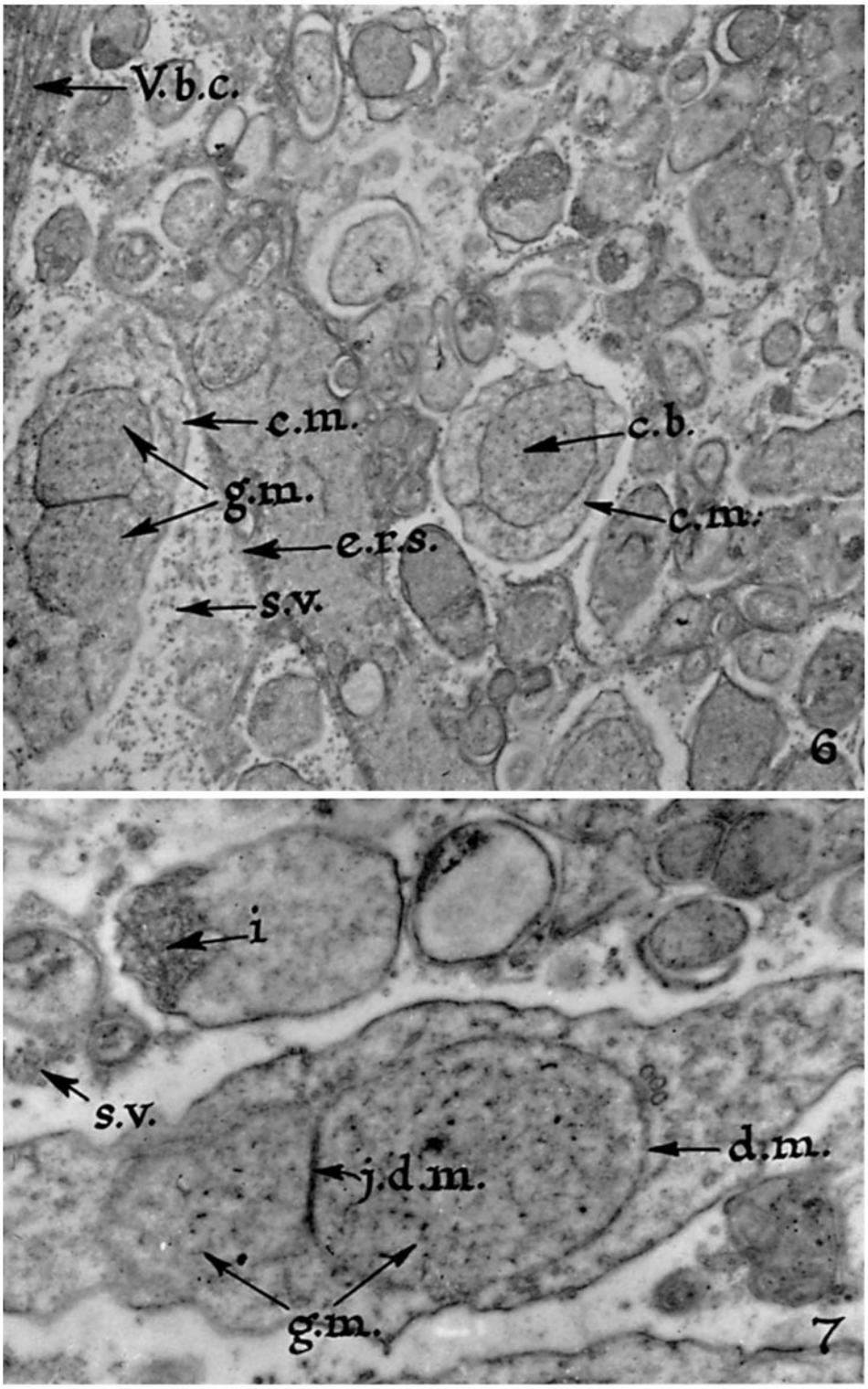


(Sotelo and Trujillo-Cenóz: Vitelline body of spider oocytes)

PLATE 98

FIG. 6. Electron micrograph of the central core of a developed vitelline body. Capsulated bodies cut at different levels can be observed. On the left side there is a typical one with the geminated masses inside. In the upper left corner the vitelline body cortex is shown (*V.b.c.*). Small vesicles (*s.v.*) like the ones described in the preceding picture are seen in all parts of the figure but in larger amounts at the lower left angle. The gray region found at the right of the endoplasmic reticulum septum (*e.r.s.*) can be regarded as derived from an inner prolongation of the cortex. *Lycosa.* × 23,000.

FIG. 7. High magnification electron micrograph of a capsulated body showing its single capsular membrane and the geminated masses (*g.m.*) limited by a double membrane (*d.m.*) joined at (*j.d.m.*). The folded appearance of the capsular membrane is best seen in capsulated bodies tangentially cut (*i*). *Lycosa.* × 33,000.



(Sotelo and Trujillo-Cenóz: Vitelline body of spider oocytes)