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Oogenesis and ovary ultrastructure in *Pseudocellus boneti* (Arachnida: Ricinulei)

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ABSTRACT Contrib. Nat. Hist. 12: 1373–1386.

This study presents first ultrastructural observations on the oogenesis of the poorly known Ricinulei. In *Pseudocellus boneti* (Bolivar y Pieltain, 1941), the oogenesis starts with a previtellogenic stage. The oocytes are located in the epithelium of the tubular ovary. Their ooplasm bears ribosomes and mitochondria which often form groups. The nucleus is located centrally. During the 1st vitellogenic stage the oocytes grow rapidly and migrate into the gap between the epithelium and the surrounding basal lamina of the dorsal portion of the ovary. The basal lamina forms a pouch around the oocyte. Epithelial cells form a broad funicle connecting the oocyte with the ovary tube. Dictyosomes, lipid and protein granules appear in the cytoplasm. The oolemma forms only few small microvilli. Oocytes in the 2nd vitellogenic stage possess elongated mitochondria and numerous dictyosomes. The oocyte's periphery is provided with many microvilli which form clusters. Between these microvilli the oocytes secrete a vitelline membrane. The nucleus contains a large nucleolus. Protein granules, which tend to fuse, and small lipid droplets are uniformly distributed in the cytoplasm. During the 3rd vitellogenic stage the oocytes grow further. The vitelline membrane gets closed. Later an electron dense layer appears between the vitelline membrane and the basal lamina. Dictyosomes form groups. Cisternae of endoplasmic reticulum are widespread in the cytoplasm. Protein yolk granules become larger. Vesicles are formed underneath the oolemma. After the ovulation of the oocytes into the lumen of the ovary the pouches are left in a shrunken shape on the surface of the ovary. They often contain cell residues from degenerated funicle cells.

Introduction

Oogenesis appears as a process of high diversity (Anderson 1974, Adiyodi & Adiyodi 1983). The ultrastructure and modes of oogenesis in Arachnida are

known only for few orders (e.g., Makioka 1987, 1988; Alberti & Nuzzaci 1996; Farley 1999; Felgenhauer 1999; Alberti & Coons 1999; Coons & Alberti 1999; Miyazaki & al. 2001; Soranzo & al. 2002; Morishita & al. 2003). This hinders generalized conclusions in respect of ongoing phylogenetic discussions. Ricinulei are one of the smallest arachnid orders with only 58 extant species belonging to the genera *Ricinoides*, *Cryptocellus* and *Pseudocellus*. Besides the Palpigradi, Ricinulei are the least investigated arachnids with regards to their anatomy and biology.

The mating behaviour of ricinuleids was described by Cooke (1967) and Legg (1977). The external morphology of the female genitalia is species specific (Legg 1977, 1982). The genital opening is located on the second opisthosomal segment. The genital atrium is two-chambered. An anterior atrium opens into a posterior bursa copulatrix. The bursa bears several blind sacs. Their number might be species specific. At least one of them functions as a spermatheca (Brignoli 1973, Legg 1977). The knowledge of the internal morph-ology of the female genital system is based only on light microscopy. Ovaries and their oviducts are described as paired tubes, located in the opisthosoma underneath the digestive system (Millot 1945, 1949b).

This study provides the first ultrastructural observations on the oogenesis of the Mexican species *Pseudocellus boneti* (Bolivar y Pieltain, 1941). Since oogenesis is a continuous process, the description of oocyte development needs to be schematized, to provide comparable data. Some authors have defined developmental stages for arachnid oocytes by evaluating the size of oocytes, the localization of oocytes in the ovarian tube, the status of vitellogenesis (yolk production), the status of vitelline membrane (vitelline envelope) formation and the appearance of cell components, e.g. nucleolus, dictyosomes, mitochondria (e.g., Alberti & Nuzzaci 1996; Miyazaki & al. 2001; Soranzo & al. 2002; Morishita & al. 2003).

Material and Methods

One adult female of *Pseudocellus boneti* was dissected and fixed in ice-cold glutaraldehyde (3.5 %) in Sörensen phosphate buffer (pH 7.4; 0.1 M) overnight. After rinsing in buffer, specimens were postfixed with bufferered OsO_4 (2 %) for 2 hours and rinsed again in buffer. Further processes included dehydration in graded ethanols and propyleneoxide and embedding in araldite. Ultrathin sections (70 nm) were made with a Reichert ultramicrotome. Sections were stained with saturated uranylacetate (5 min) and lead citrate (10 min). Transmission electron microscopy was performed on a Zeiss EM 9 S-2.

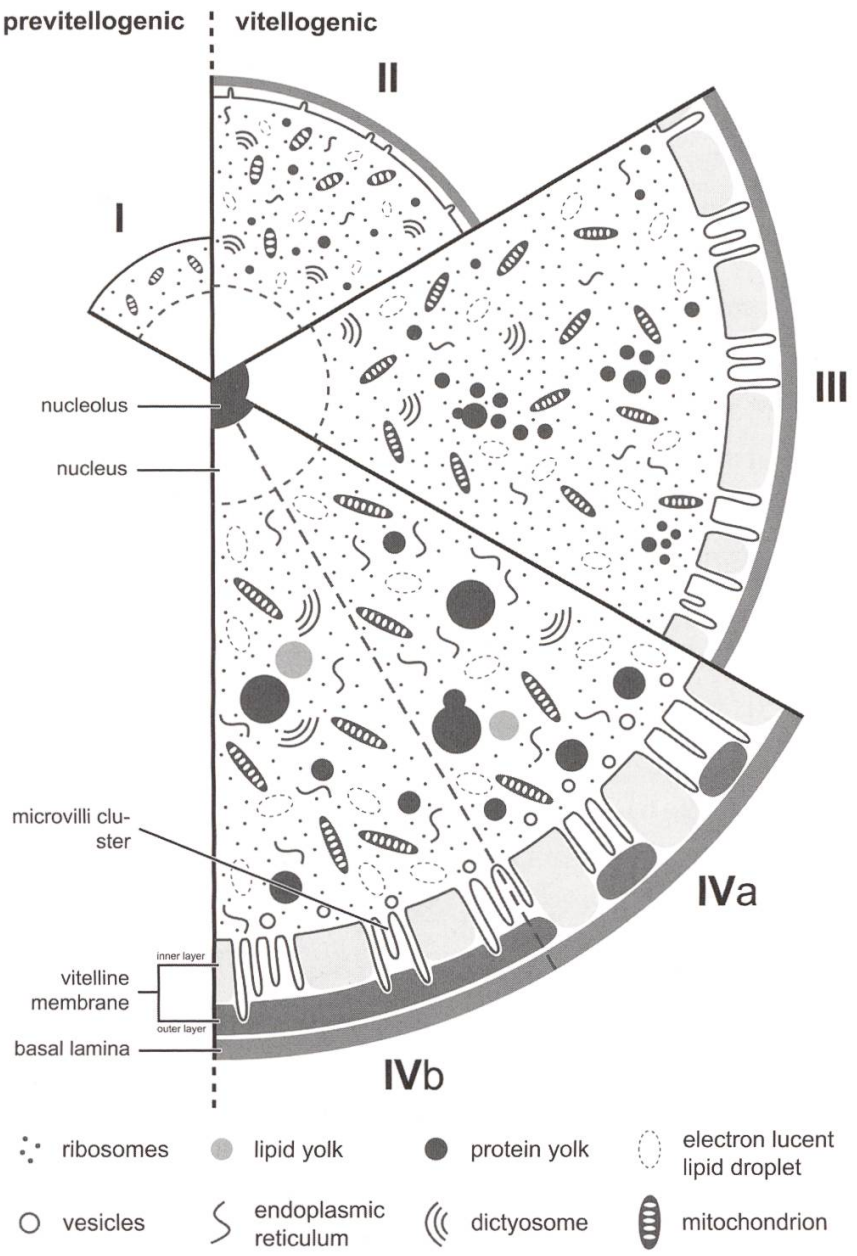


Fig. 1. Synopsis of ultrastructural changes in the oocytes during oogenesis and vitellogenesis in *Pseudocellus boneti*. Though oogenesis is a continuous process, four developmental stages can be distinguished.

Results

Ultrastructure of oocytes

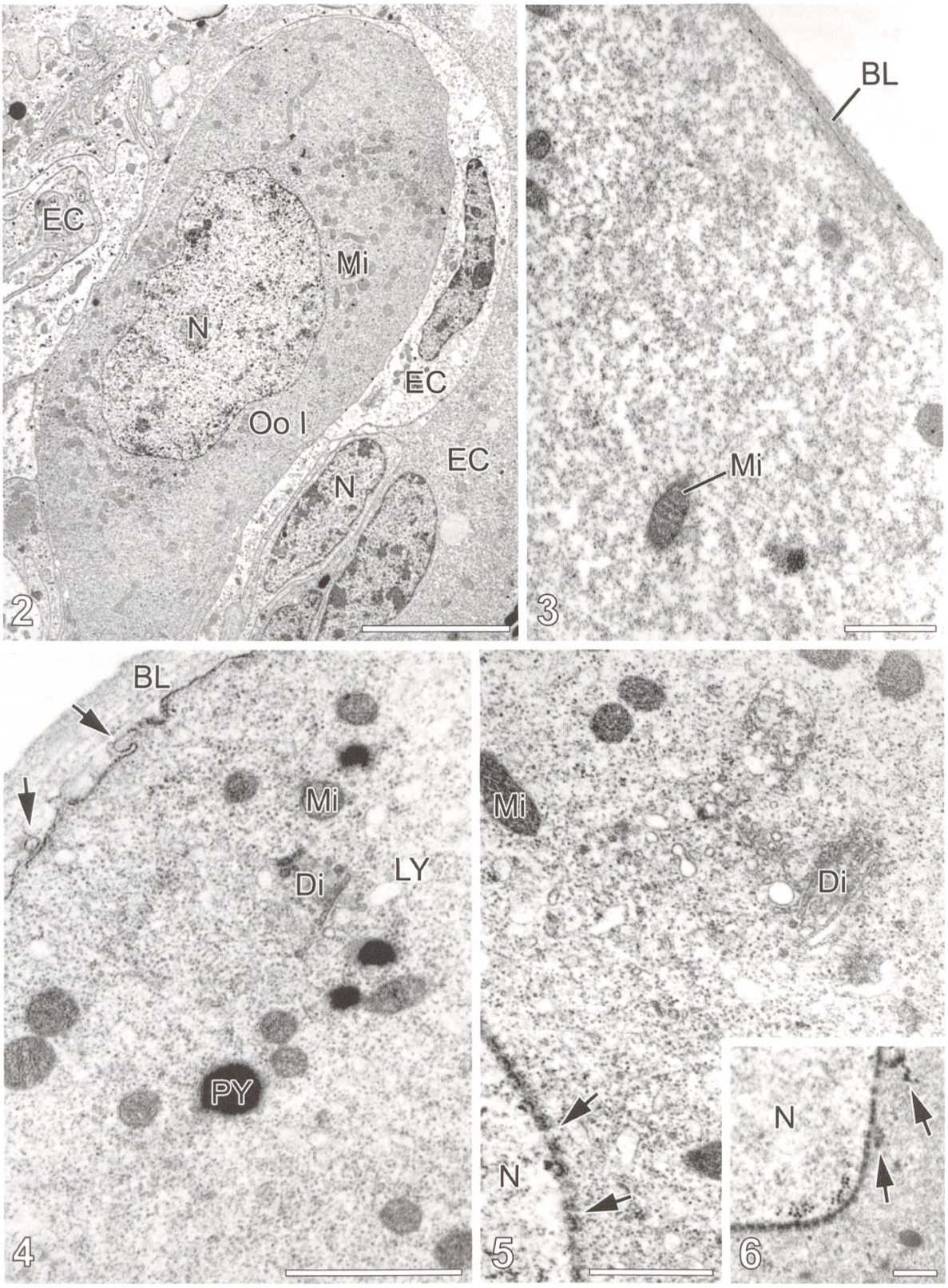
In this study, four distinct stages of oocyte development could be identified in *P. boneti*. However, the oogenesis of this species is a continuous process and does not proceed in successive stages. Hence, oocytes also occur, which are in transition between these four stages, but will not be described here. The present findings are combined in Fig. 1.

Stage I – previtellogenic oocyte: Between the small cubic epithelial cells of the ovary oogonia become spherical and start to grow (Fig. 2). The ooplasm is filled with free ribosomes and numerous mitochondria of the crista-type which often form groups. The large nucleus is located centrally. It bears homogenous chromatin. The oolemma is smooth.

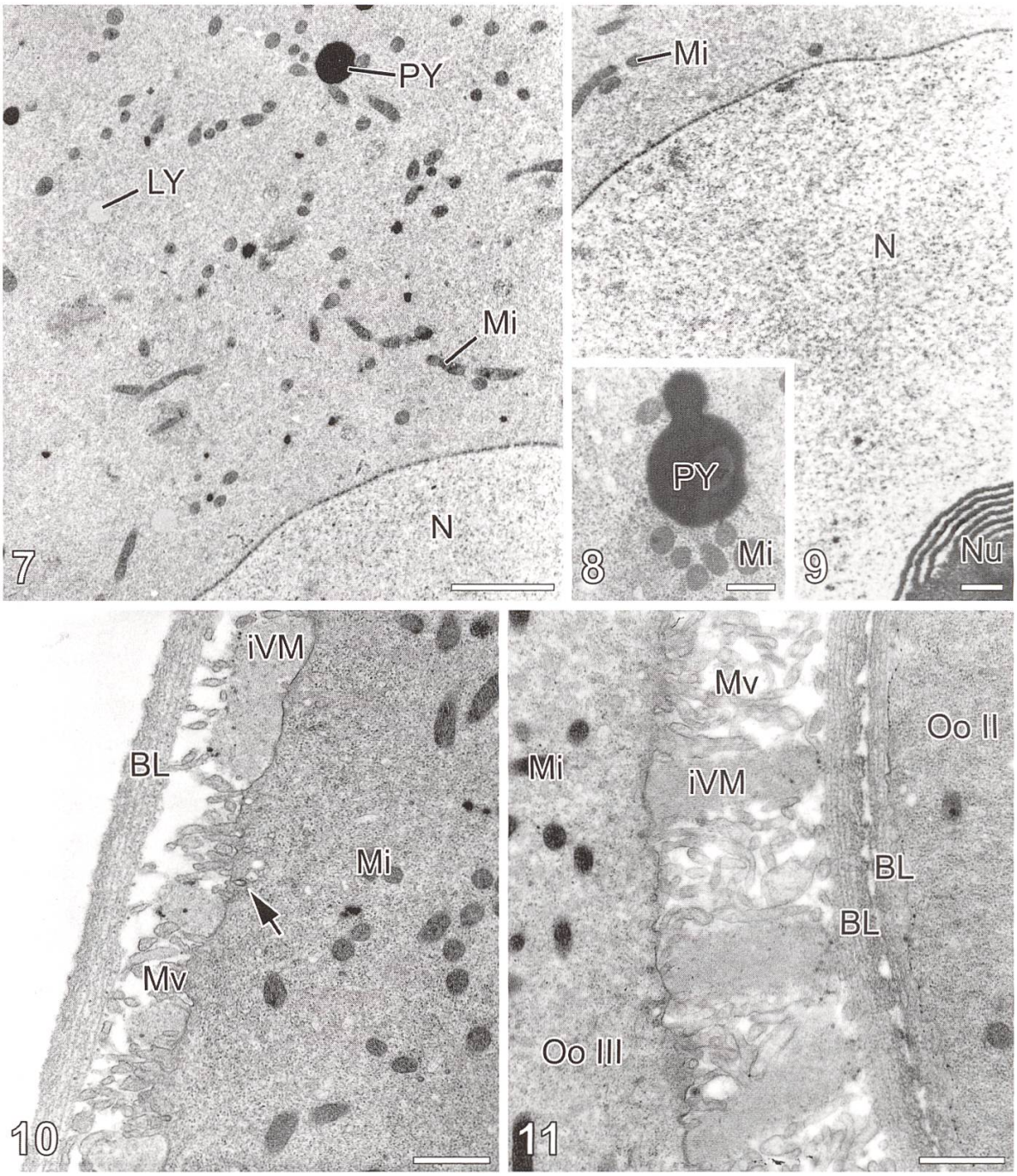
Stage II – primary vitellogenic oocyte: The oocytes increase their size further and migrate to the dorsal periphery of the ovary. Finally the oocytes are situated directly beneath the basal lamina, which surrounds the ovary (Fig. 3). During further development, the basal lamina protrudes pouch-like and is the only separation between oocyte and hemocoel. The ooplasm contains predominantly free ribosomes and mitochondria (Figs. 3, 4), also first dictyosomes with Golgi vesicles (Figs. 4, 5) and small cisternae of endoplasmic reticulum. The nucleus is located centrally. The karyolemma bears many pores (Fig. 5). Near these pores electron dense extrusions project into the ooplasm (Fig. 6). Also small electron dense granules occur near the pores of the karyolemma (Fig. 6). First bright lipid granules and dark protein granules appear (Fig. 4). The oolemma forms few small microvilli (Fig. 4).

Stage III – secondary vitellogenic oocyte: The size of the oocytes has increased again. The ooplasm also contains predominantly free ribosomes and mitochondria. The mitochondria are slightly elongated (Fig. 7). Numerous dictyosomes produce many Golgi vesicles. Numerous cisternae of endoplasmic reticulum can be observed. The production of yolk (vitellum) has started. Small electron dense proteinaceous yolk components are present in the ooplasm (Fig. 7). They tend to fuse to larger particles (Fig. 8). Also bright lipid droplets are present (Fig. 7). The central nucleus bears a large spherical electron dense nucleolus (Fig. 9). The periphery of the nucleolus shows protrusions. Nuclear extrusions are reduced. The oolemma forms clusters of microvilli (Fig. 10). Underneath the microvilli vesicles occur (Fig. 10). Some of these vesicles appear "coated" (Fig. 10). The formation of a vitelline membrane between these microvilli clusters has begun (Figs. 10, 11). The clusters of microvilli penetrate the vitelline membrane (Figs. 10, 11).

Stage IV – tertiary vitellogenic oocyte: The oocytes again become larger. The number of free ribosomes and elongated mitochondria in the ooplasm has increased (Fig. 12). Also dictyosomes, Golgi vesicles and cisternae of endoplasmic reticulum occur in higher densities. The dictyosomes often form groups. The diameter of the nucleus increases. The dark granules near the pores of the karyolemma become scarce. Protein yolk particles become larger



Figs. 2–6. Oocytes of stage I and II of *Pseudocellus boneti*. – 2: Previtellogenic oocyte inside the epithelium of the ovary. Scale bar: 5 µm; – 3: Stage II oocyte which has left the epithelium. Only a thin basal lamina seperates the oocyte from the hemolymph space. Scale bar: 1 µm; – 4: Periphery of a stage II oocyte. The oolemma forms first small microvilli (arrows). Scale bar: 1 µm; – 5: Nuclear periphery of a stage II oocyte. Dictyosomes produce numerous golgi vesicles. Note nuclear pores (arrows). Scale bar: 1 µm; – 6: Nuclear extrusions (arrows) project into the ooplasm. Scale bar: 0.5 µm. BL = basal lamina, Di = dictyosome, EC = epithelial cell, LY = lipid yolk, Mi = mitochondrion, N = nucleus, Oo I = stage I oocyte, PY = protein yolk.



Figs. 7–11. Stage III oocytes of *Pseudocellus boneti*. – 7: Nuclear periphery with elongated mitochondria and yolk components. Scale bar: 2 µm; – 8: Small protein particles fuse to form larger particles. Scale bar: 0.5 µm; –9: The nucleus bears an electron dense nucleolus. Note the conspicuous protrusions of the nucleolus. Scale bar: 1 µm; – 10: The oolemma forms microvilli clusters. Between these clusters the inner layer of a vitelline membrane is formed. Note vesicles (some of them "coated") underneath the microvilli (arrow). Scale bar: 1 µm; – 11: Adjacent oocytes of stage III and II reveal their different peripheral structure. Scale bar: 1 µm. BL = basal lamina, iVM = inner vitelline membrane layer, LY = lipid yolk, Mi = mitochondrion, Mv = microvilli, N = nucleus, Nu = nucleolus, Oo II = stage II oocyte, Oo III = stage III oocyte, PY = protein yolk.

(Fig. 12). Lipid containing yolk particles are formed (Fig. 13). They appear a little brighter than the dark protein yolk. The microvilli of the oolemma become longer. Underneath the base of the microvilli many vesicles occur (Fig. 14). Among them are again "coated vesicles" (Fig. 17). The vitelline membrane

becomes more and more closed and a second, more electron dense layer is formed between the first layer and the surrounding basal lamina (Figs. 14–17).

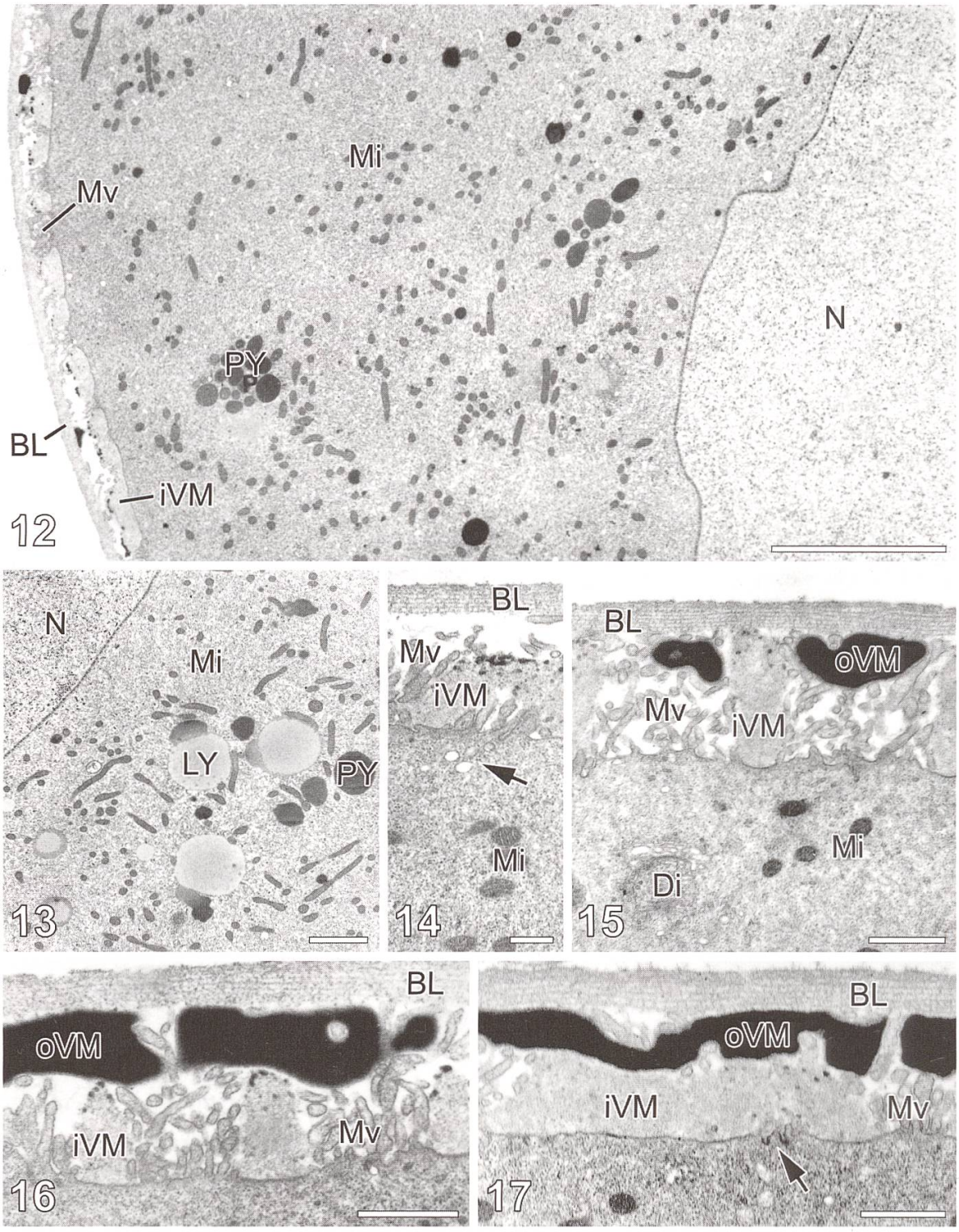
Later stages of oocyte development: The process of ovulation or the presence of mature oocytes inside the lumen of the ovaries or the oviducts could not be observed in this female of *P. boneti*. After ovulation, the pouches of the basal lamina are left in a highly folded shrunken shape on the surface of the ovary (Fig. 18). Cell residues, most likely from degenerated funicle cells, can be observed in the lumen of the basal lamina pouch.

Ovary and oviduct

Two small pearl cord like tubes form the ovaries and their oviducts (Millot 1949b). The mono-layered epithelium consists of cubic cells. A basal lamina separates the epithelium from the hemocoel (Fig. 19). Towards the lumen zonulae adhaerentes and septate junctions connect the epithelial cells (Fig. 20). Many microtubules occur in the cytoplasm (Figs. 19, 20). Often the direction of the microtubules differs in adjacent cells (Fig. 20). Dictyosomes, mitochondria and electron dense granules are present (Fig. 19). The epithelial cells of the oviduct are slightly larger, but do not differ morphologically from those of the ovary. The ovary is not surrounded by muscles. Near the ovary some muscle cells surround the oviduct (Fig. 21).

The funicle

The funicle is formed by cells of the ovarian epithelium. It connects oocytes of the vitellogenic stages (II–IV) with the ovarian tube (Fig. 22). The oolemma, or the vitelline membrane, is in close contact with the funicle cells. Protrusions of funicle cells even penetrate the vitelline membrane and come into direct contact with the oolemma (Fig. 23). Small mitochondria and numerous dictyosomes are present in the cytoplasm (Fig. 24). The nucleus of funicle cells is large (Fig. 22). The dark heterochromatin is located in its periphery. Nucleoli are present. The basal lamina surrounds the oocytes continuously, the funicle cells and the ovary epithelium. After ovulation the funicle cells most likely degenerate.

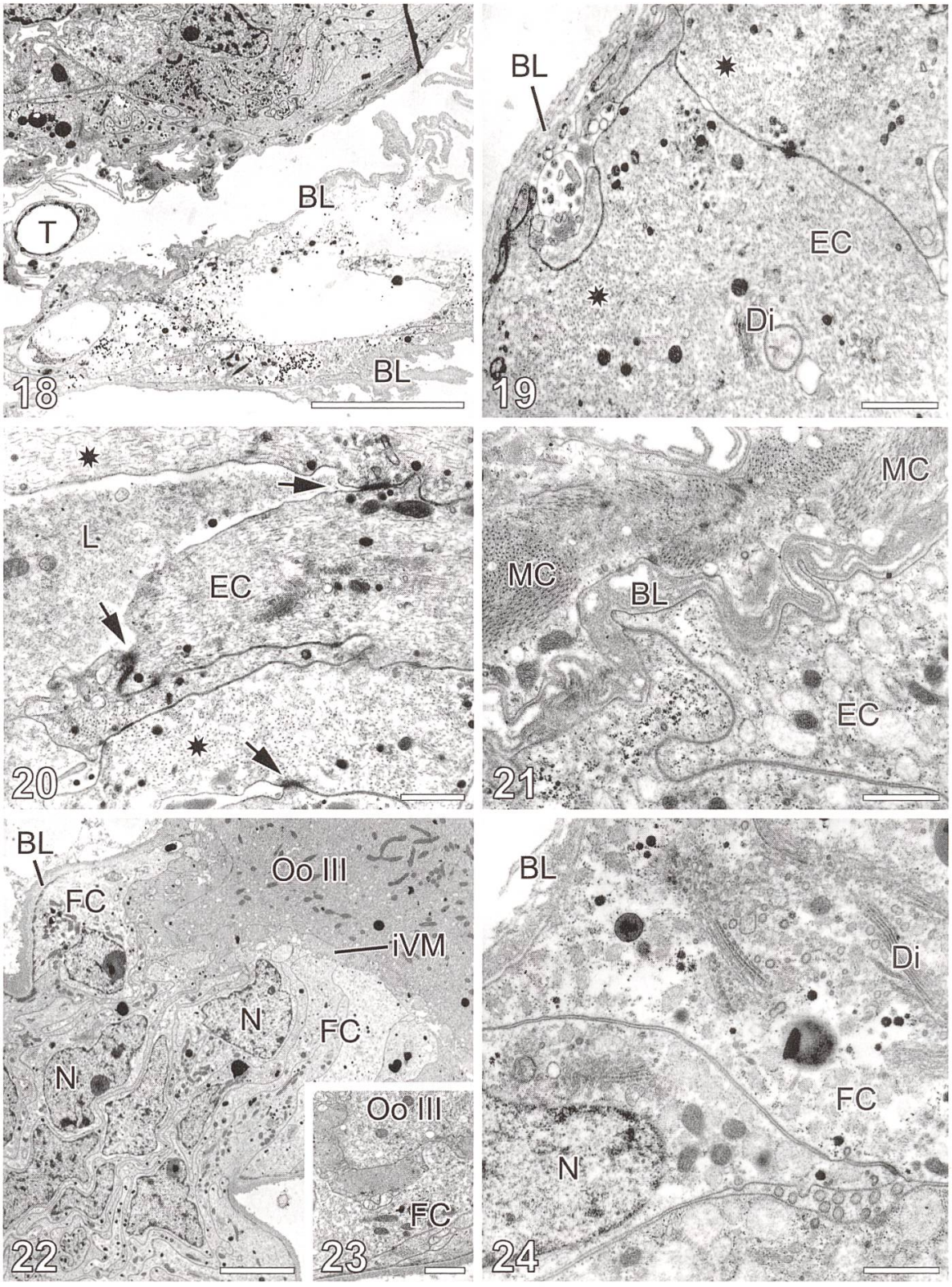


Figs. 12–17. Stage IV oocytes of *Pseudocellus boneti*. – 12: Early stage IV oocyte with numerous elongated mitochondria and protein particles forming groups. Scale bar: 5 µm. – 13: Nuclear periphery with large lipid particles. Scale bar: 2 µm. – 14–17: Successive formation of an electron dense outer vitelline membrane layer. – 14: First electron dense particles appear. Note vesicles underneath the microvilli (arrow). Scale bar: 0.5 µm. – 15: Above the microvilli clusters large electron dense plaques are formed. Scale bar: 1 µm. – 16: These plaques grow and start to fuse. Scale bar: 1 µm. – 17: The outer layer gets more and more closed. Only few microvilli penetrate the outer layer. Note "coated vesicles" (arrow). Scale bar: 1 µm. BL = basal lamina, Di = dictyosome, iVM = inner vitelline membrane layer, LY = lipid yolk, Mi = mitochondrion, Mv = microvilli, N = nucleus, oVM = outer vitelline membrane layer, PY = protein yolk.

Discussion

Oogenesis represents the precondition of any embryonal development. During vitellogenesis, energy ressources are supplied for the future embryo by the production of yolk (Anderson 1978, Palanichamy & Pandian 1983). In *P. boneti* endogenous production of yolk components could be observed in oocytes of stage II–IV. High densities of dictyosomes, mitochondria and endoplasmic reticulum point to a high metabolic activity (Figs. 4,5,15). A special function of mitochondria in protein biosynthesis is known for Araneae, Opiliones and Pseudoscorpiones (e.g., Sareen 1961, 1962, 1963, 1964, 1965; Nath 1968). A high rate of protein synthesis often is combined with an elongation of the mitochondria (Krause 1981). This is very obvious in stage IV oocytes of *P. boneti* (Figs. 7, 12, 13). In Scorpiones, Opiliones and Araneae mitochondria are also involved in the production of lipid yolk components (e.g., Nath 1925; Nath & al. 1959; Reger 1970; Seitz 1971). In these cases mitochondria show bright lipid inclusions. Such inclusions do not occur in *P. boneti*. Therefore, mitochondrial production of lipid yolk components is unlikely. Nuclear extrusions (Fig. 6), which occur in stage II oocytes of *P. boneti* are known also for Araneae (Ōsaki 1972). They are composed of RNA, DNA and lipids and are thought to initiate the endogenous yolk production (Nath 1968). Additional pinocytotic uptake of exogenous yolk components is indicated in *P. boneti* by the presences of numerous vesicles and especially "coated vesicles" underneath the oolemma of stage III and stage IV oocytes. According to Roth & al. (1976) "coated vesicles" indicate selective transport of protein yolk components. The findings for *P. boneti* widely resemble the bimodal vitellogenesis, with endogenous (in early oocytes) and additional exogenous (in late oocytes) production of yolk components, which is known for Arachnida (e.g., Aeschlimann & Hecker 1969; Weygoldt & al. 1972; Alberti & Coons 1999; Soranzo & al. 2002, Mauss-Erdmann 2004). Furthermore, this kind of vitellogenesis is very common in all animal groups (Roth & al. 1976).

Stage IV oocytes of *P. boneti* possess a double-layered vitelline membrane (Figs. 15–17). Vitelline membranes with at least two layers of different electron densities are described for actinotrichid and anactinotrichid Acari (see Alberti & Coons 1999). Also in spiders the occurrence of layered vitelline membranes is known for *Cupiennius salei* (Seitz 1971) and pictured (but not described) for the mygalomorph spider *Antrodiaetus unicolor* (Michalik & al. 2005). Thus, it seems likely that a multi-layered vitelline membrane also occurs in further arachnid groups (general feature?). Fahrenbach (1999) showed for xiphosuran oocytes the existence of two "chorion strata", but pointed out that only the electron-opaque outer layer is identical to the vitelline membrane.



The clustered microvilli of the oolemma which appear in *P. boneti* in oocytes of stage III and IV are a new feature (Figs. 10–12, 14–16). In other arachnids the microvilli of oocytes are homogenously distributed (e.g. Alberti & Nuzzaci 1996; Alberti & Coons 1999; Coons & Alberti 1999; Soranzo & al. 2002; Michalik & al. 2005).

Figs. 18–24. Ultrastructure of the ovary, the oviduct and the funicle of *Pseudocellus boneti*. – 18: After ovulation of an oocyte into the lumen of the ovary, the empty basal lamina pouch remains in a shrunken shape on the outside of the ovary. Scale bar: 10 µm; – 19: Periphery of the ovarian epithelium. The ovary is surrounded by a thin basal lamina. Note the numerous microtubules (asterisks). Scale bar: 1 µm; – 20: Zonulae adhaerentes (arrows) connect the epithelial cells of the ovary towards the lumen. Note the different direction of microtubules (asterisks) in adjacent cells. Scale bar: 1 µm; – 21: Periphery of the oviduct epithelium. Muscle cells surround the oviduct. Note the basal lamina which separates the muscle cells from the oviduct cells. Scale bar: 1 µm; – 22: Funicle cells connecting a stage III oocyte with the ovary. Scale bar: 4 µm; – 23: Protrusions of funicle cells penetrate the vitelline membrane to get in contact with the oollemma. Scale bar: 1 µm; – 24: Numerous dictyosomes are present in funicle cells. Scale bar: 1 µm. BL = basal lamina, Di = dictyosome, EC = epithelial cell, FC = funicle cell, iVM = inner vitelline membrane layer, L = ovary lumen, MC = muscle cell, N = nucleus, Oo III = stage III oocyte, T = tracheae.

The process of further oocyte-maturation in *P. boneti* remains unsolved. The investigated female most likely was fixed shortly after oviposition which may explain the lack of mature oocytes inside the genital system.

The morphology of arachnid ovaries and oviducts is diverse. Paired ovaries and oviducts, as in *P. boneti*, also occur in Solifugae (Kästner 1933; Roewer 1934; Millot & Vachon 1949), Araneae (e.g., Millot 1949a; Soranzo & al. 2002; Michalik & al. 2005) and some anactinotrichid and actinotrichid mites (e.g., Alberti 1974; Alberti & Coons 1999; Coons & Alberti 1999). With the exception of scorpions and a number of mites, the oocytes of arachnids develop solitarily, without adjacent nursing or nutritional cells, on the outside of the ovarian epithelium, surrounded only by a basal lamina pouch and connected to the ovary by an epithelial funicle (peduncle, stalk) (e.g., Makioka 1987; Alberti & Coons 1999; Coons & Alberti 1999; Miyazaki & al. 2001; Morishita & al. 2003; Michalik & al. 2005). The same situation occurs in *P. boneti*. Since muscles do not surround the ovaries (Fig. 19), ovulation, the migration of mature oocytes into the ovarian lumen, is probably induced by abdominal movements and the elasticity of the basal lamina (see Mathur & Le Roux 1970).

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