Fine Structure of Female and Male Internal Reproductive Organs in a Spider Mite *Tetranychina harti* (EWING) (Acari: Tetranychidae)

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The structure of the adult female and male internal reproductive organs of *Tetranychina harti* (EWING) was investigated mainly through electron microscopy. Some oogonia have electron-dense, slender mitochondria, while other oogonia bear electron-sparse, larger mitochondria. The supporting cells surrounding the oocytes include electron-dense mitochondria whilst the oocytes have electron-sparse mitochondria. The spermatozoal nucleus is situated in the central part of the cell within the testis, but in the vas deferens it is located near the periphery. However, in the seminal vesicle, it is in contact with the cell membrane in the posterior. The central electron-sparse part of the spermatozoal nucleus becomes as electron-dense as the other nuclear part before leaving the seminal vesicle. The plasmalemmal tubular structures radially arranged in the testicular spermatozoa become irregularly set in the vas deferens to be divided into shorter structures in the posterior part of the seminal vesicle. Finally, the spermatozoa become almost deficient in cytoplasm proper. The seminal vesicle carries two types of superficial epithelial cells (gate cells) which are located near the exit into the ejaculatory duct and provided with processes. These cellular processes possibly play an important role in the control of discharging the spermatozoa into the ejaculatory duct.

Key words: oogenesis, reproductive organs, spermatogenesis, spider mite, ultrastructure

INTRODUCTION

Up to the present, a vast number of contributions to tetranychid taxonomy, biology, ecology and control have been published in the world. However, there are only a small number of papers about the internal morphology of spider mites. With respect to the reproductive organs of spider mites, the two-spotted spider mite, *Tetranychus urticae* KOCH [= *T. telarius* (LINNAEUS)] has almost exclusively been investigated (BLAUVELT, 1945; PIJNACKER and DRENT-H-DIEPHUIS, 1973; ALBERTI and STORCH, 1976; MOTHES and SEITZ, 1981a, 1981b; MOTHES-WAGNER and SEITZ, 1984; FEIERTAG-KOPPEN and PIJNACKER, 1982; MOTHES-WAGNER, 1984, etc.). By contrast, the reproductive organs of such other spider mite species as *Panonychus ulmi* (KOCH), *Bryobia eharai* PRITCHARD and KEIFER, and *Porcupinychus abutilioni* ANWARULLAH were not duly studied (SNIEDER-

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BERKENBOSCH, 1955; EHARA, 1960; ANWARULLAH, 1963; ANWARULLAH and QUREISH, 1967). In the present paper, the fine structure of the adult female and male reproductive organs is reported of a common spider mite, *Tetranychina harti* (EWING), which belongs to the subfamily Bryobiinae.

MATERIALS AND METHODS

Adult female and male *Tetranychina harti* (EWING) were collected from *Oxalis* on the campus of Tottori University, Koyama, Tottori. In preparation for light microscopy, the specimens were fixed in BOUIN's solution, and sectioned at 6–8 μm . The sections were stained with DELAFIELD's hematoxylin and eosin. The preparations were used mainly for the reconstruction of organs.

For electron microscopy, the mites were fixed for 3 h in 2.5% glutaraldehyde–2% paraformaldehyde that had been adjusted to pH 7.4 with 0.1 M cacodylate. Next, they were postfixed in a 1% OsO_4 solution containing 0.1 M cacodylate buffer (pH 7.4) for 1 h. The fixation procedures were performed at 4°C, with the exception of the initial 30 min of the first fixation at room temperature. The specimens were dehydrated in a series of ethanols, passed through propylene oxide, and embedded in Epon–Araldite resin. Sections were stained with uranyl acetate and lead citrate, and examined with a JEM-100 CXII electron microscope.

RESULTS

Female organs

The female reproductive system of *Tetranychina harti* accords with the general plan of that of the Tetranychidae. Namely, there are an unpaired ovary, an oviduct consisting of an anterior and posterior part, a vagina and a spermatheca (=seminal receptacle) (Fig. 1). The female reproductive organs often occupy the ventral half of the body cavity.

Ovary

The ovary is a large sack-like organ immediately posterior to the central nervous mass. The lateral parts of the ovary are surrounded by the midgut, and the dorsal parts adjoin the hindgut. The ovary is also adjacent to the body wall ventrally.

The ovarian wall is a one-layered epithelium which encloses the posterior part of the ovary (Fig. 4). The wall is composed of slightly flattened cells that are 4 μm tall. Immediately outside the ovary there is a membranous connective tissue including thin starlike cells that are sparsely situated and in contact with the exterior basement membrane (Fig. 3).

In the anteriormost portion of the ovary, many oogonial cells are closely packed (Fig. 3); each of them is 7 μm in diameter, and has a nucleus the size of 4 μm . The mitochondria of the oogonia are ellipsoidal or rodlike; many of them occur in the periphery of the nucleus. Numerous ribosomes were found to occur in the oogonia. Some oogonia include electron-dense, slender mitochondria, while in the other oogonia electron-sparse, larger mitochondria are present. In addition, the plasmalemmal connections between the oogonia were observed sporadically.

In the middle and posterior part of the ovary, the oocytes ranging from 20 to 50 μm

Fig. 1. Schematic figure of the female reproductive organs in *Tetranychina harti* (lateral view). ODI: anterior oviduct, ODII: posterior oviduct, OV: ovary, SP: spermatheca, V: vagina.

Fig. 2. Schematic figure of the male reproductive organs in *T. harti* (dorsal view). AD: aedeagus, ED: ejaculatory duct, VD: vas deferens, SV: seminal vesicle, T: testis.

in size, are arranged. The oocytes have one or three rounded nuclei; each nucleus includes a well developed nucleolus. The three-nucleate cells are so-called nurse cells (Fig. 6). Among the oocytes, the supporting cells are intercalated and encircle the oocytes themselves.

The mitochondria of the oocytes and nurse cells are electron-sparse, and densely aggregated around the nuclei. Numerous ribosomes are present, while the rough endoplasmic reticulum (ER) are poorly developed and flattened. On the oocytes, the synaptonemal complexes were often clearly observed (Fig. 5).

The supporting cells surrounding the oocytes are irregular in shape, often flattened, and one-nucleate (Fig. 7). In the supporting cells the nucleolus is poorly developed, and a good deal of heterochromatin is present within the nucleus. The cytoplasm of these cells is provided with electron-dense mitochondria. In the cytoplasm, Golgi fields and ribosomes are present, and several masses of reticular inclusions are also located. Further, the cytoplasm of the supporting cells was recognized to be electron-sparse, compared with that of the oocytes. In addition, there are tight junctions between the supporting cells and between the cells and oocytes (Fig. 6).

Each adult female usually harbors two or three mature ova simultaneously. The mature ova are not present in the ovary but in the body cavity, keeping close to the ovary and midgut. These ova, ranging mostly 70 to 100 μm in diameter, include a number of yolk spheres of various sizes. The maturing ova were found to be in contact with the midgut by minute bridges of microvilli (Fig. 8).

Oviduct

The oviduct is a large, fleshy organ leading the ovarian wall into the vagina, and is encircled by the hindgut, midgut and body wall. The oviduct consists of an anterior part and a much smaller posterior part. The ovarian wall connects with the anterior part of the oviduct.

The anterior oviduct is a convoluted tube composed of one-layered, columnar epithelial cells. In these cells, there are large ellipsoidal mitochondria. The distal portions of the cells are filled with mucous secretions (Fig. 9).

The posterior oviduct, surrounded by the midgut and body wall, is formed of a single layer of slender ellipsoidal epithelial cells enclosing the lumen. The vagina and spermatheca were not studied here.

Male organs

The male reproductive system comprises a pair of testes, a pair of vasa deferentia, a seminal vesicle and an ejaculatory duct entering the aedeagus (Fig. 2). These organs are located in the posterior ventral part of the body cavity, and are adjacent to the hindgut dorsally, and to the body wall and midgut laterally and ventrally.

Testes

In each side of the caudal ventral portion of the body, there is a slender sack-like testis. The testis is sparsely surrounded by starlike cells directly. No wall cells, as seen around the posterior part of the ovary, were found. Each testis is packed with a large number of germ cells at various stages of spermatogenesis, and their supporting cells (Fig. 10).

The spermatogonia, irregular in shape, occupy the posteriormost portion of the testis (Fig. 10). These cells are 4 μm in size, with a nucleus measuring 2 μm in diameter. In each of the cells there are a well developed nucleolus, many ribosomes, and electron-dense mitochondria.

The supporting cells surrounding the spermatogonia are distinctive in being multinucleate, and in having irregularly shaped nuclei and electron-sparse cytoplasm (Fig. 10). Among the supporting cells there are some globular cells of 4.5 μm diameter. These cells can be classified as spermatocytes. The cytoplasm bears two kinds of inclusions, reticular and corpuscular.

The spermatocytes develop into rounded spermatids that are 2.5 μm in size, having nuclei the size of 1.5 μm (Fig. 14). The spermatids are provided with many peripheral plasmalemmal invaginations with a length of 0.1 μm (Fig. 15). In the spermatids, the nucleus includes a good deal of heterochromatin, and the cytoplasm has rough ER, ribosomes and mitochondria that decrease in number later (Fig. 15). Sometimes, the intercellular plasmic bridge between two spermatids was observed.

The spermatozoa are located in the anteriormost portion of each testis. They are nearly spherical, measuring 2 μm in diameter. Their peripheral plasmalemmal invaginations are 0.4 μm long and 0.03 μm wide, and form an approximate radial pattern (Fig. 16). Further, the invaginations gradually detach from the cell membrane proper, to form radial tubular structures which include amorphous substance of medium electron density (Fig. 16). The spermatozoal nucleus measures 1 μm in diameter, having an electron-sparse central part (Fig. 16).

In almost mature spermatozoa, the tubular structures are considerably irregular

in arrangement (Fig. 17). The cisterna of the nuclear envelope gradually expands to attain a width of $0.2\ \mu\text{m}$. Some nuclear pores connect the nucleus and cytoplasm (Fig. 16). The mitochondria and other organelles are absent in the cytoplasm. No flagella, cilia or acrosomes were found.

Vasa deferentia

The vasa deferentia are wide, tubular organs, located anterior to the testes that are narrower. Each vas deferens leads from the anterior region of the testis on the same side to a short, narrow duct, the entrance to the seminal vesicle.

The wall of the vas deferens is composed of a single layer of ellipsoidal epithelial cells (Fig. 11). The epithelial cells near the testis are lower than those near the seminal vesicle. The nucleus is very variable in shape, with the nucleolus well developed. The rough ER occupy the greater part of the cytoplasm, and Golgi fields and mitochondria were also found.

The lumen of the vas deferens is filled with secretory material from the epithelial cells. There occur a few spermatozoa embedded in the secretion. The tubular structures of the spermatozoa present in the vas deferens are more irregularly arranged than those in the testis. The nucleus of the spermatozoa in the vas deferens is located near the periphery. In several males, the lumen of the vas deferens harbors a number of bacteria of $0.2\ \mu\text{m}$ width.

Seminal vesicle

The seminal vesicle is a single, median, large spherical organ lying slightly caudal to the center of the body. The periphery of this vesicle is covered by a thick, non-cellular membranous structure. The wall of the vesicle comprises flattened epithelial cells. Most of these cells are arranged in a single layer and have hardly any microvilli on the free surface.

However, in the posteriormost part of the vesicle, the epithelial cells are multi-layered, and some superficial epithelial cells which are set near the vesicular exit, are furnished with a number of processes (Fig. 12). Two types of process-bearing cells (gate cells) were discerned: Cells of one type have long processes (length $12\ \mu\text{m}$, width $0.3\ \mu\text{m}$), and those of the other type bear short processes (length $5\ \mu\text{m}$, width $0.1\ \mu\text{m}$) (Fig. 13), while the former cells are situated anterior to the latter. Inside the cellular processes, there are microfilaments along the longitudinal axis.

The lumen of the seminal vesicle is filled with spermatozoa and a secretion similar to that in the vasa deferentia. The spermatozoa present in the central part of the lumen are provided with irregularly arranged, distinct tubular structures (Fig. 18). The spermatozoal nucleus continues to have the electron-sparse central region. All over the periphery of the plasmalemma, theca-like structures were recognizable. Incidentally, in the vesicular lumen, there occur some bacteria which are possibly the same as those seen in the vasa deferentia.

There are numerous spermatozoa in the posterior part of the vesicular lumen (Fig. 12). The spermatozoal nucleus, which is homogeneously electron-dense, is located in contact with the cell membrane (Fig. 19). The tubular structures in the cytoplasm are divided into shorter ones of various thicknesses. The cytoplasm proper becomes scarcely present. In the caudally situated spermatozoa, the outer theca-like structures, attaining to a thickness of $40\ \text{nm}$, are more clearly discerned than those of the sper-

matheca in the central region of the lumen.

Ejaculatory duct

The very narrow ejaculatory duct (diameter of lumen $0.7\ \mu\text{m}$) issuing from the posterior end of the seminal vesicle runs caudally to pass through the aedeagus. The wall of the ejaculatory duct is non-cellular and firmly membranous. The exterior of the wall is connected with the plasmalemmas of the outer cells; the plasmalemmas are complicatedly invaginated. The lumen of the ejaculatory duct was observed to contain a great deal of secretion.

DISCUSSION¹

As described above, the gross anatomy of female and male reproductive organs of *Tetranychina harti* is in accordance with that of *Tetranychus urticae*, *Bryobia eharai*, etc.

In the present study, the ovary was observed to be covered externally by a membranous connective tissue consisting of sparsely arranged, flat starlike cells. This tissue

¹ The articles cited in the Discussion, unless otherwise mentioned, deal with the two-spotted spider mite, *Tetranychus urticae* KOCH [= *T. telarius* (LINNAEUS)].

Fig. 3. Anterior part of the ovary of *T. harti*. Arrow indicating an oogonium with electron-dense mitochondria. BM: basement membrane, OG: oogonium, SL: starlike cell. Scale bar: $2\ \mu\text{m}$.

Fig. 4. Wall surrounding posterior part of the ovary of *T. harti*. EP: epidermis, OC: oocyte, OW: ovarian wall, SC: supporting cell. Scale bar: $2\ \mu\text{m}$.

Fig. 5. Oocyte of *T. harti*, showing synaptonemal complexes (arrow). Scale bar: $1\ \mu\text{m}$.

Fig. 6. Nurse cells in the ovary of *T. harti*. Arrow indicating a tight junction between the supporting cells. N1-N3: nuclei, SC: supporting cell. Scale bar: $2\ \mu\text{m}$.

Fig. 7. Supporting cells with reticular inclusions (arrow) in the ovary of *T. harti*. Scale bar: $1\ \mu\text{m}$.

Fig. 8. Maturing ovum connected to the midgut cell via microvillous bridges (arrows) in *T. harti*. MGC: midgut cell, MO: maturing ovum. Scale bar: $1\ \mu\text{m}$.

Fig. 9. Epithelium of the anterior oviduct of *T. harti*, sagittal section. MS: mucous secretions. Scale bar: $2\ \mu\text{m}$.

Fig. 10. Part of the testis of *T. harti*. Arrow indicating an intercellular bridge between two spermatids. C: corpuscular inclusions, EP: epidermis, N: nucleus of supporting cell, R: reticular inclusions, SG: spermatogonium, ST: spermatid, SY: spermatocyte, SZ: spermatozoon, VD: vas deferens. Scale bar: $2\ \mu\text{m}$.

Fig. 11. Epithelial cell of the vas deferens of *T. harti*. G: Golgi apparatus, LU: lumen. Scale bar: $1\ \mu\text{m}$.

Fig. 12. Posteriormost part of the seminal vesicle of *T. harti*, exhibiting gate cells with processes (arrows) and spermatozoa. SZ: spermatozoon. Scale bar: $2\ \mu\text{m}$.

Fig. 13. High magnification of a gate cell bearing short processes in the seminal vesicle of *T. harti*. Each process enclosing microfilaments (arrow). SZ: spermatozoon. Scale bar: $0.5\ \mu\text{m}$.

Figs. 14-19. Stages of spermioteleosis in *T. harti*. Scale bar: $0.5\ \mu\text{m}$. 14: early spermatid, 15: later spermatids connected by a plasmic bridge (arrow), 16: early spermatozoon showing plasmalemmal tubular structures (arrow), 17: later spermatozoon within testis, 18: spermatozoon present in the central part of seminal vesicle, 19: spermatozoon occurring in the posteriormost part of seminal vesicle.

was called the epithelium by FEIERTAG-KOPPEN and PIJNACKER (1982). The ovarian wall comprising a single layer of flattened epithelial cells was observed as enclosing the posterior part of the ovary. The present observation accords with previous data (FEIERTAG-KOPPEN and PIJNACKER, 1982; ALBERTI and CROOKER, 1985).

In this study, several masses of reticular inclusions were recognized to exist in the cytoplasm of the supporting cells. These inclusions closely resemble protein reserve substances demonstrated in mammalian oocytes (ENDER, 1971), and are possibly consumed as nutrition by the oocytes.

Apart from the supporting cells, so-called nurse cells (often referred to as nutritive cells) have been reported by previous researchers, and these cells are known to develop as sister cells of the oocytes (LANGENSCHIEDT, 1973; WEYDA, 1980; FEIERTAG-KOPPEN and PIJNACKER, 1985). It is also known that each maturing oocyte penetrates the ovary wall to protrude from the ovarian surface, and that this oocyte invades the body cavity where it receives the nutrients from the nurse cell via a cytoplasmic bridge (KOPPEN, 1982; FEIERTAG-KOPPEN and PIJNACKER, 1982; MOTHES-WAGNER and SEITZ, 1984).

Also in *Tetranychina harti*, the three-nucleate nurse cells are present within the ovary, and the maturing ova are placed in the body cavity. However, the intercellular bridge between the oocyte and nurse cell was not observed here. It has been reported that nutrition of the maturing ova are also supplied by the hemolymph and midgut (WEYDA, 1980; MOTHES-WAGNER and SEITZ, 1984). In this study, the maturing ova were found to be connected with the midgut via microvillous bridges. The minute bridges are regarded as supplying nutrition to the maturing ova.

The term vas deferens is not used in BLAUVELT's article (1945), who did not distinguish this organ from the testis. EHARA (1960) used this term in *Bryobia charai*, and then JEPSON et al. (1975) also did. However, many authors have not used the term vas deferens for the organ, instead, adopted "Drüsenteil der Hoden" (ALBERTI and STORCH, 1976), "glandular region of testis" (MOTHES and SEITZ, 1981a), and "vesicular seminalis" (PIJNACKER and DRENTH-DIEPHUIS, 1973; PIJNACKER, 1985). Further, most of these authors referred to a short duct, each of the paired entrances of the seminal vesicle, as the "vas deferens." The present authors postulate that it is more reasonable to use the term vas deferens for the wide duct which leads the testis into the seminal vesicle, because it comprises a glandular epithelium that encloses a large lumen with secretion and a few spermatozoa.

ALBERTI and STORCH (1976) described that the single multinucleate supporting cell which envelops the germ cells had tubular structures within the nuclei. In each testis of the present material, there occur numerous germ cells from spermatogonia to spermatozoa, as well as multinucleate supporting cells. No nuclear tubular structures were detected in the testicular supporting cells. In the cytoplasm of the spermatocytes, the present authors could observe two kinds of inclusions, reticular and corpuscular; the reticular inclusions were also found in the cytoplasm of ovarian supporting cells.

According to ALBERTI and STORCH (1976), the spermatids are connected by cytoplasmic bridges in groups of four or eight cells. Also in this study, sometimes, two spermatids interconnected by an intercellular bridge were found to occur.

Summarizing previous work on spermatogenesis, the structure of the spermatozoa hardly changes in the vas deferens and seminal vesicle (PIJNACKER, 1985). The present observations show that the plasmalemmal tubular structures radially set in the testicular spermatozoa become irregularly arranged in the vas deferens, and are finally divided into

shorter structures in the caudal part of the seminal vesicle. The nucleus is located in the central part of the spermatozoa within the testis, but in the vas deferens it is situated near the periphery to occur in contact with the cell membrane in the posterior part of the seminal vesicle. The spermatozoan nucleus is electron-sparse only in its central part, but becomes homogenously electron-dense before the spermatozoa leave the seminal vesicle. Finally, the cytoplasm proper becomes scarcely present. Moreover, when the spermatozoa occur in the seminal vesicle, theca-like structures are developed all over the periphery of the cell membrane.

Within the plasmalemmal tubular structures, there exists an amorphous substance of medium electron density. The authors are inclined to think that this substance originates in the nutrients taken at the early plasmalemmal invaginations, and accumulates inside the tubular structures formed by the invaginations. This substance is possibly consumed in the course of the metabolism of the spermatozoa.

So far as the present materials are concerned, the seminal vesicle is furnished with two types of the superficial epithelial cells, gate cells, which are present near the exit into the ejaculatory duct and provided with processes: Cells of one type bear long processes, whereas those of the other have noticeably shorter ones. The former cells are set anterior to the latter. Within these cellular processes, there exist microfilaments along the long axis. However, two singlets and nine doublets that are seen in the cilia and flagella of other animals were not detected here. Therefore, these processes appear to be not always mobile by themselves, but are able to move owing to the contraction of the seminal vesicle. The processes possibly play an important role in controlling the discharge of spermatozoa into the ejaculatory duct. The gate cells of these two types seem to share these roles between them.

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