Recent Advances in Insect Embryology in Japan
Edited by H. Ando and K. Miya.
ISEBU Co. Ltd., Tsukuba 1985

Panoistic Ovarioles of the Dobsonfly, *Protohermes grandis* (Megaloptera, Corydalidae)

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Synopsis

The morphology of ovarioles of the megalopteran *Protohermes grandis* is described. Each of the paired ovaries of this insect consists of 145-150 panoistic ovarioles having no nurse cells. A fully developed ovariole contains a linear array of about 14 developing oocytes of different stages; first four anterior oocytes show the late previtellogenic, next 4-5 the vitellogenic, and about five posterior the fully grown ones. The process of the ovariole development roughly resembles to those of the most insects with the panoistic ovaries. However, this is entirely different from that of the sister-groups, the megalopteran Sialidae and the Raphidioptera which have the telotrophic ovarioles.

Introduction

The order Megaloptera is classified into two families, Sialidae and Corydalidae respectively. On the oogenesis of *Sialis* belonging to the family Sialidae, two electron microscopic studies were published by Matsuzaki and Ando (1977) and Büning (1979). According to them, the ovariole type of Sialidae is the telotrophic one which is fundamentally similar to those of the Hemipteran and polyphagous Coleopteran insects. Recently it has also been reported that insects belonging to the order Raphidioptera closely related to the Megaloptera have the same telotrophic ovarioles (Büning, 1980; Matsuzaki and Kano, 1980). In the another family Corydalidae included to the Megaloptera, however, the female reproductive system has not been investigated up to the present, therefore it is not known on the type of ovariole present in the insects of this family.

The present study was designed to investigate the ovarian structure, development of the oocytes and the related tissue (follicular cells) during the early oogenesis by means of electron microscopy.

Materials and Methods

In this study, female adults and larvae of *Protohermes grandis* Thumberg were used. The ovary was fixed in either 1% solution of osmium tetroxide buffered with 0.1M sodium cacodylate at pH 7.4 or 4% glutaraldehyde buffered with same buffer (pH 7.4) for 3-4 hours at about 4°C. In the latter case, the materials rinsed in cacodylate buffer were then postfixed in 1% OsO_4 in the same buffer for 3 hours. Then they were stained in saturated uranyl acetate for 60 min. Following dehydration, the ovaries were embedded in Epon 812. Ultrathin sections were stained with lead citrate for 60 sec. and observed with JEM-T7 electron microscope.

Observations

Morphology of the Ovarioles

Each ovary of the dobsonfly, *Protohermes grandis* consists of 145-150 panoistic ovarioles, segmentally arranged on the lateral oviducts. In this respect *Protohermes* shows rather a close affinity to the Thysanura belonged to the Apterygota, and hemimetabolan panoistic ovaries, such as the Odonata, Orthoptera, Grylloblattodea and Thysanoptera etc.

Fully developed ovarioles of females just before the oviposition are about 10mm from the tip of the germarium to the base of the vitellarium, and three regions can be distinguished; the terminal filament, germarium and vitellarium. The terminal filament measured about 13 μm in diameter is composed of a row of flattened mesodermal cells with elongated nuclei generally lying their long axis perpendicular to the long axis of terminal filament (Fig. 1). No transverse septum may be observed in the region between the terminal filament and the germarium. These ovariole structures are similar to those of the sister-groups, such as megalopteran *Sialis* (Matsuzaki and Ando, 1977; Büning, 1979) and neuropteran *Chrysopa* (Matsuzaki, 1978). The terminal filament posteriorly continues into the germarium maximum width of which is enlarged up to about 40 μm.

The germarium is composed of the oogonia, young oocytes and prefollicular cells, and the oogonia occupy the anterior region of the germarium. In the larval stage oogonial mitosis is occasionally observed in the anterior portion of the germarium. The oogonia clustered in the anterior germarium are subspherical or ovoid in shape, measured 13-15 μm in diameter, and contain large spherical or subspherical nuclei (10-12 μm in diameter). The chromatin material in the nuclei of the oogonia is in a dispersed state. Three or four small masses of the nucleolar material (1.0-1.5 μm in diameter) are dispersed to closely opposite to the inner layer of the nuclear membrane. The oogonial cytoplasm contains mitochondria, rough-surfaced endoplasmic reticulum, a few Golgi bodies and numerous free ribosomes. The mitochondria are randomly distributed in the cytoplasm, and they are largely spherical (about 0.3 μm in diameter) or oval (0.6 × 0.3 μm) in shape and have less developed cristae,

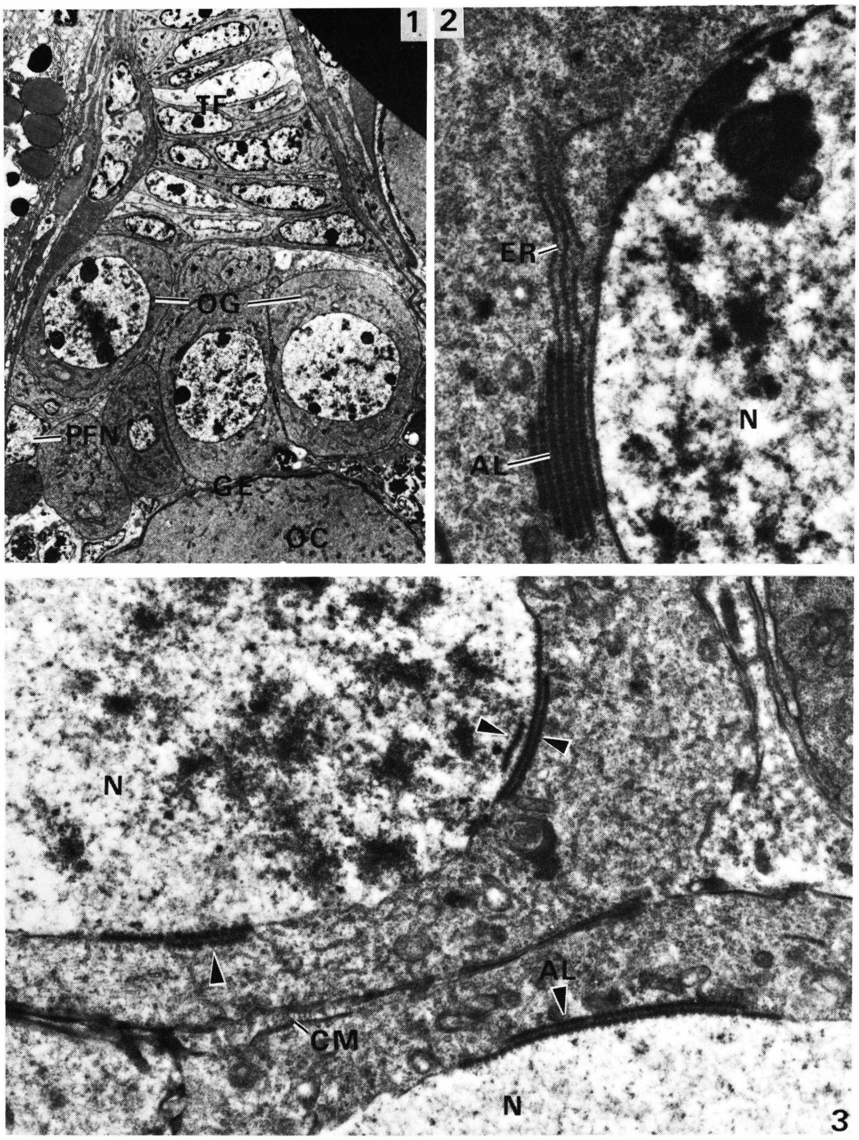

Fig. 1. Low electron micrograph of the boundary between terminal filament (TF) and germarium (GE). OG oogonia, OC young oocyte, PFN prefollicular cell nucleus. X 2,300

Fig. 2. A stack of annulate lamellae (AL) associated directly with the rough-surfaced endoplasmic reticulum (ER) observed in close association with the oogonial nucleus (N) in the anterior portion of germarium. X 15,000

Fig. 3. Electron micrograph showing adjacent two oogonia in the anterior part of germarium. A single strand of annulate lamellae (AL) is seen in contact with the outer or inner nuclear membrane. N oogonial nucleus, CM oogonial cell membrane. Arrow heads indicate another annulate lamellae. X 10,000

but highly elongated forms can not be observed. The rough-surfaced endoplasmic reticulum of various length and forms are small in number most of which distribute around the nucleus in the ooplasm. Annulate lamellae are often observed in the oogonia. In many cases they are positioned close to the nuclear membrane, and are a single to several strands in occurrence (Figs. 2 and 3). As observed in Fig. 2, the interlamellar spacing is quite uniform, and frequently both ends of each strand of the annulate lamellae are directly associated with the rough-surfaced endoplasmic reticulum in continuity. Young oocytes in the posterior region of the germarium slightly increase in volume, and its nucleus likewise enlarges to about 17 X 13 μm and contains usually two masses of nucleoli. Prefollicular cells surrounding the oogonia and early young oocytes are poorly developed similar to those in other panoistic ovarioles.

The vitellarium of the ovariole is situated between the germarium and pedicel. In the case of the late larval ovarioles, the oocytes grow very slowly and they are retained in the early previtellogenic stage. In the most anterior portion of the vitellarium the first young oocyte arranged in a single file is somewhat oblong (ca. 55 X 70 μm), and its long axis is perpendicular to that of the ovariole. The 14th oocyte located in the most posterior portion of the vitellarium becomes more elongated and measured approximately 200 X 86 μm in size. In the ovarioles of females just before the oviposition, on the other hand, the number of oocytes in the vitellarium is also about 14; anterior about four oocytes are about 140 X 70 μm to 300 X 100 μm in size and are in a late previtellogenic stages, next 4-5 oocytes of about 320 X 120 μm to 360 X 150 μm are in the early to middle vitellogenic, and the last average five oocytes are approximately 1,300 X 550 μm in size and are extremely the same with mature oocytes. This fact may suggest that a female produces at least approximately 1,500 eggs at the same time. The mature eggs are cylindrical, with rounded end, and a conspicuous micropylar apparatus is observed at the one side of their anterior end.

Morphological Features of Developing Oocytes and Follicular Cells during Oogenesis

Germinal vesicle As described above, the development of oocytes is comparatively slow during the larval period. Accompanying by the oocyte growth, the germinal vesicle becomes also enlarged and round in shape, and somewhat irregular in the outline. The first oocyte located in the most anterior portion of the vitellarium measures about 32 X 32 μm in size and three times of the maximum diameter of the germarial oogonia, the size of the 14th oocyte is about six times of that of the first oocyte in the fully developed vitellarium of adult females. At the late stage of the vitellogenesis the germinal vesicle becomes somewhat ellipsoidal in shape and reaches its maximum size (ca. 120 X 86 μm). That is, this is about ten times in the major axis of the oogonial nucleus. During this process, the nucleolar masses appear in numerous small fragments which unevenly disperse throughout the nucleoplasm, and these nucleoli disappear in the late vitellogenesis. This condition is similar to those of the panoistic ovarioles of hemimetabolan insects and primitive polytrophic ovarioles of neuropteran *Chrysopa* (Gruzova *et al.*, 1972; Matsuzaki, 1978) and *Stenoponia* of the Siphonaptera (King and Teasley, 1980).

Mitochondria During the early previtellogenesis at the late larval period, the mitochondria are the most numerous and conspicuous organelle found in the ooplasm. In the early

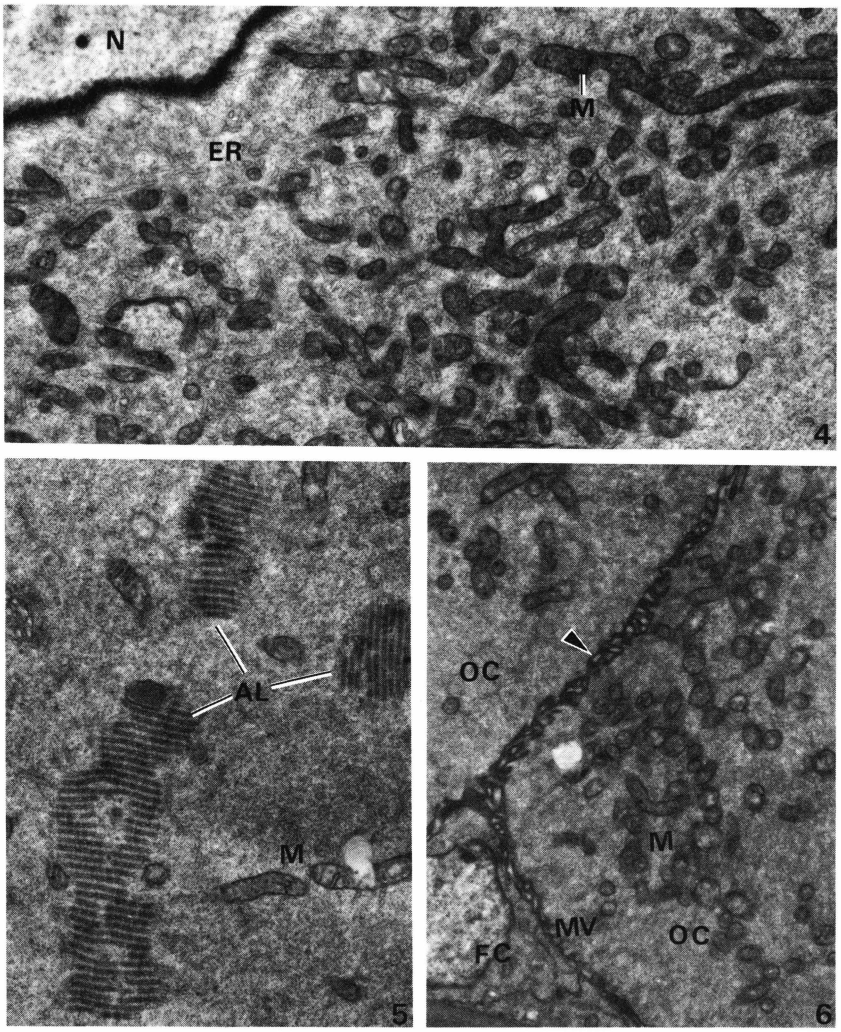

Fig. 4. Perinuclear cytoplasm of the larval previtellogenic oocyte. Numerous mitochondria (M) and smooth-surfaced endoplasmic reticulum (ER) are observed. N nucleus. X 10,000

Fig. 5. Annulate lamellae (AL) in the late larval previtellogenic oocyte. M mitochondria. X 9,000

Fig. 6. Previtellogenic young oocyte (OC) and flattened follicular cells (FC). MV microvilli between oocyte and follicular cells. Arrow head indicates microvilli between two oocytes. M mitochondria. X 9,000

oocytes situated in the anterior position of the vitellarium, the mitochondria fairly increase in number and somewhat grow in size (about 1.5 X 0.3 μm) than those in the germarial oogonia. Subsequently, as the oocytes grow the mitochondria conspicuously increase in number especially in the cytoplasm around the germinal vesicle (Fig. 4). These mitochondria are mostly round or short-rod shaped with irregular cristae, and rod-shaped mitochondria are 1.5-3.3 μm in length. However, sometimes the very long rod-shaped (maximum length aproximately 6.0 μm), Y-shaped and dumbbell-shaped mitochondria are observed, and it is thought that they are to be interpreted as the terminal stage of mitochondrial division as reported by Liu and Davies (1973) and others. Moreover, numerous smooth-surfaced endoplasmic reticulum which may be originated from the nuclear membrane are found within the ooplasm embedded numerous mitochondria around the germinal vesicle (Fig. 4). In the late previtellogenic oocytes of the adult ovarioles the mitochondria are dispersed into the cortical and subcortical ooplasm. While their number decreases in the ooplasm close to the germinal vesicle. These mitochondria are largely subspherical or short rod-shaped with many transverse cristae and are slightly smaller in size (0.6 X 0.5-1.0 X 0.6 μm) than those found in the former stage.

Annulate lamellae In the germarial oogonia, as mentioned above, the annulate lamellae occur in contact with the nuclear membrane, and are also connected to the rough-surfaced endoplasmic reticulum (Fig. 2). In some cases the annulate lamellae are found as a single strand within the nucleus (Fig. 3) as observed in the oocyte nucleus of *Ophion* (King and Richard, 1968). *Anagasta* (Cruickshank, 1972), *Aedes* (Fiil, 1974) and preblastodermal nuclei of *Oncopeltus* eggs (Gassner and Sears, 1977). In *Protohermes*, in the young vitellarial oocytes the annulate lamellae are scattered in stacks in the endoplasm and subcortical ooplasm (Fig. 5). From the early to the late vitellogenic stage, the stacks of annulate lamellae developed within the cytoplasmic electron dense masses are observed here and there in the cortical and subcortical ooplasm. Similar results were also obtained in the *Libellula* oocytes (Kessel and Beams, 1969), in the nurse cells of trichopteran *Parastenopsyche* (Matsuzaki, 1972), and homopteran *Bothrogonia* (Matsuzaki, 1975).

Follicular epithelium In *Protohermes* ovarioles, during larval period the epithelium enclosing the young previtellogenic oocytes is incompletely formed by scattered squamous follicular cells, because the oocytes and their follicular cells during this period grow slowly in size and number. Accordingly, the cytoplasm of these cells is poor in the organelles, *i. e.*, only some mitochondria and rough-surfaced endoplasmic reticulum may be seen (Fig. 6). In the boundary between the oocyte and follicular epithelium small microvilli develop, among which an electron opaque substance may be seen. Subsequently, as the oocyte growth, the follicular cells gradually increase in number by means of mitotic division and their size markedly increase at the same time (Fig. 7). Consequently, at the early stage of the vitellogenesis the oocyte becomes to be enclosed in the cuboidal follicular epithelium which is approximately 8 μm in height (Fig. 8). The cytoplasm of follicular cells contains numerous ribosomes, and other organelles such as the mitochondria, rough-surfaced endoplasmic reticulum etc., also increased in number. The microvilli are more numerous as compared with those of the previtellogenic stages, and the micropinocytotic vesicles or pinosomes become to be found in the cortical ooplasm (Fig. 8). From the middle to the late

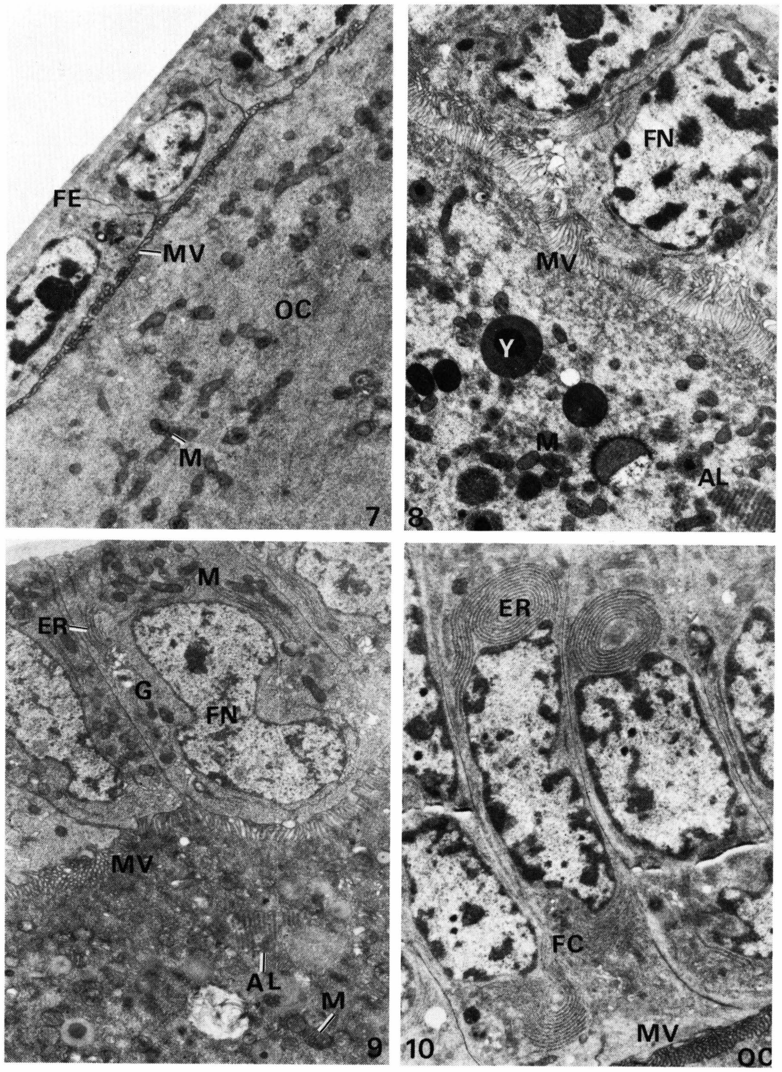

Fig. 7. Late previtellogenic oocyte (OC) and somewhat flattened follicular epithelium (FE). M mitochondria, MV microvilli. X 6,000

Fig. 8. Early vitellogenic oocyte and cuboidal follicular epithelium. AL annulate lamellae, FN follicular cell nucleus, M mitochondria, MV microvilli, Y proteid Yolk. X 6,000

Fig. 9. Late vitellogenic oocyte and surrounding the columnar follicular epithelium. AL annulate lamellae, ER rough-surfaced endoplasmic reticulum, FN follicular cell nucleus, G Golgi body, M mitochondria, MV microvilli. X 6,000

Fig. 10. Conspicuously elongated follicular cells (FC) on the anterior most portion of oocyte (OC). Whorls of the endoplasmic reticulum (ER) is developed in the cytoplasm near the follicular cell nucleus. MV microvilli. X 6,000

vitellogenic stage the follicular epithelium attains their maximum size (approximately 9 μm in height) and is columnar in shape (Fig. 9). As shown in Fig. 9, the mitochondria with the electron dense matrix and rough-surfaced endoplasmic reticulum increase remarkably in number. The Golgi bodies are also found in some places of the follicular cells. The part of the follicular epithelium investing the anterior pole of the oocyte is significantly thick (18-20 μm in height) (Fig. 10). The cells in this part have the synthetic function of the micropylar apparatus and the egg membranes *i. e.* vitelline membrane and chorion. Therefore the development of the cell organelles especially the whorls of rough-surfaced endoplasmic reticulum is noticeable.

Discussion

The above mentioned ovarian development in *Protohermes grandis* belonging to Corydalidae of the Megaloptera roughly agrees with that known in many other insects having panoistic ovaries, they are the Thysanura (Bitsch, 1980a, b; Bitsch and Bitsch, 1982; Cone and Scalzi, 1967) included in the Apterygota, several primitive orders belonging to the Hemimetabola, such as Odonata (Ando, 1962; Beams and Kessel, 1969: Halkka and Halkka, 1968; Kessel and Beams, 1969; Kessel and Ganion, 1979; Matsuzaki, 1971; Seshachar and Bagga, 1963), Orthoptera (Allen and Cave, 1968; Bassemir, 1977; Cave and Allen, 1969; Favard-Séréno, 1966; Favard-Séréno and Durand, 1963a, b; Gupta, 1968; Kunz, 1969; Matsuzaki, 1971), Blattaria (Anderson, 1964; Gresson and Threadgold, 1962; Ksiazkiewicz-Ilijewa, 1977; Ogi, 1973; Scheurer, 1969; Tanaka, 1973; Wüest, 1979; Zinsmeister and Davenport, 1970), Mantodea (Ogi and Iwaikawa, 1980), Grylloblattodea (Matsuzaki et al, 1979), Isoptera (Truckenbrodt, 1970), and Thysanoptera (Haga and Matsuzaki, 1980), although some variation of the style of ovarian development may be observed in some of these insects. The ovaries of these insects have no nurse cells, but their oocyte nuclei or germinal vesicles develop well instead. For instance, the germinal vesicle of *Protohermes* ovarioles grows about ten times in the maximum diameter larger than that of the germarial oogonia. In these insects RNA synthesis during the oogenesis would reasonably be carried out only by the oocyte nucleus. Same results are also obtained in some primitive polytrophic ovaries of *Chrysopa* (Gruzova et al, 1972; Matsuzaki, 1978) and *Stenoponia* (King and Teasley, 1980). Namely, in *Chrysopa* the germinal vesicle of the middle vitellogenic stage 5 shows a maximum major axis, which is about ten times longer than that of stage 1 (Matsuzaki, 1978). On the other hand, King and Teasley (1980) have described the relative growth rates of the nuclei of oocytes and those of nurse cells of *Stenoponia* and *Drosophila* during the oogenesis. According to them, in *Drosophila* the volume of each oocyte nucleus grows only 1.5 times, whereas that of each nurse cell nucleus grows between 4 and 5 doublings. In *Stenoponia* this tendency was reversed. The volume of the oocyte nucleus increased 5 times, whereas each nurse cell nucleus only doubled its volume.

In general the follicular cells are fully developed by the onset of the vitellogenesis. For instance, in *Galloisiana* ovaries the columnar follicular cells attain their maximum thickness (ca. 35 μm) during the vitellogenesis (Matsuzaki et al., 1979). On the other hand, in *Protohermes* ovaries in the present study, the follicular cells show the comparatively slow growth and are only about 9 μm in their maximum thickness. The precursors of the proteid yolk substances are supplied from the follicular cells to the oocyte. After this process ceased, the follicular cells secrete the material for the vitelline membrane and chorion, and then degenerate.

Several differences in the fine structure of *Protohermes grandis* oogenesis were noticed among the other panoistic ovaries described in the present paper, although those ovaries are very similar from a functional point of view. Another interesting group having a panoistic ovaries is the mecopteran *Boreus* and Siphonaptera which are often placed in advanced groups because they are considered close to the Diptera. As described above, King and Teasley (1980) found that *Stenoponia* has the primitive polytrophic ovaries as well as those of the Neuroptera. It is very interesting to elucidate the evolutional correlation between the panoistic and polytrophic ovaries in the holometabolous insects.

Acknowledgements

We wish to express our sincere gratitude to Dr. H. Ando, Professor of University of Tsukuba for his cordial guidance and helpful criticism of the manuscript.

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