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Morphological Study of Ovarian Structures in Scolopendromorph Centipedes (Myriapoda: Chilopoda) with Special Reference to the Position of Oocyte Growth

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Abstract

The ovarian structures of scolopendromorph centipedes, *Scolopocryptops rubiginosus* and *S. sexspinosus*, are described based on histological and ultrastructural observations. Particular attention was paid to the position of growing germ cells. In the *Scolopocryptops* species examined, the ovary was a single longitudinal sac-like organ that consisted of a layer of ovarian epithelium. Oogonia and young oocytes were sparsely distributed or closely clustered among ovarian epithelial cells all along the ventral region of the ovary. Early previtellogenic oocytes surrounded by a single layer of vitelline membrane were also presented among ovarian epithelial cells and irregularly distributed along the ventral region of the ovary. In contrast, late previtellogenic and vitellogenic oocytes surrounded by two layers of vitelline membrane occupied their own individual follicular pouches. Each follicular pouch appeared as a dent in the ovary and was formed by a continuous layer of the ovarian epithelium accompanied by a continuous lining of basement membrane. Therefore, oogenetic growth of these folliculated oocytes proceeded in hemocoelic spaces rather than in the ovarian lumen. Oocyte growth within hemocoelic spaces settled in the follicular pouches, *i. e.* growth outside of the ovary, could be regarded as a shared derived feature of myriapods, and this trait is never observed in other arthropods.

Introduction

Several differences in ovarian structure have been represented in the two major arthropod subphyla, the Chelicerata and the Mandibulata (Makioka, 1988). One of the most noticeable differences is the position of oocyte growth within the ovary (Fig. 1). In the type found in most chelicerates (the chelicerate-type; Fig. 1A), the early oocytes leave the germarium, not to enter the ovarian lumen, but to ride on the outer surface of the ovarian wall, where they grow sandwiched between the ovarian epithelium and its basement membrane during the oogenetic period. The ripe oocytes are then ovulated into the ovarian lumen through the ovarian wall epithelium. The other type is found in many mandibulates (the mandibulate-type; Fig. 1B). In this type of ovary, the oocytes leave the germarium to enter the ovarian lumen, where they grow during the oogenetic period.

This histological understanding of arthropod ovaries was, however, challenged by an ultrastructural study of diplopod ovaries. Kubrakiewicz (1991a) observed the ultrastructure of ovaries in the julid diplopod, *Ophyiulus pilosus*, and reported that the oocytes underwent oogenetic growth in a hemocoelic space outside of and immediately adjacent to the ovary. Oocyte-growth in a hemocoelic space is never known in the other mandibulates (also in the chelicelates). In the ovary of this julid diplopod, each growing oocyte was surrounded by a follicular epithelial layer that was continuous with the ovarian epithelium and accompanied by the basement membrane. Therefore, the inner space of the follicular pouch was hemocoelic. Such an ovarian structure is quite different from those of the both mandibulate- and chelicelate-type of ovary. Until now, only a few ultrastructural studies have been done in other myriapod species: a lithobiomorph chilopod (Herbaut, 1974), a symphylan (Biliński, 1979) and some diplopods (Kubrakiewicz, 1991b, c). However, they provided very few details on the position of germ cells at different developmental stages within and/or around the ovary. Therefore, it remains to be determined whether oocyte growth occurs in the hemocoel in some myriapods and whether it is common among myriapod groups.

The growing oocytes are commonly connected with the ovarian epithelium via their own follicle layers in all of four myriapod groups (*e. g.*, in Chilopoda: Jangi, 1957; Herbaut, 1974; Knoll, 1974; in Symphyla: Tiegs, 1940; in Pauropoda: Tiegs, 1947; in Diplopoda: Sareen and Adiyodi,

1983; Yahata and Makioka, 1994). Such a follicular connections between oocytes and the ovarian epithelium is unique among arthropod groups, and may be a shared distinctive feature of the all myriapod groups.

Recently, Miyachi and Yahata (2011) suggested the possibility that oocyte growth occurs in the hemocoel in some centipedes. The present study histologically and ultrastructurally describes the ovaries in two scolopendromorph centipede species, *Scolopocryptops rubiginosus* and *S. sexspinosus*. Special attention was paid to the position of female germ cells at different developmental stages to compare with the findings of Kubrakiewicz (1991a).

Materials and Methods

Adult specimens of *Scolopocryptops rubiginosus* (L. Koch, 1878) and *S. sexspinosus* (Say, 1821) were collected from leaf litter, decayed tree, and under stones in the Ibaraki, Fukuoka, Miyazaki and Shizuoka Prefectures of Japan.

For light microscopy, dissected ovaries or whole bodies of which the legs were removed out were fixed with Bouin's solution. Some fixed specimens were dehydrated in a graded ethanol-acetone series, embedded in methacrylate resin, and were cut into serial sections in 1 or 2 μm thick. Other specimens were dehydrated in a graded ethanol-*n*-butanol series, embedded in paraffin and were cut into serial sections of 5 or 8 μm thick. Both the paraffin and the resin sections were stained with Mayer's hematoxylin and eosin, alcian blue-periodic acid SCHIFF (PAS)-hematoxylin, or azocarmine G-aniline blue-orange G.

For transmission electron microscopy, dissected ovaries were pre-fixed with Karnovsky's fixative buffered with 0.2 M HCl-sodium cacodylate in a few hours. After post-fixation with 1% osmium tetroxide in two hours, specimens were dehydrated in a graded acetone series, embedded in Quetol 651 resin, and cut into ultrathin sections with an ultramicrotome (Leica ULTRACUT-S or RMC MT-7000). Sections were un-stained or double stained with uranyl acetate and lead citrate and were observed under a transmission electron microscope (Hitachi H-7650, JEOL JEM-1010 or TOPCON LEM-2000) at 80 kV.

Results

Gross anatomy of female reproductive organ

The reproductive systems of adult female *Scolopocryptops rubiginosus* and *S. sexspinosus* were very similar in morphology. In both species, the adult ovary was a single, long, sac-like organ located dorsaly to the alimentary canal along the median axis (Fig. 2). An oviduct extended posteriorly from the most posterior end of the ovary. The ovarian wall, which surrounded an ovarian lumen (Figs. 2, 3), consisted of a layer of ovarian epithelial cells ranging from 0.5–6 μm in height (Figs. 3, 4). These ovarian epithelial cells were connected to each others by desmosome junctions (Fig. 5). On the outer surface of the ovary, the ovarian epithelium was lined with a thick basement membrane from 350–1000 nm in thickness (Fig. 4). The basement membrane was distinctive in that it was unusually thick and it had a homogeneous mono-lamina structure that lacked distinct lamina lucida, lamina densa, and zona reticularis layers (Figs. 4, 5).

Oogonia, young oocytes, and early previtellogenic oocytes were sparsely distributed or closely clustered among ovarian epithelial cells throughout the ventral wall of the ovary (Fig. 2). In contrast, late previtellogenic and vitellogenetic oocytes were separated into their own follicular pouches (Fig. 3). The follicular pouch was an extended inward hollow formed by a continuous layer of ovarian epithelium, which was lined with a continuous

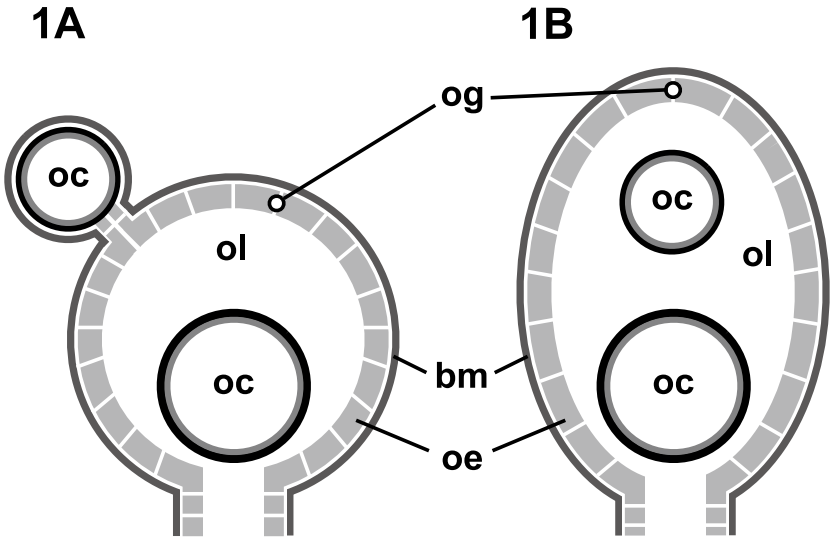


Fig. 1 Schematic drawings of two types of arthropodan ovaries (modified from Makioka, 1988). A) Chelicerate-type; oocytes grow between ovarian epithelial layer and its basement membrane. B) Mandibulate-type; oocytes grow within ovarian lumen. bm: basement membrane, oc: oocyte, oe: ovarian epithelium, og: oogonia, ol: ovarian lumen.

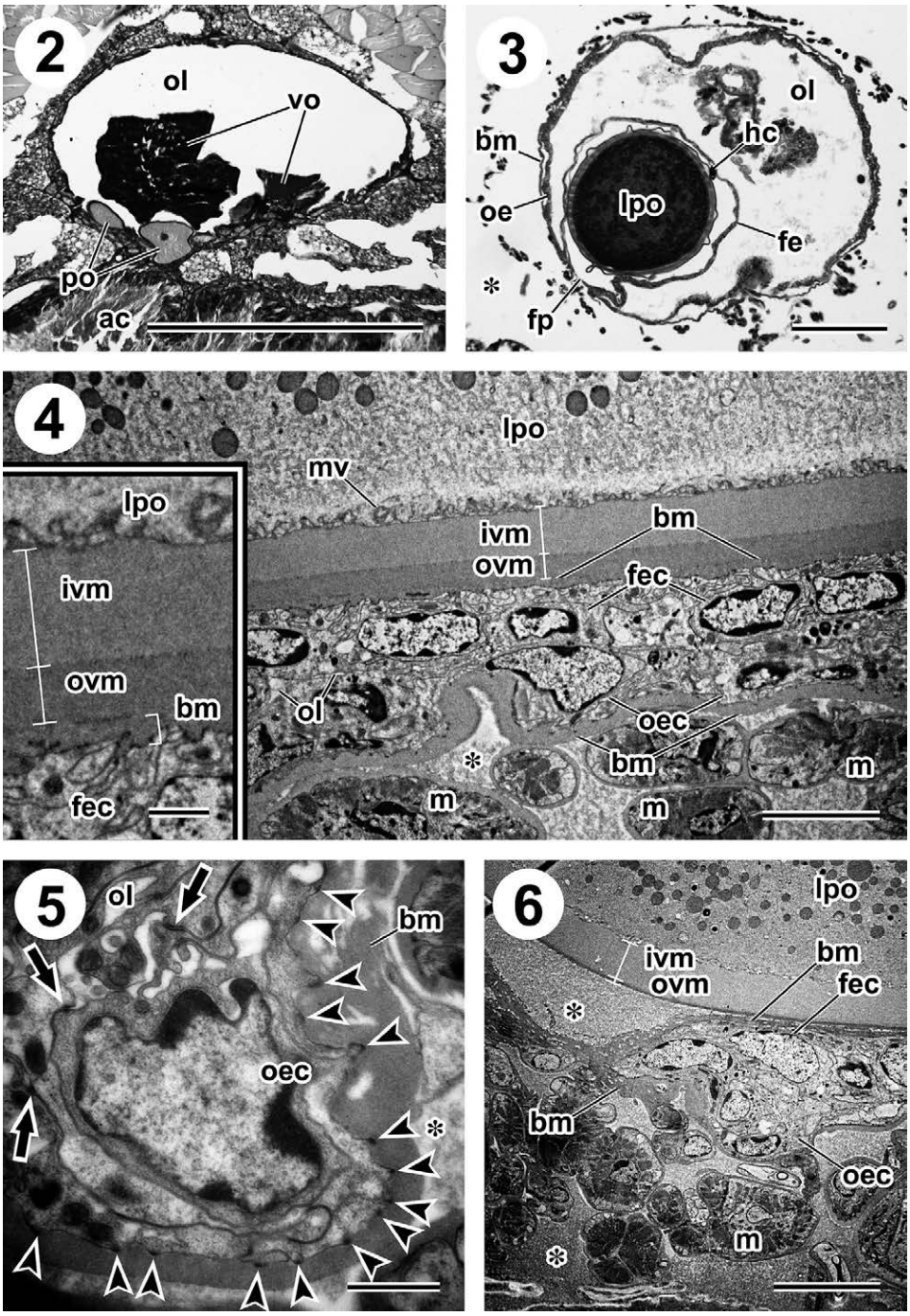


Fig. 2 Cross-section of adult ovary in *Scolopocryptops sexspinosus*. Paraffin. Alcian blue-PAS-hematoxylin. Dorsal side is oriented towards figure top. Previtellogenic (po) and vitellogenic oocytes (vo) within the ovary at ventral region of the ovary. ac: alimentary canal, ol: ovarian lumen. Scale = 500 μm.

Fig. 3 Cross-section of adult ovary in *Scolopocryptops rubiginosus*. Paraffin. Azocarmine G-aniline blue-orange G. Dorsal side is oriented towards figure top. Ovarian lumen (ol) surrounded by ovarian epithelium (oe), and late previtellogenic oocyte (lpo) growing in hemocoelic space within follicular pouch. Note the presense of hemocyte (hc) between the late previtellogenic oocyte (lpo) and follicle epithelium (fe). Asterisk indicates the hemocoelic space. bm: basement membrane, fp: follicle pore. Scale = 100 μm.

Fig. 4 Ovary in *Scolopocryptops rubiginosus*. TEM. Un-stained. Ovarian and follicle epithelial layers accompanied by their own basement membrane (bm), and narrow ovarian lumen (ol) between the both layers. Note that the late previtellogenic oocyte (lpo) with developed microvilli (mv) is enveloped by the outer (ovm) and inner layer of vitelline membrane (ivm), and the enveloped oocyte is directly surrounded by the layer of follicle epithelial cells (fec) and its basement membrane (bm). Asterisk indicates the hemocoelic space. Inset: Extended part of the inner surface of follicular pouch. m: muscle, oec: ovarian epithelial cell. Scales = 5 μm in main and 1 μm in insetted figure.

Fig. 5 Ovarian epithelial cells in *Scolopocryptops rubiginosus*. TEM. Un-stained. Arrows indicate the desmosome junctions between adjacent ovarian epithelial cells (oec). Arrowheads indicate the hemidesmosomes by which the epithelial cells are anchored with the basement membrane (bm). Asterisk indicates the hemocoelic space. ol: ovarian lumen. Scale = 1 μm.

Fig. 6 Ovary around the fold of ovarian and follicular epithelial layer in *Scolopocryptops rubiginosus*. TEM. Un-stained. Continuous construction of follicle epithelium with the ovarian epithelium. Asterisks indicate the hemocoelic space. bm: basement membrane, fec: follicular epithelial cell, ivm: inner layer of vitelline membrane, lpo: late previtellogenic oocyte, m: muscle, oec: ovarian epithelial cell, ovm: outer layer of vitelline membrane. Scale = 10 μm.

basement membrane (Fig. 6). Such construction of follicle epithelium proves the hemocoelic nature for the inner space of follicular pouch. Each follicular pouch had a follicle pore that opened to the hemocoel (Fig. 3). Based on the histological analysis of whole-body sections, the follicle pores opened towards the alimentary canal all along the ovary (Fig. 2).

Female germ cells in ovarian epithelium

Oogonia, young oocytes, and early previtellogenic oocytes were distributed among the ventral ovarian epithelial cells. These germ cells could be distinguished from the epithelial cells based on the cellular shape and the staining condition of nucleus (Fig. 7). The nuclei of the ovarian epithelial cells were irregular in shape, but the nuclei or early germinal vesicles of germ cells were round (Fig. 8).

Oogonia of about 12 μm in diameter had relatively large nuclei of about 6 μm in diameter with several chromatin granules but no nucleoli (Figs. 7, 9). Young oocytes, those that had not begun oogenetic growth, of about 12 μm in diameter had early germinal vesicles of about 5 μm in diameter with one or a few nucleoli (Fig. 7). Early previtellogenic growth of the oocytes proceeded among the ovarian epithelial cells (Fig. 7). These oocytes of more than 20 μm in diameter were surrounded by a thin layer of egg envelope of about 500 nm thick (Fig. 10). These enveloped early previtellogenic oocytes had a numerous microvilli, and the surrounding ovarian epithelial cells showed no evidence of secretory activity (Fig. 10). Thus the egg envelope should be autosynthetic vitelline membrane.

Each of these female germ cells–oogonia, young oocytes, or early previtellogenic oocytes were wholly surrounded by a few ovarian epithelial cells (Figs. 7, 9), and were never contacted with the basement membrane of the ovarian epithelium (Fig. 9). The epithelial cells were elongated and curved to surround the female germ cell (Figs. 7, 9). The basal surfaces of the epithelial cells had a large number of protuberances that projected deep into the basement membrane. At the tips of these protuberances, electron dense granular structures, possibly hemidesmosomes, were very prominent (Figs. 7, 9). The ovarian epithelium and its basement membrane of the regions surrounding oogonia, young oocytes or early previtellogenic oocytes were thicker than other regions: They became 15–25 μm and 450–1400 nm in thick, respectively (Figs. 7, 9).

Female germ cells in follicular pouches

Oocytes larger than 60 μm in diameter were not distributed among ovarian epithelial cells, but were located within the inner space of each individual follicular pouch (Figs. 3, 11–13). Epithelial cell layer of the follicular pouch was about 0.3–5 μm in thick (Figs. 3, 11–13), and its inner surface was lined with a basement membrane that was 240–750 nm in thick (Figs. 4, 6, 7, 10). The inner space of each pouch was continuous with the hemocoel (Figs. 3, 6, 11–13), and hemocytes were often found within the space and adjacent to oocytes (Fig. 3).

Most oocytes in follicular pouches larger than 80 μm in diameter were surrounded by two layers of vitelline membrane (Figs. 4, 6, 7, 10), but some of these folliculated oocytes had only one layer of vitelline membrane. The microvilli were well developed in the oocytes with two layers of vitelline membrane (Fig. 4). The outer and inner vitelline membranes were about 2 μm and 5 μm thick, respectively. In previtellogenic oocytes more than 80 μm in diameter, the outer layer of vitelline membrane was somewhat basophilic and more electron dense than the strongly PAS positive inner layer (Figs. 4, 6, 7).

Oocytes larger than 230 μm in diameter were categorized into the vitellogenic stage. In the early vitellogenic oocytes, small acidophilic yolk granules of 2–4 μm in diameter as well as a large number of very prominent lipid droplets of 2–20 μm in diameter (Fig. 11) first appeared in the periplasm. During vitellogenic growth, the yolk granules and the lipid droplets increased in size respectively via successive fusions (Fig. 12). In late vitellogenic oocytes larger than 300 μm in diameter, the yolk granules become large polygonal yolk blocks of 15–85 μm at the widest point. The yolk blocks nearly filled the ooplasm, and the lipid droplets, 2–50 μm in diameter, were distributed between them (Fig. 13).

Discussion

Location of germ cells

Our histological observations of two *Scolopocryptops* centipedes revealed that the germ cells grew only in the ventral region of ovaries along the longitudinal axis. Jangi (1957) also described a similar location of the germ cells in other scolopendromorph centipede, *Scolopendra morsitans*. Thus the location of germ cells in the ventral region of ovary seems to be common among the scolopendromorph centipedes. In contrast, Knoll (1974) demonstrated that the germ cells developed in the dorsal region of the ovaries in scutigeromorph species. The location of germ cells in ovary possible varies among higher level taxa, and more comprehensive observations are required covering a wider taxonomic range.

Position of oocyte growth

Several authors have described ovarian structure and oogenesis in several centipede taxa (in scutigeromorph: Knoll, 1974; in lithobiomorph: Herbaut, 1974; in scolopendromorph: Jangi, 1957). These authors suggested that the follicular pouches were the hollows of the ovary, *i. e.* the epithelial layer of the pouch was continuous with the epithelial layer of the ovarian wall. The oocytes grew within the inner spaces of these pouches, but it was

unclear whether the oocytes were situated in the hemocoelic space or were sandwiched between the follicle layer and its basement membrane.

Here, we described the position of oocyte growth in *Scolopocryptops* centipedes in detail based on histological and ultrastructural analyses (Fig. 14). We clearly

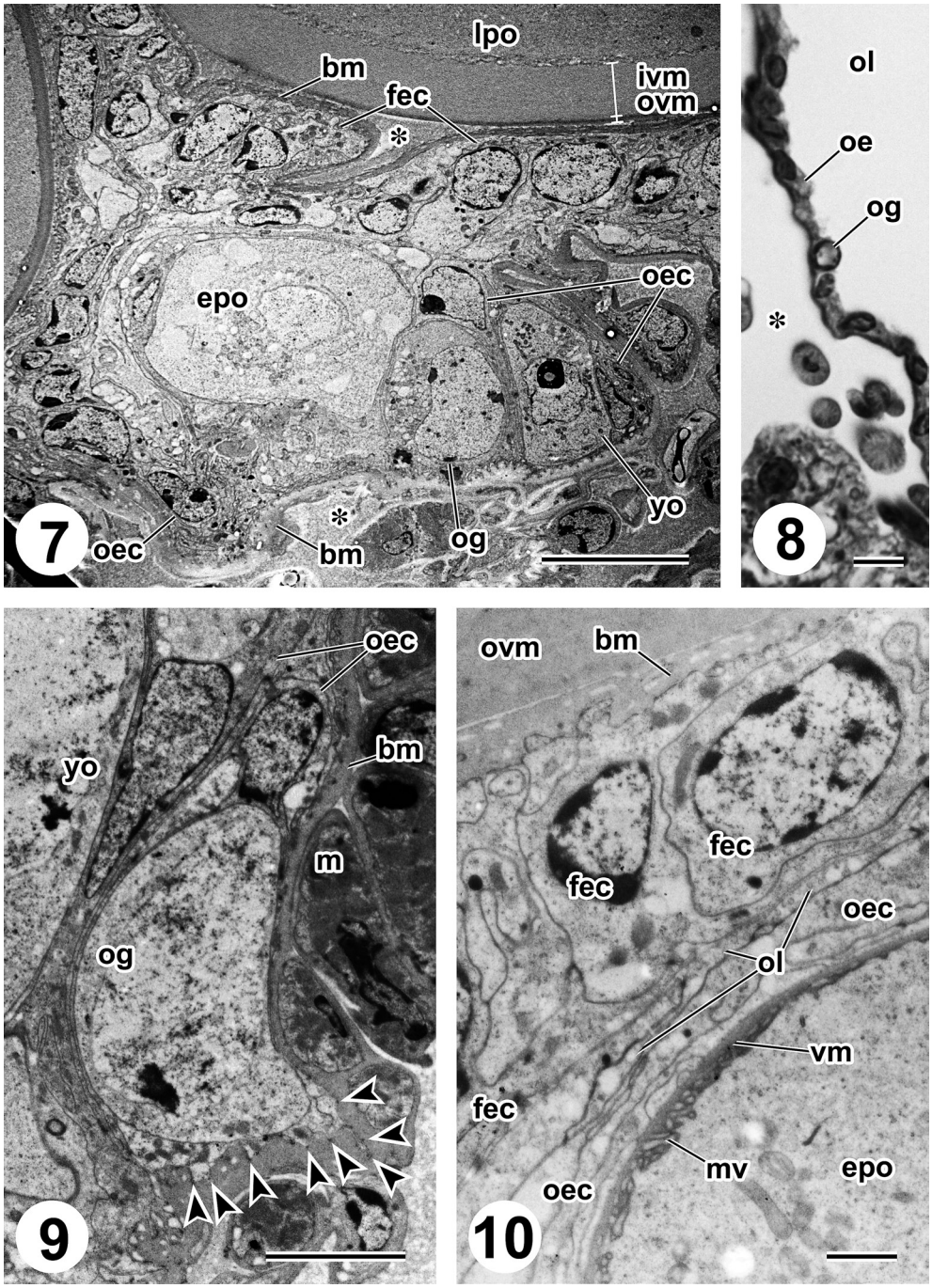
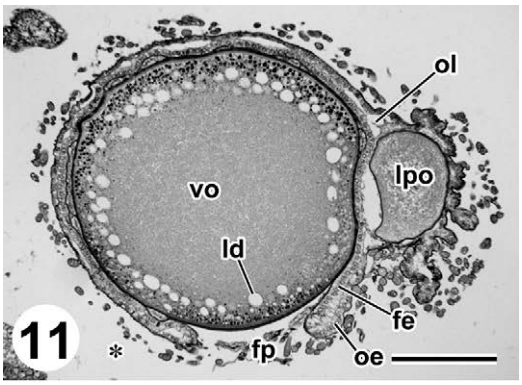


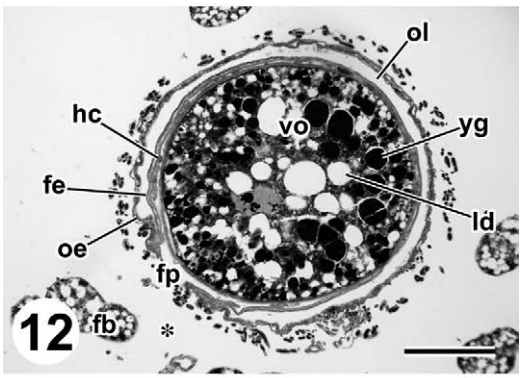
Fig. 7 Ovarian epithelium surrounding young germ cells in *Scolopocryptops rubiginosus*. TEM. Un-stained. Oogonium (og), young oocyte (yo) and early previtellogenic oocyte (epo) presented among ovarian epithelial cells (oec). Note that many protuberances project deep into the basement membrane on the basal surfaces of the epithelial cells in this area. Asterisks indicate the hemocoelic space. bm: basement membrane, fec: follicle epithelium, ivm: inner layer of vitelline membrane, lpo: late previtellogenic oocyte, ovm: outer layer of vitelline membrane. Scale = 10 μm.

Fig. 8 Ovarian epithelium surrounding oogonium in *Scolopocryptops sexspinosus*. Paraffin. Azocarmine G-aniline blue-orange G. Oogonium (og) embedded in ovarian epithelium (oe). Asterisk indicates the hemocoelic space. ol: ovarian lumen. Scale = 10 μm.

Fig. 9 Oogonium and adjacent epithelial tissue in *Scolopocryptops rubiginosus*. TEM. Double-stained. Oogonium (og) surrounded by a few ovarian epithelial cells (oec), and epithelial cells with many protuberances on the basal surface projecting deep into the basement membrane (bm). Note the prominant hemidesmosomes (arrowheads) at the tips of the epithelial protuberances. m: muscle, yo: young oocyte. Scale = 5 μm.

Fig. 10 Ovary in *Scolopocryptops rubiginosus*. TEM. Double-stained. Early previtellogenic oocyte (epo) with microvilli (mv) and vitelline membrane (vm) settled among the ovarian epithelial cells (oec). Note the absence of basement membrane between the oocyte and the ovarian epithelial cells, and a thick basement membrane (bm) between the follicular epithelial cells (fec) and outer layer of vitelline membrane (ovm) of folliculated late previtellogenic oocyte. ol: ovarian lumen. Scale = 1 μm.





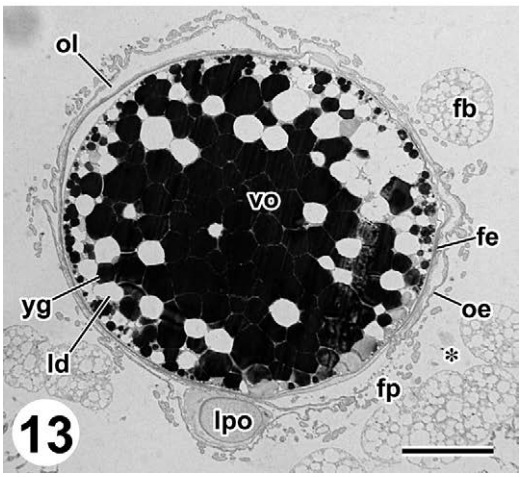


Fig. 11 Cross-section of adult ovary in *Scolopocryptops rubiginosus*. Paraffin. Alcian blue-PAS-hematoxylin. Dorsal side is oriented towards figure top. Early vitellogenic oocyte (vo) and late previtellogenic oocyte (lpo) within individual follicular pouches. Note the strongly stained small yolk granules (not indicated) and lipid droplets (ld) in the periplasm of the vitellogenic oocyte. Asterisk indicates the hemocoelic space. fe: follicle epithelium, fp: follicle pore, oe: ovarian epithelium, ol: ovarian lumen. Scale = 50 μm.

Fig. 12 Cross-section of adult ovary in *Scolopocryptops rubiginosus*. Paraffin. Azocarmine G-aniline blue-orange G. Dorsal side is oriented towards figure top. Vitellogenic oocyte (vo) in the follicular pouch with a number of late yolk granules (yg) and lipid droplets (ld). Note the presence of hemocytes (hc) between the oocyte and its follicle epithelium, indicating the hemocoelic nature of the inner space of the follicular pouch. Asterisk indicates the hemocoelic space. fb: fat body, fe: follicle epithelium, fp: follicle pore, oe: ovarian epithelium, ol: ovarian lumen. Scale = 100 μm.

Fig. 13 Cross-section of adult ovary in *Scolopocryptops sexspinosus*. Resin. Azocarmine G-aniline blue-orange G. Dorsal side is oriented towards figure top. Ripe vitellogenic oocyte (vo) within the follicular pouch with number of large block-shaped yolk granules (yg) and lipid droplets (ld). Asterisk indicates the hemocoelic space. fb: fat body, fe: follicle epithelium, fp: follicle pore, lpo: late previtellogenic oocyte, oe: ovarian epithelium, ol: ovarian lumen. Scale = 100 μm.

demonstrated that the follicular pouches were hollows of the ovary, and that the oocytes grew within the inner spaces of these pouches during the late previtellogenic and vitellogenic stages. The space where oocytes grow was conclusively proved to be hemocoelic rather than the space between the follicular epithelial layer and its basement membrane.

Comparison of ovarian structure among myriapods

In the julid diplopod, *Ophyiulus pilosus*, Kubrakiewicz (1991a) described the presence of oocytes in hemocoelic spaces of follicular pouches. This morphological feature is shared with the *Scolopocryptops* centipedes examined in the present study.

The observation that growing oocytes were connected to the ovarian epithelium via a part of their follicle layers was commonly reported for species of all myriapod groups (*e. g.*, in Chilopoda: Jangi, 1957; Herbaut, 1974; Knoll, 1974; in Symphyla: Tiegs, 1940; in Puropoda: Tiegs, 1947; in Diplopoda: Sareen and Adiyodi, 1983; Yahata and Makioka, 1994), and reports of this type were absent for other arthropods. Also in the present study, the continuity between follicle and ovarian epithelium was observed in the ovaries of the *Scolopocryptops* centipeds examined. The fact that many previously examined myriapods have such a follicular continuity could strengthen the idea that the ovaries of the all four myriapod groups have a common plan.

Both morphological (*e. g.*, Anderson, 1973; Dohle, 1980; Edgecombe, 2004; Giribet *et al*., 2005) and molecular analyses (*e. g.*, Podsiadlowski *et al*., 2007; Gai *et al*., 2008) tend to indicate that the myriapod relationship is as follows (Chilopoda (Symphyla (Pauropoda + Diplopoda))). Oocyte growth in hemocoelic follicular pouches has been confirmed in the distantly related myriapod groups, Diplopoda (Kubrakiewicz, 1991a) and Chilopoda (present study), but never observed in other arthropods. Occurence of similar follicular pouches in symphylan (Tiegs, 1940) and pauropodan (Tiegs, 1947) ovaries strongly suggests that the hemocoelic manner of oocyte growth is a common feature among myriapods. If so, the hemocoelic manner would represent the ground plan of myriapod oogenesis, and furthermore become a strong candidate of the synapomorphy of the Myriapoda. To confirm these assertions, symphylan and pauropodan species should be subjected to ultrastructural analysis in the future.

Phylogenetic significance of position of oocyte growth

Makioka (1988) suggested that there are several differences in the structure of the ovaries between two major arthropod subphyla, the Chelicerata and the Mandibulata. In the mandibulate-type ovary, the oocytes grow within the ovarian lumen (Fig. 1B), whereas in the chelicerate type, the growing oocytes are sandwiched between the ovarian epithelial layer and its basement

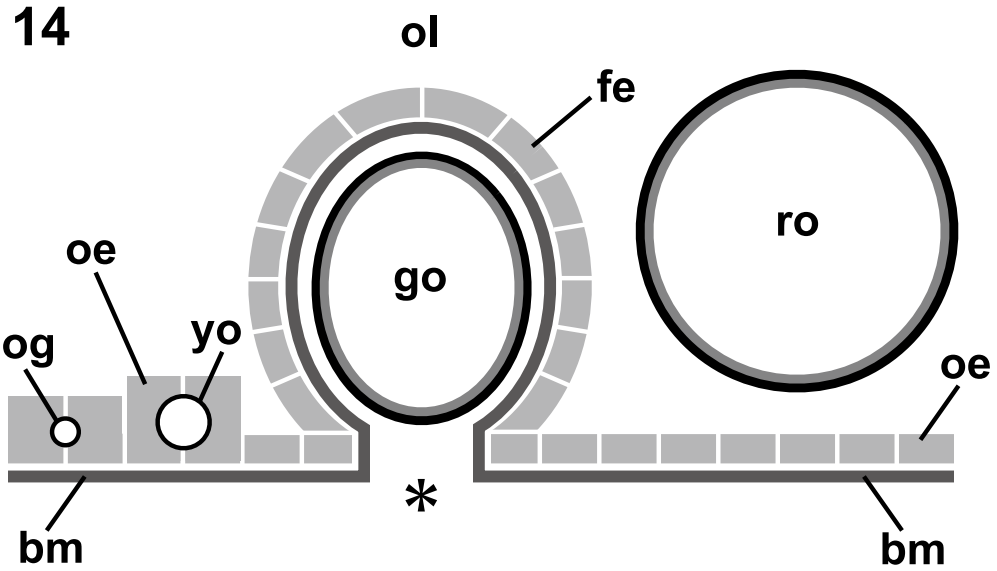


Fig. 14 Schematic drawing of ovarian structure and oogenesis in *Scolopocryptops* centipedes. Oogonia (og) and young oocyte (yo) are surrounded by some cells of ovarian epithelium (oe). Growing oocyte (go) is surrounded by follicle epithelium (fe) and its basement membrane (bm), and thus growing oocyte is located in hemocoelic space (asterisk). Ripe oocyte (ro) is released from its follicular pouch into ovarian lumen (ol).

membrane (Fig. 1A). The hemocoelic position of oocyte growth described in a julid diplopod (Kubrakiewicz, 1991a) and the *Scolopocryptops* centipedes (present study) is completely different from the above mentioned two types. Hence, we now reached a tentative conclusion that another type of ovary can be recognized in arthropods. In this third ovarian type, the myriapod type, oocytes grow within the hemocoelic space of the follicular pouches, though more observations are reqired on the ovarian structures of Symphyla and Pauropoda. If the myriapod type is established, we would propose that the type hitherto known as the mandibulate type should be renamed to the pancrustacean type or the tetraconate type.

Morphological evidence for myriapod monophyly is often described as elusive (Edgecombe, 2010). If oocyte growth in the hemocoelic space of follicular pouches is a shared in the all myriapod groups, it could be a robust morphological support for myriapod monophyly. To ascertain this, future research should be undertaken in order to examine symphylan and pauropodan ovaries.

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