Ovarian Structure and Oogenesis in Chelicerates and Other Arthropods

Toshiki MAKIOKA

Institute of Biological Sciences, University of Tsukuba
Tsukuba, Ibaraki 305, Japan

In chelicerates including xiphosurans and arachnids, many studies have been done on the oogenesis and some related subjects, but their ovarian structures and mode of oogenesis have not yet been scrutinized to the extent allowing a general comparison with those in insects, in which ovaries have already been categorized into three nutritional types (Gross, 1903; Bonhag, 1958). Recently, common characteristics in the chelicerate ovarian structures and oogeneses were preliminarily summarized by the present author (Makioka, 1987) in horseshoe crabs, scorpions, whip-scorpions, spiders, opilions, ticks, and pseudoscorpions. In the present review, a generalized model of the chelicerate ovarian structures and oogeneses is presented with comparison to those in some other arthropods.

1. Ovarian structures and oogeneses in chelicerates

The generalized mature ovary is a simple tube, forming a loop with distal ends of paired oviducts anastomosing each other (Fig. 1). A large number of developing oocytes at late previtellogenic and vitellogenic stages and mature eggs cluster around the ovarian tube. Each oocyte or mature egg is connected with the ovarian wall by a cellular egg-stalk, instead of occurring in the ovarian lumen. Such a looped tubular ovary has no blind terminals as seen in the insect ovarioles.

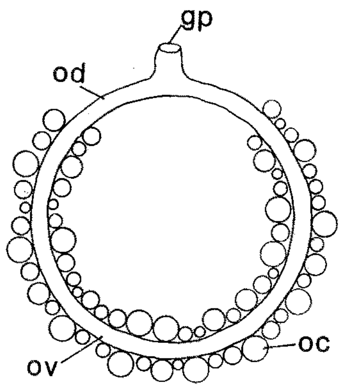

Fig. 1 Generalized model of chelicerate ovary. gp: gonopore, oc: oocyte, od: oviduct, ov: ovary.

Egg cells are first recognized in the ovarian epithelium or the inner layer of ovarian wall, not scattered among the epithelial cells, but localized in the germarium which contains oogonia, early previtellogenic oocytes, and somatic interstitial cells. The younger the egg-cells are, the more centripetally, near the ovarian lumen, they lie in the germarium (Fig. 2).

The oogonium is a small spherical cell with a large nucleus including several dispersed chromatin granules. The oogonia make homogeneous clusters often accompanied with mitotic figures. Various sizes of the early previtellogenic oocytes are characterized with a distinct nucleolus, and interstitial cells having a small eliptic nucleus are scattered among these oocytes and now around the germarium. The interstitial cells develop into the epithelial cells of the ovarian tube and egg-stalks, and in some scorpions and pseudoscorpions they also develop into the follicle cells. The elongated germarium runs along the entire length of the ovary, lying on the ventro-median line of the ovarian tube in many arachnids, but on the dorso-median line in the horseshoe crabs.

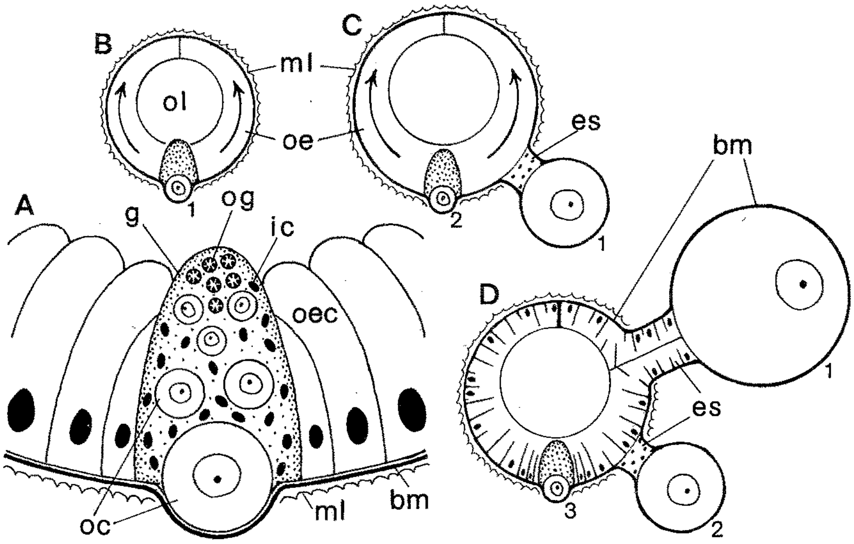

Fig. 2 Cross sections through generalized chelicerate ovary. A. Germarium in ovarian epithelium. B-D. Ovaries with stalked oocytes in order of development. 1-3: Order of developing oocytes protruded from germarium, arrow: direction of stream of ovarian epithelium. bm: basement membrane, es: egg-stalk, g: germarium, ic: interstitial cell, ml: muscle layer, oc: oocyte, oe: ovarian epithelium, oec: ovarian epithelial cell, og: oogonium, ol: ovarian lumen.

The largest oocytes in the most centrifugal region of the germarium migrate outwards, raising the basement membrane of the ovarian epithelium and penetrating the muscle layer or the other layer of the ovarian wall. Some interstitial cells following these oocytes make the egg-stalks. These oocytes sitting on their stalks are protruded out of the ovarian wall to the body cavity, and gradually leave the germarial region with the ovarian epithelial movement by the successive production of new epithelial cells in the germarium (Fig. 2). The oocytes are not surrounded by follicle cells in many chelicerates throughout the oogenetic period. Some scorpions and pseudoscorpions, however, have a thin follicle layer around the growing oocytes. These follicle cells look too rudimentary to have any role in formation of the yolk and the egg-membrane (Vachon, 1938; Makioka, 1979; Makioka and Koike, 1979).

During the rapid vitellogenesis in most chelicerates, the yolk-precursors are taken into the oocytes directly from the haemolymph without any assistance by follicle cells or stalk cells. In some ticks, only previtellogenic oocytes are seen in the ovary before sucking the host blood. The ticks begin to lay eggs within a few days after the blood-sucking. In some whip-scorpions and spiders, the vitellogenesis takes a few weeks (Makioka, unpublished).

The primary egg-membrane is formed around the oocytes during the period from the previtellogenic stage to the end of vitellogenesis. Throughout the vitellogenic period, the yolk precursors are taken into the oocyte through the egg-membrane becoming thicker.

Egg-maturation takes place on the egg-stalks, and mature eggs are ovulated into the ovarian lumen through the cavities of their stalks. The ovulated eggs can migrate for either directions in the ovarian lumen until entering the oviduct.

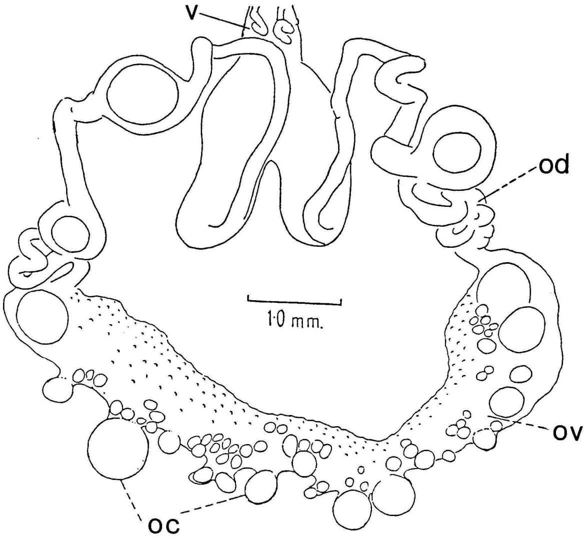

Fig. 3 Female reproductive system of tick, *Ornithodorus* (Leas and Beament, 1948). oc: oocyte, od: oviduct, ov: ovary, v: vagina.

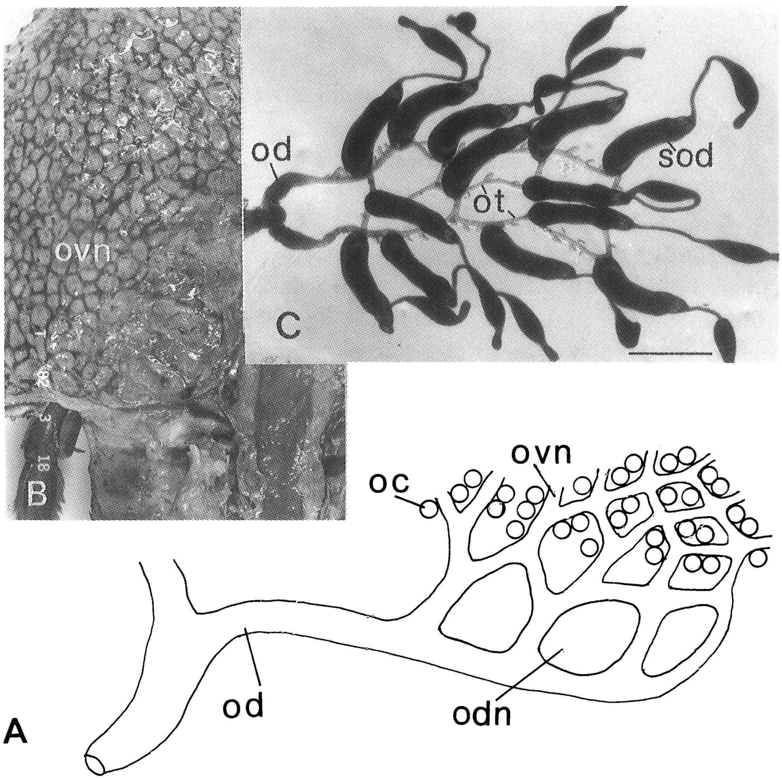

Fig. 4 Female reproductive systems of primitive chelicerates. A. Diagrammatic representation of ovary and oviduct of horseshoe crab. B. A part of fine ovarian network of horseshoe crab, *Tachypleus tridentatus*, after vital staining. C. Rough ovarian network of the viviparous scorpion, *Liocheles australasiae* (Scale: 1mm). oc: oocyte, od: oviduct, odn: oviductal network, ot: ovarian tube, ovn: ovarian network, sod: swollen ovarian diverticulum including embryo. (c: Makioka and Koike, 1985).

In the horseshoe crabs and some scorpions, no germaria have been found in mature ovaries and no oogonia have been observed in the germaria of young adult ovaries (Munson, 1898; Gardiner, 1927; Makioka and Koike, 1979; Makioka and Saito, 1984). Consequently, young oocytes cannot be newly supplied in adult ovaries of these chelicerates. In other chelicerates, such as pseudoscorpions, however, the mature ovaries have the germaria including oogonia (Makioka, 1979).

There are various shapes of ovaries in chelicerate groups, but the simplest ovaries representing the generalized chelicerate ovary are seen in opilions and ticks (Figs. 1 and 3). The complicated ovarian networks in horseshoe crabs and scorpions consist of their reticulated ovarian tubes (Fig. 4). These complicated ovaries can be simplified into the generalized looped ovary mentioned above, because these ovarian tubes have the same structure at any regions of the network and have no terminal portions. In pseudoscorpions and amblypygids, the ovaries are of a single tube which anteriorly divides into two tubules jointed to paired oviducts and posteriorly ends as a blind terminal (Fig. 5). Seemingly it is different from the generalized ovary, but it can be regarded as a loop fused on the median line. The fact that various paired structures are found in a single ovarian tube of the pseudoscorpion (Makioka, 1979) supports this idea. A pair of the ovarian tubes in whipscorions and spiders are also different superficially from the generalized ovary (Fig.6). Anteriorly each ovarian tube of them is connected with the corresponding oviduct and posteriorly it makes a blind terminal. It is easily presumed that these ovarian tubes are originated from a single loop separated along the median line. Each ovarian tube has the same structure at any regions. The germarium is not localized in the posterior terminal, but lies in the ovarian epithelium along the entire length of the ovarian tube.

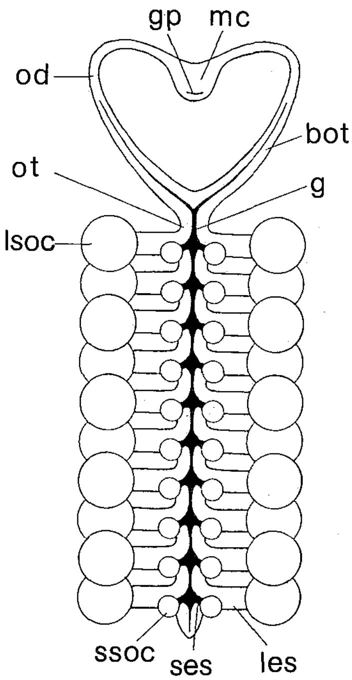

Fig. 5 Diagrammatic representation of single tubular ovary of pseudoscorpion, *Garypus japonicus* (ventral view) (Makioka, 1979). bot: branch of ovarian tube, g: germarium, gp: gonopore, les: large egg-stalk, lsoc: large stalked oocyte, mc: median chamber of oviduct, od: oviduct, ot: ovarian trunk, ses: small egg-stalk, ssoc: small stalked oocyte.

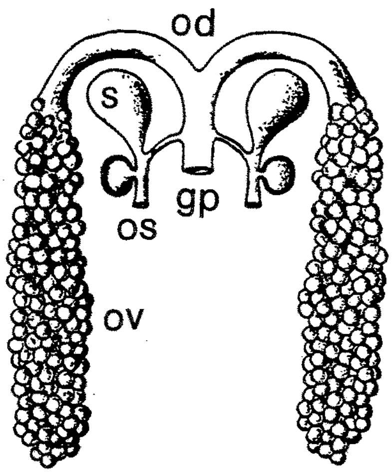

Fig. 6 Diagrammatic representation of paired ovarian tubes of spider (Comstock, 1913). gp: gonopore, od: oviduct, os: opening of spermatheca, ov: ovary, s: spermatheca.

2. Ovarian structure and oogenesis in other arthropods

In most insects except collembolans (Matsuzaki, 1973), each ovariole has a terminal germarium and a long vitellarium in which growing oocytes are arranged in a file in order of size. These oocytes are surrounded by a layer of the follicle cells which help in yolk-formation and finally secrete the chorion, the secondary egg-membrane. Such a type of ovarioles or ovaries is seen among the mandibulates (Fig. 7).

Ovaries in millipedes have often been said to be similar to those in chelicerates, because of their growing oocytes seemingly protruded outwards from the ovarian surface (Osche, 1963; Nair, 1981; Sareen and Adiyodi, 1983). However, a recent study has shown that a long tubular ovary of the milliped, *Spirostreptus*, has a terminal germarium and a long vitellarium filled with many growing oocytes arranged in order of size and accompanied with follicle cells (Nadarajalingam and Subramoniam, 1984) (Fig. 7c). This type of the ovary seems to correspond to an ovariole of insects. Also in centipedes, growing oocytes of *Lithobius* enter the ovarian lumen accompanied with follicle cells (King, 1925; Herbaut and Joly, 1972), but the germarium runs throughout the ovary, not localized in the ovarian terminal.

Crustaceans have various shapes of ovaries (Matthews, 1962; Adiyodi and Subramoniam, 1983), but basically, their ovaries are composed of the tube with one or two terminals, and growing oocytes enter the ovarian lumen. The germarium runs throughout the tubular ovary in the anostracan, *Chilocephalopsis* (Linder, 1959), the cirriped, *Chthamalus* (Iwaki, 1975) and many malacostracans (Fig. 8) (Charniaux-Cotton, 1965; Ryan, 1967; Payen, 1974; Thampy and John, 1974; Zerbib, 1976; Dhas, *et al.*, 1980; *etc.*) or locates in the ovarian terminal in notostracans (Longhurst, 1955), the conchostracan, *Limnadia* (Zaffagnini, 1968), the copepod, *Canthocamptus* (Haecker, 1912), the syncarid, *Bathynella* (Kaestner, 1970), and the isopod, *Armadillidium* (Makioka, unpublished). The ovarian structure of the former type seems similar to that in the chilopods and of the latter to those in the diplopods and insects. In any cases, the ovarian structures or oogenetic modes of the chelicerate type have never been found among mandibulates.

In pycnogonids, the U-shaped ovarian tube in the body trunk has four pairs of branches extending into the walking legs (Sanchez, 1959; King and Jarvis, 1970; Jarvis and King, 1972, 1975, 1978). The germarium runs along the whole length of the ovarian tube and its branches. The growing oocytes do not protrude outwards from the ovarian wall, but enter the ovarian lumen (Miyazaki and Makioka, 1988).

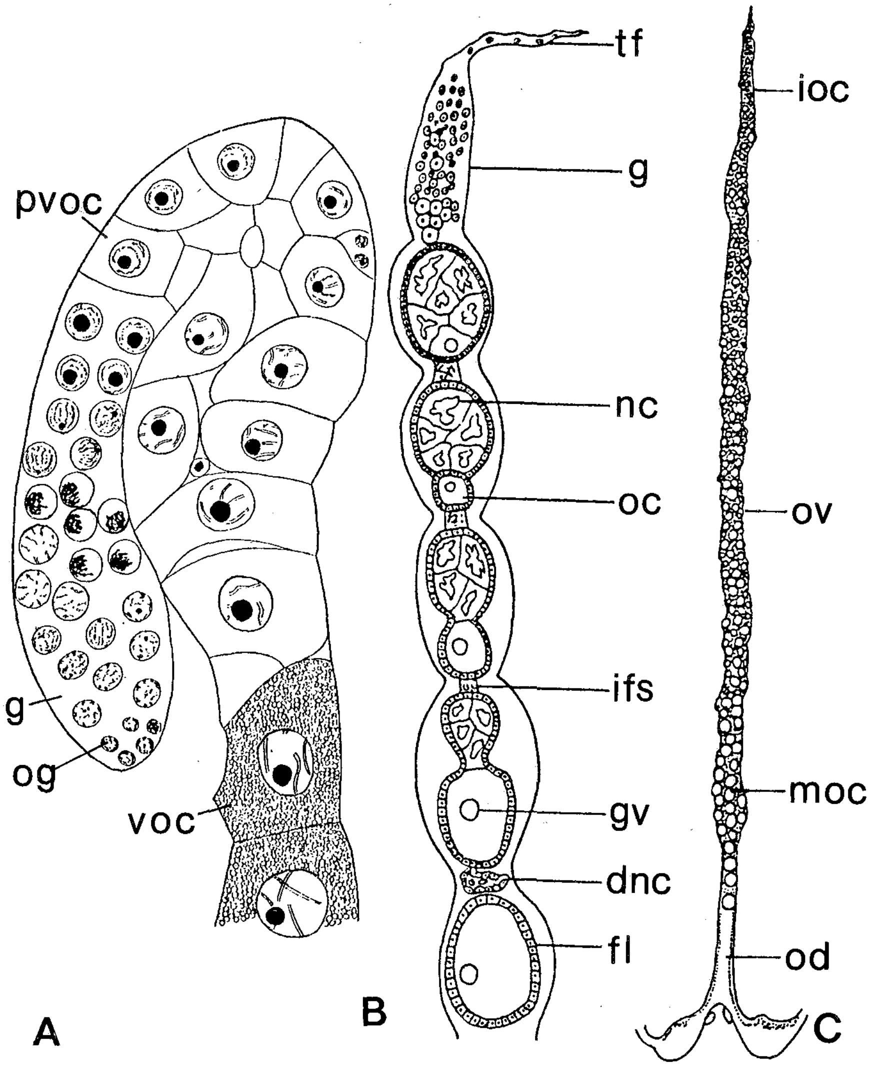

Fig. 7 Ovaries in mandibulates. A. copepod crustacean, *Canthocamptus* (Haecker, 1912). B. Lepidopteran insect, *Philosamia* (Mohanty, 1982). C. Milliped, *Spirostreptus* (Nadarajalingam and Subramoniam, 1984). dnc: degenerated nurse cell, fl: follicle layer, g: germarium, gv: germinal vesicle, ifs: interfollicular stalk, ioc: immature oocyte, moc: mature oocyte, nc: nurse cell, oc: oocyte, od: oviduct, og: oogonium, ov: ovary, pvoc: previtellogenic oocyte, tf: terminal filament, voc: vitellogenic oocyte.

In onychophorans, a single tubular ovary has the growing oocytes, not in the ovarian lumen, but on the surface of the ovarian wall, sitting on their stalks, and mature eggs are ovulated into the ovarian lumen (Matthews, 1962; Herzberg *et al.*, 1980). Follicle cells are not observed around these growing oocytes. The "Follikelzellen" of Herzberg *et al.* (1980) probably correspond to the interstitial cells in chelicerate ovaries. The germarium seems to run throughout the ovary. In the pentastomes also, growing oocytes are protruded outwards from the ovarian surface accompanied with the stalks and with no follicle cells (Fig. 9) (Haffner, 1922; Haffner and Rack, 1971; Nørrevang, 1983; Böckeler, 1984), and mature eggs are ovulated into the ovarian lumen through the stalk cavities. The dorso-median germarium runs along the entire length of the ovary.

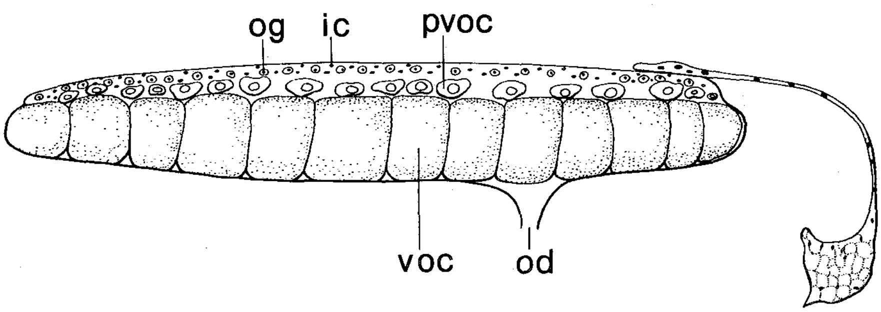

Fig. 8 Longitudinal section of ovarian tube in amphipod crustacean, *Orchestia gammarella* (Charniaux-Cotton, 1965). ic: interstitial cell, od: oviduct, og: oogonium, pvoc: previtellogenic oocyte, voc: vitellogenic oocyte.

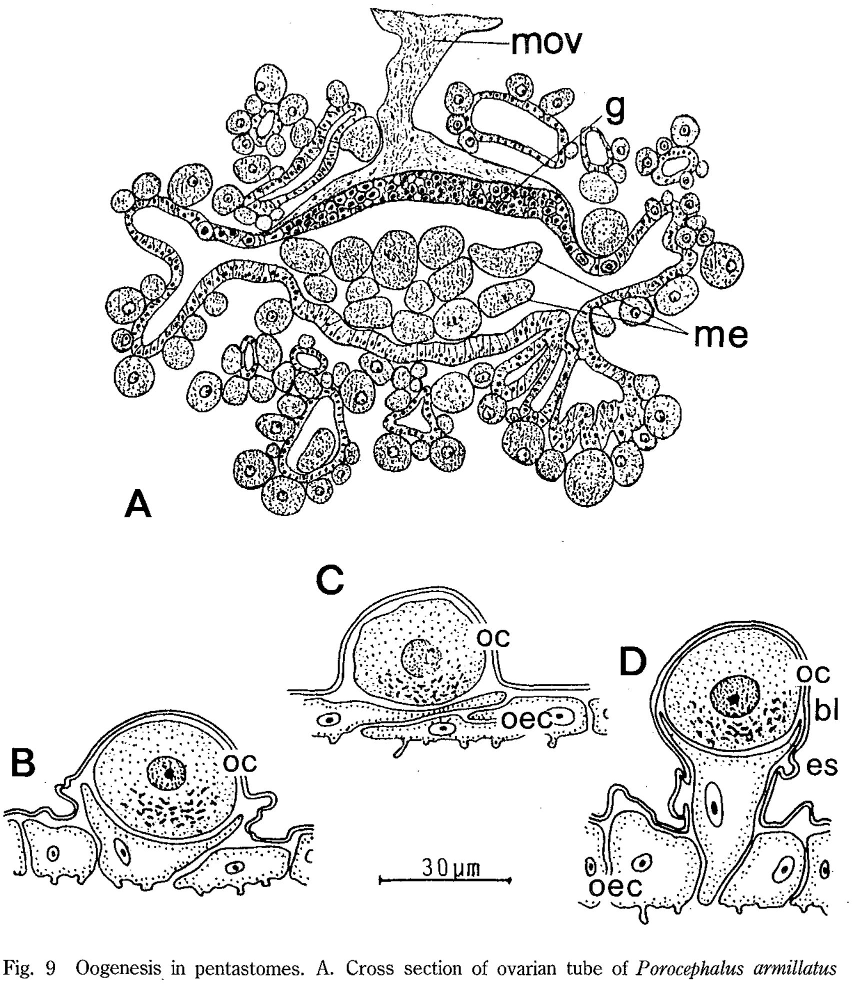

Fig. 9 Oogenesis in pentastomes. A. Cross section of ovarian tube of *Porocephalus armillatus* (Haffner, 1922). B-D. Protrusion of oocyte from ovarian epithelium in *Reighardia sternae* (Böckeler, 1984). bl: basal lamina, es: egg-stalk, g: germarium, me: mature egg, mov: mesovarium, oc: oocyte, oec: ovarian epithelial cell.

3. Conclusions

There are three types of the ovarian structures and oogenetic modes recognized in the arthropods. The first type is seen in almost all insects, the diplopods, and some crustaceans. The germarium of this type is localized at the blind terminal of the ovary or the ovariole, and growing oocytes which are usually surrounded by a follicle-cell layer are in the ovarian or ovariolar lumen (Fig. 10A). The second type is found in almost all chelicerates, some pentastomes, and some onychophorans. In this type the germarium runs throughout the tubular ovary, and growing oocytes not accompanied with functional follicle cells are protruded outwards from the ovarian wall, sitting on their stalks (Fig. 10B). The third type is seen in some pycnogonids, crustaceans, and myriapods. The germarium runs throughout the ovary, and growing oocytes appear in the ovarian lumen (Fig. 10C). Follicle-cell layers surrounding oocytes are in the crustaceans and myriapods, but not in the pycnogonids.

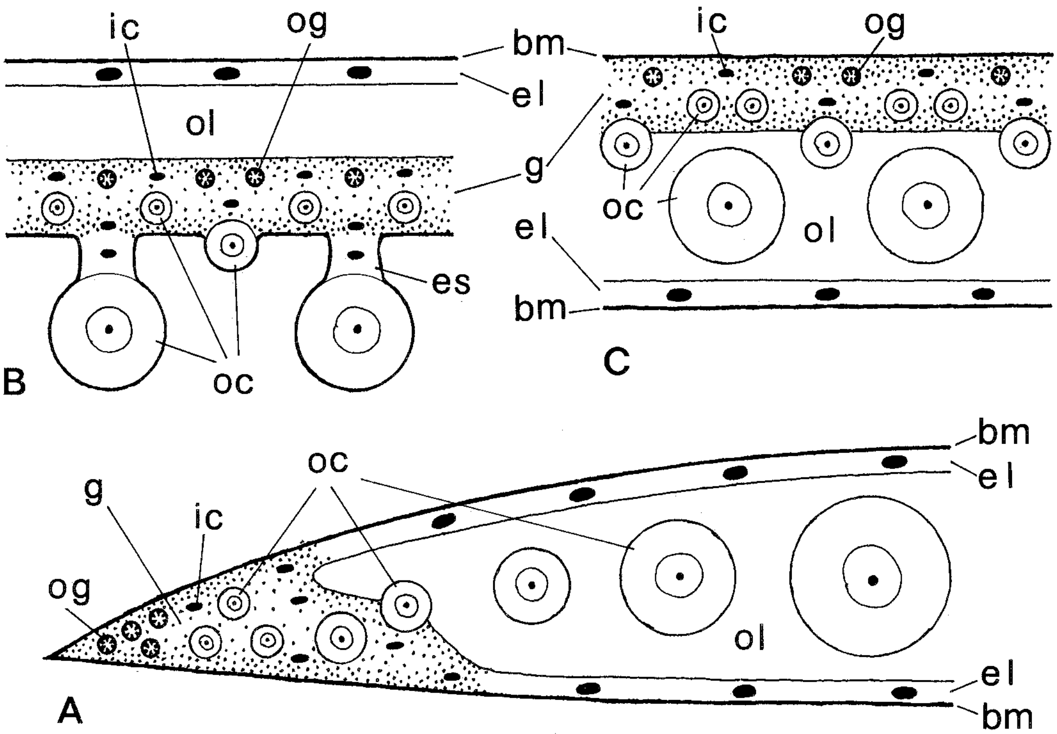

Fig. 10 Diagrammatic representation of three types of arthropod ovaries. A. ovariole of first type. B. Ovarian tube of second type. oc: oocyte, og: oogonium, ol: ovarian lumen. Follicle cells and muscle layers are excluded.

Differences between the first and the second type, especially on the locality of the growing oocytes are decisive. Any intermediate types between the both types have not yet been found among the arthropods. The third type seemingly has some intermediate characteristics such as the growing oocytes occurring in the ovarian lumen as in the first type and the germarium lying throughout the ovary as in the second one. The third one, however, seems basically similar to the first one, not to the second one. The elongated germarium in the third type can easily be modified into the localized germarium in the blind ovariolar or ovarian terminal of the first one, and growing oocytes occur in the ovarian lumen in both types. On the other hand, the elongated germarium running throughout the ovary is common in both, second and third types. The oogonia and early previtellogenic oocytes lie in the germarium in order of size. In the second type, larger egg-cells locate more centrifugally, but in the third, larger egg cells locate more centripetally. This fact is thought as the most fundamental difference between the second and the third type.

Schimkevitch (1906) remarked for the first time the location of the growing oocytes of chelicerates from the phylogenetic viewpoints, and compared it with that of the growing oocytes in some polychaetous annelids in which the oocytes leave the germarium and float in th body cavity. At present, however, the body cavities of polychaetes and of arthropods are considered to be different in origin: the former is the true coelom, and the latter is the secondary haemocoel. In arthropods only the pericardiac space and the lumen of the reproductive system are considered as remnants of the true coelom. If it is certain, the location of the growing oocytes corresponding to that in polychaetes would be found in the first and the third type, not in the second type. For more detailed discussions on the origin and evolution of the ovarian structure and oogenesis of the second type, it seems necessary to study not only development of the gonads and germ cells, but also that of the coeloms.

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