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Structure of the Ovary and Mode of Oogenesis in a Freshwater Crayfish, *Procambarus clarkii* (Girard)

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ABSTRACT—The adult ovary was examined in a freshwater crayfish, *Procambarus clarkii*, to clarify the ovarian structure and the mode of oogenesis. A Y-shaped ovary consisting of a pair of anterior ovarian sacs and a single posterior ovarian sac was located in the cephalothorax, on the dorsal side of the stomach. An oviduct connected each of the posterior ends of the paired anterior ovarian sacs with the genital pore on the coxa of the 6th appendage. The wall of the ovarian sacs, consisting of a layer of the ovarian epithelium, folded inwards to form a number of oogenetic pouches of various sizes. Each oogenetic pouch contained one egg or large oocyte, vitellogenic or previtellogenic, sometimes followed by a few early previtellogenic oocytes in the oogenetic pouch lumen. Germaria containing oogonia, very early previtellogenic oocytes and somatic interstitial cells were located in the ovarian epithelium near the bases of the oogenetic pouches. In a cross-section of the ovarian sac, the germaria were concentrated in the center of the ovarian sac as a central germarial cluster. An early previtellogenic oocyte beginning to grow left its germarium and raised the ovarian epithelium to form a new oogenetic pouch, in which it remained until mature. Mature eggs were ovulated from the oogenetic pouches into the central ovarian lumen, transferred into the oviducts, and oviposited through the genital pores. The female reproductive system was surrounded wholly and tightly by a thin muscular sheath, which has often been mistaken as the ovarian epithelium in some decapod crustaceans.

INTRODUCTION

Two structural and functional types of ovaries corresponding to the two major arthropod taxa, the Chelicerata and the Mandibulata, were distinguished by Makioka (1988) based on various descriptions of arthropod ovaries.

One type is found in most chelicerates (the chelicerate type), the network- or loop-shaped tubular ovary has both ends as exits to the oviducts and no terminal portion. A long germarium runs in the ovarian epithelium through the whole length of the ovary. In the germarium, the oogonia are located in the region near the ovarian lumen, whereas the earliest oocytes are found in the region near the ovarian surface. The oocytes then leave the germarium, not to the ovarian lumen, but to ride on the outer surface of the ovarian epithelium. They grow there, sandwiched between the ovarian epithelium and its basement membrane during the oogenetic period, then the mature eggs are ovulated into the ovarian lumen through the ovarian epithelium.

The other type of ovary is found in many mandibulates (the mandibulate type). In general, the sac-like ovary has a terminal germarium and an exit to the oviduct. In the germarium, the oogonia are located far from the ovarian lumen, and the earliest oocytes are found in the region near the ovarian lumen. The oocytes then leave the germarium to enter the ovarian lumen, in which they grow during the oogenetic period.

This differentiation has been confirmed in some other arthropod groups, such as the Pycnogonida (Miyazaki and Makioka, 1990, 1991, 1992a, b), the Diplopoda (Yahata and Makioka, 1991, 1994, 1995, 1997), the Branchiopoda (Ando and Makioka, 1992), and the Branchiura (Ikuta and Makioka, 1995, 1996, 1997a, b). However, in decapod crustaceans, one of the major mandibulate groups, the ovaries have not been described from the viewpoint that they are of the mandibulate type or the chelicerate type.

There have been many studies on the ovary of the decapod crustaceans, but most have concentrated on the oocyte growth (Hard, 1942; Ryan, 1967; Talbot, 1981; Cau *et al*., 1988; Yano, 1988; Lee *et al*., 1994), in particular the vitellogenesis (Kessel, 1968; Hinsch and Cone, 1969; Yano and Chinzei, 1987; Minagawa *et al*., 1993; Chang and Shih, 1995), the ovarian muscle physiology (Howard and Talbot, 1992), the maturation of the ovary (Cuzin-Roudy and Amsler, 1991), and seasonal changes in the ovarian activity (Hanaoka and Otsu, 1957; Chiba and Honma, 1972; O'Donovan *et al*., 1984; Meusy and Payen, 1988), rather than upon the basic struc-

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ture of the ovary. One reason may be that the phylogenetic implications of the basic ovarian structure have been accounted of little importance in the decapod crustaceans and another reason may be the structural complication of decapod ovaries.

Most studies have been made in large marine decapods with large and extremely complicated ovaries producing a great number of eggs for a spawning (Ryan, 1967; Eurenius, 1973; Talbot, 1981; Adiyodi and Subramoniam, 1983; Cau *et al*., 1988; Minagawa *et al*., 1993). Such large and complicated ovaries with numerous oocytes and yolky eggs pose difficulties to histological analysis and prevent exact understanding of the basic structure of the ovary and mode of oogenesis. Therefore, it is not easy to compare the structural and functional features of decapod ovaries with those of other crustaceans and arthropods.

In the present study, we used a freshwater crayfish, *Procambarus clarkii*, which produces large eggs but of small quantity in a single spawning. This species was expected to have an ovary simple in structure and therefore suitable for allowing an understanding of its basic structure and oogenetic mode.

MATERIALS AND METHODS

Adult females of *Procambarus clarkii* were collected from ponds on the campus of the University of Tsukuba in Ibaraki, Japan, from May to July, 1995. The specimens, ranging from 7 to 12 cm from head to telson, were kept in the laboratory at room temperature, and the ovaries were excised at various oogenetic stages before and after oviposition. The female reproductive system was removed from each specimen and fixed with Bouin's solution, dehydrated in a graded ethanol-n-butanol series, and embedded in paraffin. Serial sections 6 to 10 μm thick were stained either with Mayer's hematoxylin and eosin (H-E) or with periodic acid-Schiff and Mayer's hematoxylin (PAS-H).

RESULTS

Structure of the female reproductive system

A Y-shaped ovary consisting of a pair of anterior ovarian sacs and a single median posterior ovarian sac (Fig. 1) was located in the cephalothorax, on the dorsal side of the stomach. Just before oviposition, the ovary included several hundred mature eggs of fully grown, dark violet oocytes about 1.8 mm in diameter. The maximum length of the ovary was about 4 cm and the maximum width of the ovarian sac was about 5

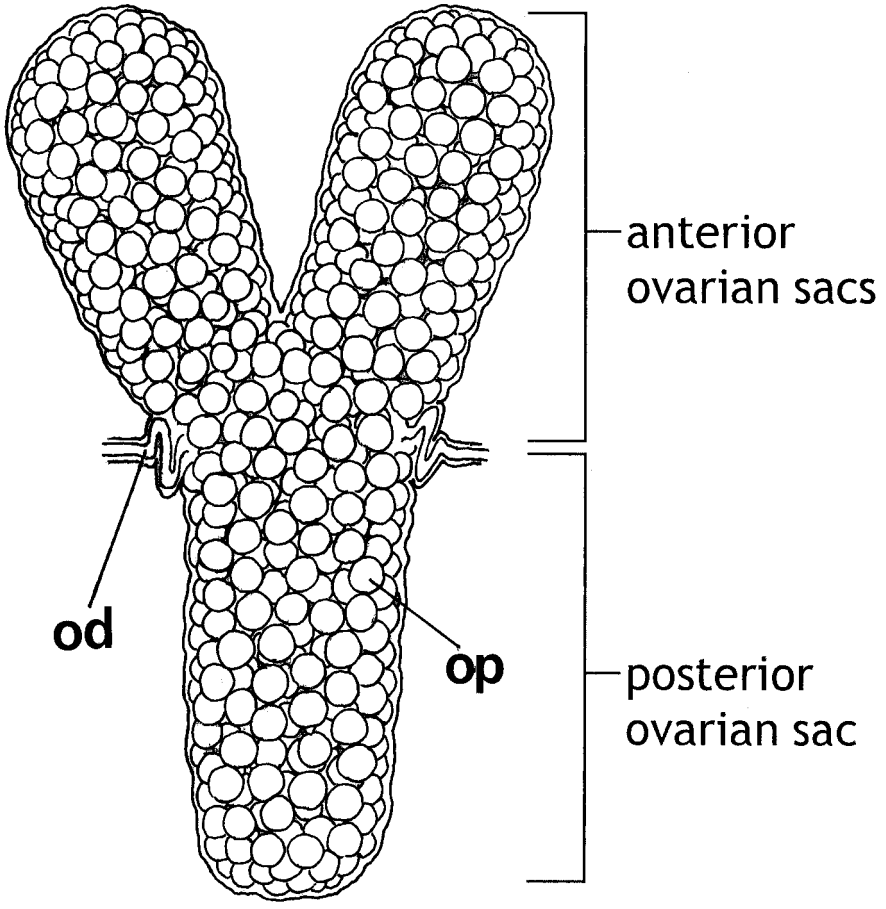

Fig. 1. Schematic drawing of a dorsal view of the female reproductive system of *Procambarus clarkii*. A Y-shaped ovary consisting of a pair of anterior ovarian sacs and a single posterior ovarian sac. A number of oogenetic pouches containing a single egg or oocyte constitute the ovarian sac surfaces. A short oviduct is connected with the posterior end of each anterior ovarian sac. od, oviduct; op, oogenetic pouch.

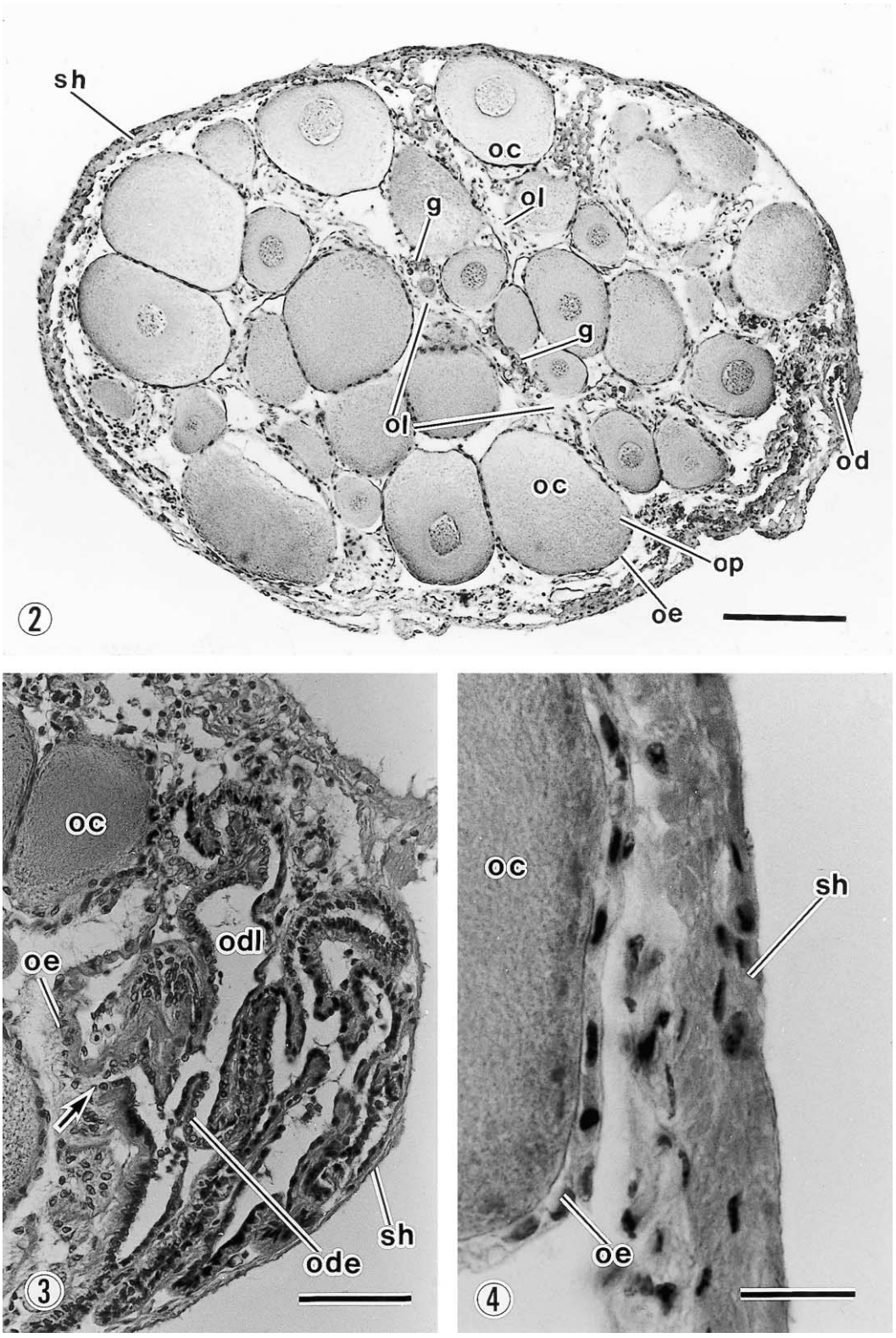

Fig. 2. Cross-section of a young ovarian sac. A thin muscular sheath surrounds the ovarian sac surface. Each oocyte is surrounded by a serial ovarian epithelium extended to form oogenetic pouches. Two germaria are seen in the ovarian epithelium near the center of the ovarian sac. PAS-hematoxylin (PAS-H) staining. Scale bar, 150 μm.

Fig. 3. Irregular cork screwed oviduct. Oviductal epithelium connecting to the ovarian epithelium (arrow). PAS-H staining. Scale bar, 50 μm.

Fig. 4. Outermost muscular sheath of the ovary, covering the oogenetic pouch. Hematoxylin and eosin staining. Scale bar, 30 μm. g, germarium; oc, previtellogenic oocyte; od, oviduct; ode, oviductal epithelium; odl, oviductal lumen; oe, ovarian epithelium; ol, central lumen of ovarian sac; op, oogenetic pouch; sh, outermost muscular sheath of the ovary.

mm. Just after oviposition, the ovary contained only white oocytes (previtellogenic and early vitellogenic) less than 1 mm in diameter, and was about 3 cm long, and the ovarian sac was 2 to 3 mm wide. Other adult ovaries of intermediate size contained yellow to dark orange oocytes, 1.0 to 1.4 mm in diameter. The size of the ovary depended not only on the body size of the crayfish, but also on the sizes of the oocytes or eggs within the ovary.

From each base of the paired anterior ovarian sacs, a narrow oviduct protruded laterally. It first cork screwed irregularly near the ovarian sac, and then ran straight to the genital pore on the coxa of the 6th appendage. No distinct seminal receptacles were present throughout the oviduct (Figs. 1 and 3).

The female reproductive system, composed of the ovary and the oviducts, was tightly surrounded by a thin muscular sheath about 30 μm thick (Figs. 2 and 4). When the sheath was removed from the surface of the ovarian sacs in physiological saline, a number of oogenetic pouches or swellings of the ovarian sac walls, including mature eggs or large oocytes, rose up on the ovarian sacs, and the width of the ovarian sacs apparently increased.

Internal structure of the ovary

Oogenetic pouch

The wall of the ovary consisted of a single layer of thin epithelium 5 to 12 μm thick. The epithelium of the ovarian sacs bulged at irregular intervals to form a number of oogenetic pouches of various sizes containing eggs or oocytes (Figs. 2, 5-7). The epithelium in the distal portions of the oogenetic pouches containing eggs or large oocytes was stretched to a thickness of about 5 μm, the epithelial cells contained flat nuclei about 4 × 9 μm. On the other hand, the epithelium at the basal portions or the portions between the pouches was about 10 to 12 μm thick and had nuclei about 8 μm in diameter.

A number of oogenetic pouches stood side by side around the narrow central lumen of the ovarian sacs. Each oogenetic pouch contained one egg (about 1.8 mm in diameter) or a vitellogenic or previtellogenic oocyte larger than 150 μm in diameter in its lumen. The size of the oogenetic pouch depended upon the size of the egg or the oocyte contained in it. In the ripe ovary, no oogenetic gradation was seen throughout the ovarian sacs. In the young ovary or adult ovary just after oviposition, there were many young oogenetic pouches

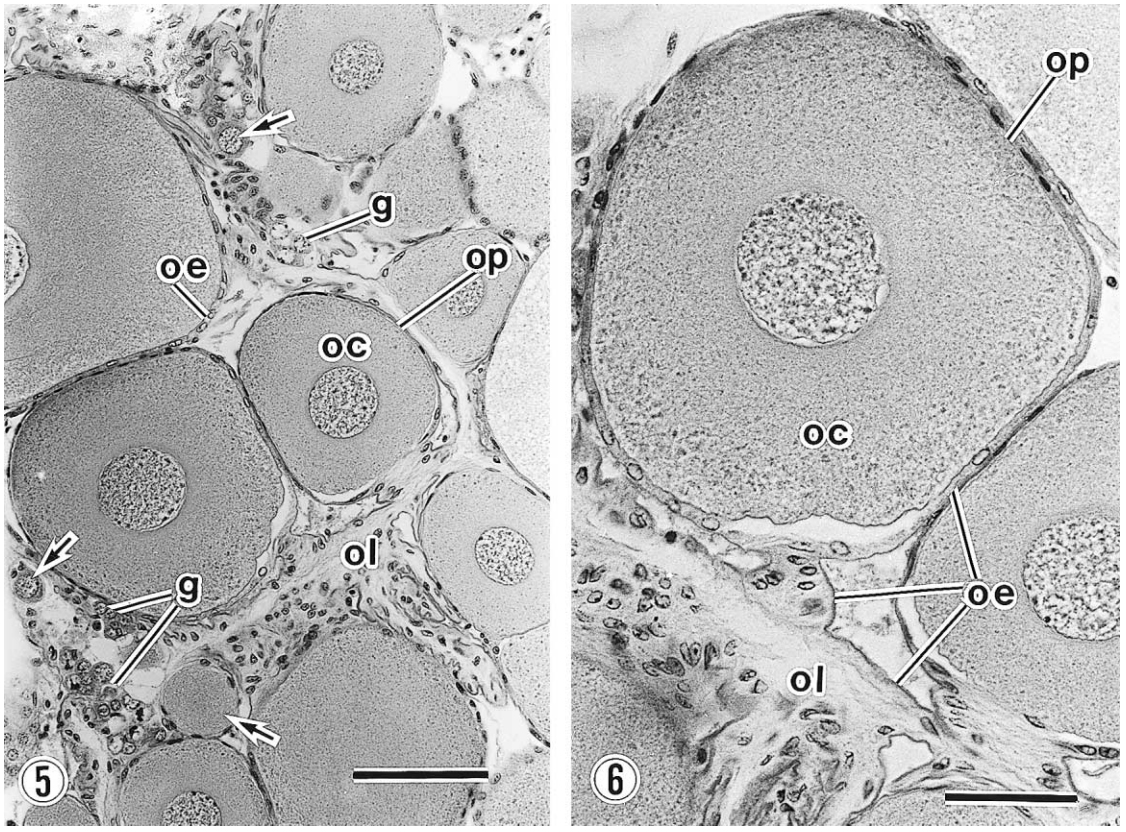

Fig. 5. Oogenetic pouches containing a single oocyte and surrounding central lumen of the ovarian sac. A few very early previtellogenic oocytes (arrows) without their oogenetic pouches are attached to the ovarian epithelium near the germaria and near the bases of other oogenetic pouches. PAS-H staining. Scale bar, 100 μm.

Fig. 6. A large previtellogenic oocyte surrounded by the ovarian epithelium constituting its own oogenetic pouch and continuing with the adjacent one. PAS-H staining. Scale bar, 50 μm. g, germarium; oc, previtellogenic oocyte; oe, ovarian epithelium; ol, central lumen of ovarian sac; op, oogenetic pouch.

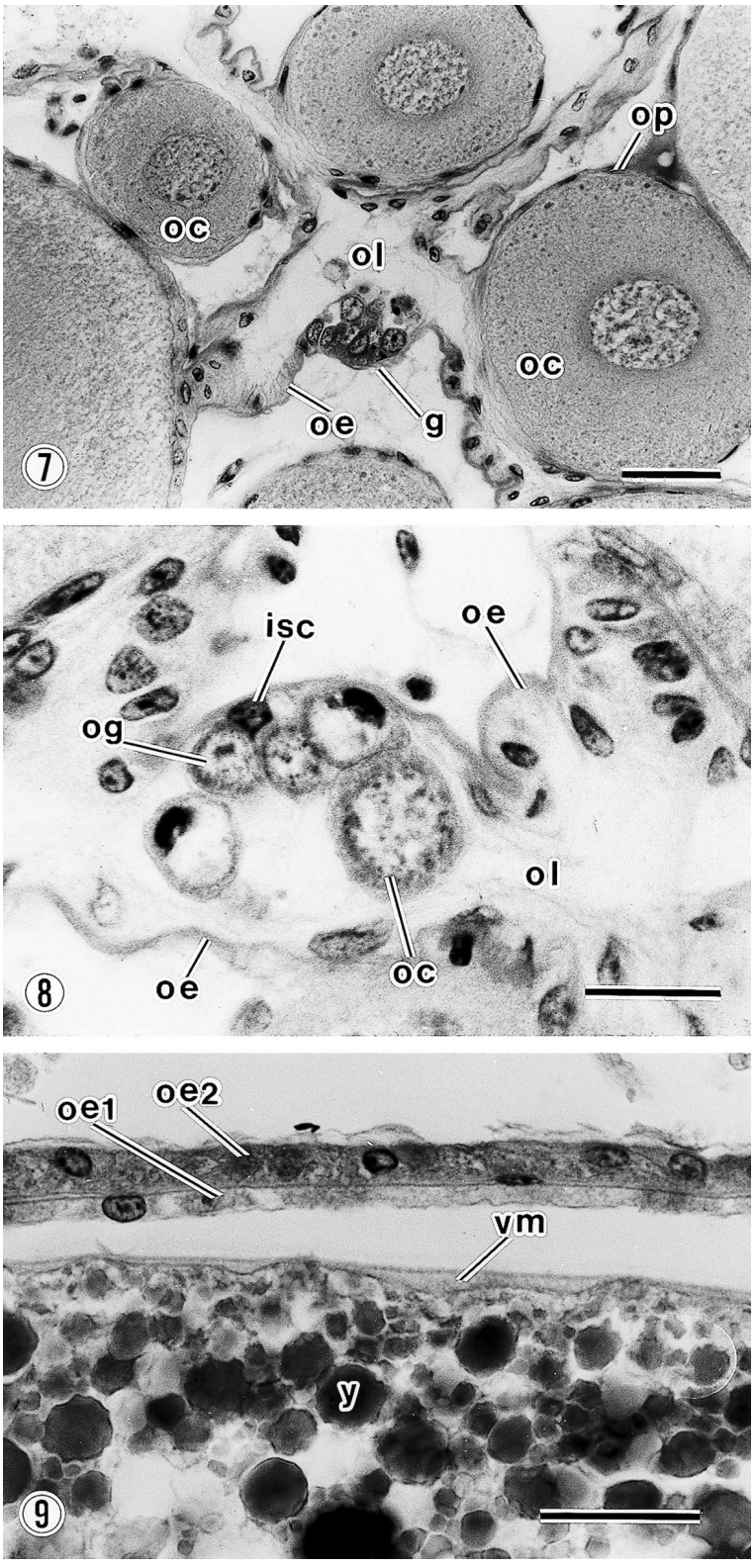

Fig. 7. Germarium in the ovarian epithelium near the oogenetic pouch. A few early previtellogenic oocytes without their own oogenetic pouches are attached to the ovarian epithelium near the germarium. PAS-H staining. Scale bar, 50 μm.
Fig. 8. Oogonia, very early previtellogenic oocytes and interstitial cells in a germarium. PAS-H staining. Scale bar, 30 μm.
Fig. 9. Periphery of a late vitellogenic oocyte in the oogenetic pouch. A thin vitelline membrane is seen on the surface of the periplasm. PAS-H staining. Scale bar, 30 μm. g, germarium; isc, interstitial cell; oc, previtellogenic oocyte; oe, ovarian epithelium; oe1, ovarian epithelium of the present oogenetic pouch; oe2, ovarian epithelium of a neighboring oogenetic pouch; og, oogonium; ol, central lumen of ovarian sac; op, oogenetic pouch; vm, vitelline membrane; y, yolk granule.

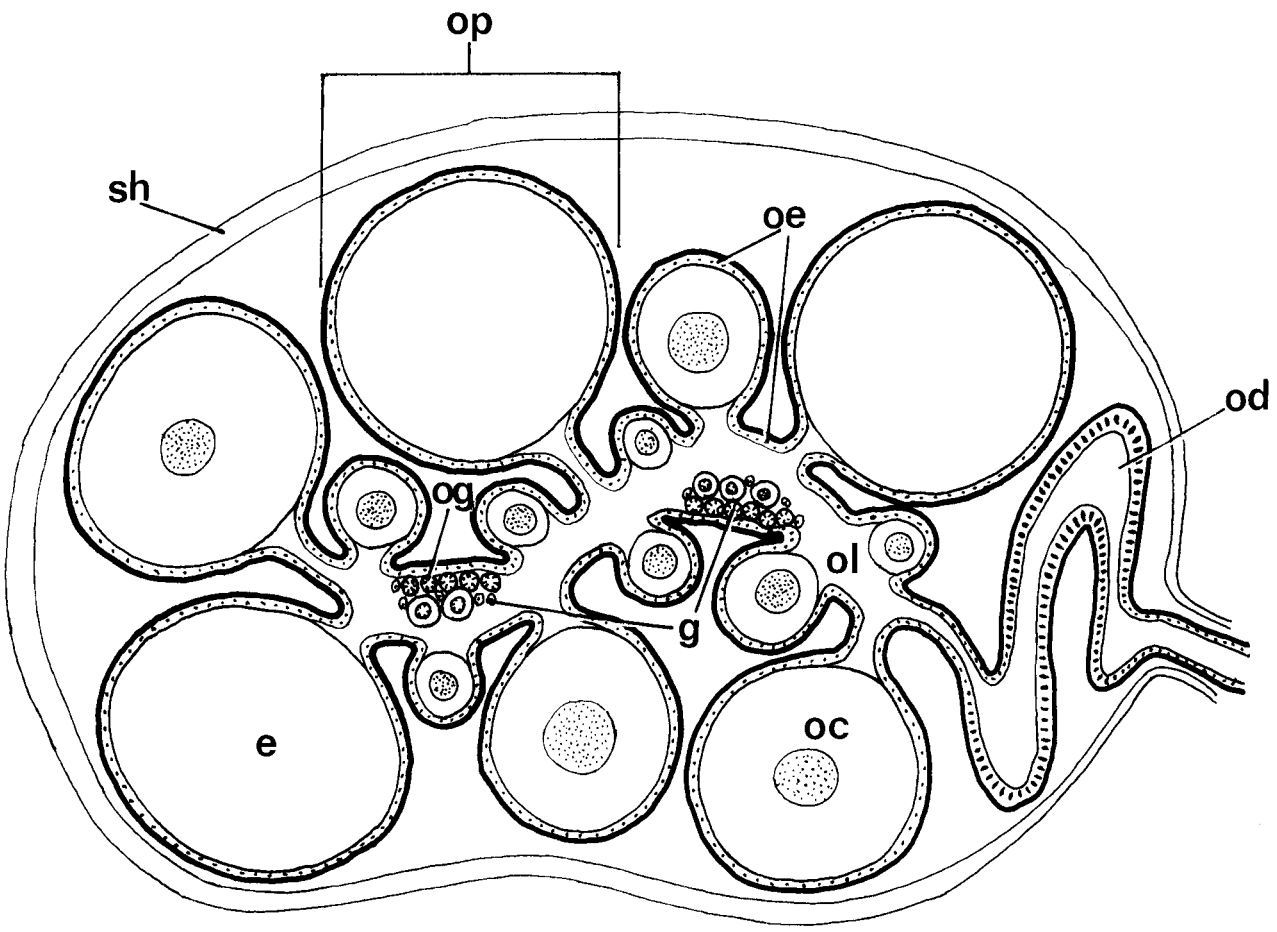

Fig. 10. Schematic drawing of a cross-section of an anterior ovarian sac of *P. clarkii*. Ovarian sac and oviduct are surrounded by the outermost muscular sheath. Eggs and large oocytes are enclosed in their own oogenetic pouches, but younger oocytes are imperfectly enclosed. Two germaria are in the ovarian epithelium near the center of the ovarian sac. Ovarian epithelium as a serial sheet (constituting the ovarian wall) is connected with the oviductal epithelium. e, egg; g, germarium; oc, previtellogenic oocyte; od, oviduct; oe, ovarian epithelium; og, oogonium; ol, central lumen of ovarian sac; op, oogenetic pouch; sh, outermost muscular sheath of ovary.

containing young white oocytes less than 150 μm in diameter throughout the ovarian sacs (Fig. 2).

In the well developed oogenetic pouches, the ovarian epithelium tightly surrounding the eggs or oocytes occasionally resembled follicle epithelia. The ovarian epithelium traced in the serial sections was a continuous epithelial sheet, repeating evagination and invagination in a number of oogenetic pouches and connecting with the oviductal epithelium at the bases of the anterior ovarian sacs (Figs. 2 and 3).

Germarium

Germaria, special germ areas of the ovarian epithelium, were located separately at the bases of well developed oogenetic pouches throughout the ovary. Oogonia, very early previtellogenic oocytes, and young somatic interstitial cells were localized in the germaria. An average size germarium contained ten or more oogonia, several very early previtellogenic oocytes, and several tens of interstitial cells (Figs. 7 and 8). In cross sections of the ovarian sac, the germaria located at the bases of the oogenetic pouches were arranged radially around an extremely narrow central ovarian lumen, and were seemingly concentrated into a central germarial cluster (Figs. 2 and 10).

Oogenesis

Oogonia and very early previtellogenic oocytes less than 30 μm in diameter were found only in the germarium. The oogonia, 12 to 14 μm in diameter, included a large nucleus with some chromatin granules specifically agglutinated and without a nucleolus. The oocytes in the germarium included a large germinal vesicle with a single nucleolus and some leptonemas. The weak basophilic ooplasm included neither yolk granules nor oil drops. In the germarium, the oogonia were arranged peripherally, far from the central lumen of the ovarian sac, and the oocytes were nearer to the lumen. The nuclei of the interstitial cells about 5 μm, in diameter were scattered among the oocytes (Fig. 8).

Early previtellogenic oocytes 30 to 50 μm in diameter did not remain in the germarium, but were attached to the inner surface of the ovarian epithelium near the germaria. They were not yet enclosed by the oogenetic pouches, but they had begun to raise the ovarian epithelium outward to form their own

oogenetic pouches (Figs. 2, 5 and 6). Oocytes larger than 50 μm in diameter were found in their own oogenetic pouches (Figs. 2, 5 and 6). A number of small oil drops occurred in the ooplasm around the germinal vesicles of the largest previtellogenic oocytes which were about 300 μm in diameter. The cytoplasm stained weakly with hematoxylin, and very short irregular shaped nucleoli were seen mainly in the periphery of the germinal vesicle (Fig. 6). Subsequently, fine yolk granules stained with eosin or PAS appeared first in the periplasm of oocytes about 500 μm in diameter. The yolk granules increased in size, up to about 80 μm in diameter, and in number eventually filling the ooplasm (Fig. 9). A thin egg membrane appeared first around the vitellogenic oocyte of about 1.4 mm in diameter. The membrane thickened up to 3 to 5 μm in the fully grown vitellogenic oocytes or the mature eggs (Fig. 9). No follicles were formed around the oocytes throughout oogenesis, indicating that the egg membrane was not the chorion but the vitelline membrane (Fig. 9).

Maturation divisions should take place in the fully grown oocytes in the oogenetic pouches, because mature eggs with small egg nuclei were present in the largest oogenetic pouches. Neither mature eggs nor growing oocytes were found in the central lumen of each ovarian sac, suggesting that mature eggs should be ovulated simultaneously from their oogenetic pouches and immediately transferred into the oviduct through the central lumen of the ovarian sac after spawning.

DISCUSSION

In some decapod species, including *P. clarkii*, the ovary is a long sac-like organ, and a thin "ovarian wall" or the outermost cellular layer of the ovary surrounds the oocytes and eggs, of which most have their own "follicle epithelia" or "follicle cells" (Carayon, 1941; Suko, 1954; Ryan, 1967; O'Donovan *et al*., 1984; Papathanassiou and King, 1984; Yano and Chinzei, 1987; Meusy and Payen, 1988; Cuzin-Roudy and Amsler, 1991; Kulkarni *et al*., 1992; Chang and Shih, 1995; Courtney *et al*., 1995). In these ovaries, the germaria, including oogonia and very early previtellogenic oocytes, are often concentrated into a central germarial cluster in the ovarian lumen, not bound to the ovarian epithelium (Ryan, 1967; Kon and Honma, 1970; Chiba and Honma, 1972; Eurenius, 1973; Haefner, 1977; Dhas *et al*., 1980; Minagawa *et al*.,1993). Such structural features of the decapod ovary, however, are unusual among the crustaceans and other arthropods, making the structural and phylogenetic relationships of the ovaries unclear. In most arthropods, including crustaceans, the germarium produces not only germ cells but also somatic cells, in particular ovarian epithelial cells, and therefore, the germarium is usually bound to the ovarian epithelium, not isolated from it.

In the present study, cross-sections of the ovarian sacs of *P. clarkii* showed the germaria were localized independently in the ovarian epithelium at the bases of the oogenetic pouches and appeared to be concentrated into a central germarial cluster. This central germarial cluster may correspond to those described in some other decapods as floating in the center of the ovarian lumen (Ryan, 1967; Kon and Honma, 1970; Chiba and Honma, 1972; Eurenius, 1973; Haefner, 1977; Dhas *et al*., 1980; Adiyodi and Subramoniam, 1983; Minagawa *et al*., 1993). In some other decapod ovaries, the outermost cellular sheath has been reported as the ovarian epithelium and the true ovarian epithelium of the oogenetic pouches as the follicle epithelium (King, 1948; Ryan, 1967; Cau *et al*., 1988; Howard and Talbot, 1992). In those decapod ovaries, the central germarial cluster had to float in the ovarian lumen because the germaria could not be included in the follicle epithelium. In disagreement with earlier reports, results of the present study establish that the ovarian epithelium resembled the follicle epithelium was a serial sheet, and connected with the oviductal epithelium, and the germarium did not float in the ovarian lumen but located in the infolded ovarian epithelium. One of the most important differences between the chelicerate type and the mandibulate type is the location of the growing oocytes. In the chelicerate type, growing oocytes protrude to the haemocoel but are not in the ovarian lumen, whereas in the mandibulate type, the oocytes never get outside the ovarian lumen surrounded by the ovarian epithelium. Therefore, it is important identify the true ovarian epithelium in order to clarify the structure of the ovary in *P. clarkii*.

In the *P. clarkii* ovary, examined in the present study, the outermost layer of the ovary was a thin muscular sheath. It surrounded not only the ovary but also the oviducts, showing itself to be, not as the ovarian epithelium, but as the outer sheath of the female reproductive system. Such a muscular sheath has been found in some lobsters and crabs, and interpreted as the ovarian wall or the ovarian epithelium (Kessel, 1968; Talbot, 1981; Howard and Talbot, 1992; Minagawa *et al*., 1993). In the present specimens, the ovarian epithelium lay just under the sheath and folded deeply and repeatedly to form a number of oogenetic pouches containing the growing oocytes or mature eggs. The ovarian epithelium constituting the walls of the oogenetic pouches partly surrounded the oocytes or mature eggs and sometimes looked like their follicles, although the oocytes and eggs had no real follicles. The oogenetic pouches in *P. clarkii* may correspond to the "germinal nest" in *Ranina ranina* (Minagawa *et al*., 1993) or the "sac-like structure" in *Portunus sanguiolentus* (Ryan, 1967).

The oogenesis in *P. clarkii* is of the mandibulate type. The oocytes grow only in their own oogenetic pouches, the lumens of which are branches of the central ovarian lumen (Fig. 10). Mature eggs should be ovulated from the oogenetic pouches into the central ovarian lumen, transferred into the oviduct and oviposited from the female gonopore. Fertilization may take place in the oviducts, in particular in the irregular cork screw region near the ovary, which possibly plays a role as the seminal receptacle. The epithelial cells of this region were tall and stained strongly with hematoxylin, closely resembling the epithelial cells of the seminal receptacle in a freshwater crab, *Potamon dehaani* (Ando and Makioka, 1998).

P. clarkii, laying a small number of large eggs in a spawn-

ing, has an ovary simpler in structure than that of many other decapods laying a great number of small eggs. This simple ovary has some distinct mandibulate type features, such as the oocytes growing in the ovarian lumen in the oogenetic pouches. The *P. clarkii* oogenetic pouch, containing a single oocyte or mature egg, is a simple structure suitable for investigation of the basic structure of the ovary. The present findings may contribute to discussions on the basic ovarian structure and functions in other decapod ovaries.

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