

The *Oikopleura* coenocyst, a unique chordate germ cell permitting rapid, extensive modulation of oocyte production

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Abstract

The ability to adjust reproductive output to environmental conditions is important to the fitness of a species. The semelparous, chordate, *Oikopleura dioica*, is particularly adept in producing a highly variable number of oocytes in its short life cycle. Here we show that this entails an original reproductive strategy in which the entire female germline is contained in a single multinucleate cell, the “coenocyst”. After an initial phase of syncytial nuclear proliferation half of the nuclei entered meiosis whereas the other half became highly polyploid. The inner F-actin network, with associated plasma membranes, formed a highly ramified infrastructure in which each meiotic nucleus was contained in a pseudo-compartmentalized pro-oocyte linked to the common cytoplasm via ring canals. At a set developmental time, a subset of the pro-oocytes was selected for synchronous growth and the common coenocyst cytoplasm was equally partitioned by transfer through the ring canals. Examination of related species indicated that the coenocyst arrangement is a conserved feature of Appendicularian oogenesis allowing efficient numerical adjustment of oocyte production. As Appendicularia are the second most abundant class of zooplankton, with a world-wide distribution, the coenocyst is clearly a common and successful reproductive strategy on a global scale.

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Introduction

Oogenesis begins with a founder germ cell, or cystoblast, undergoing incomplete divisions to form interconnected germ cells referred to as the germline cyst (Pepling et al., 1999). In vertebrates, cysts appear as clusters of germ cells, also called nests. They can be visualized within the ovary as groups of adjacent cells staining positively for the germ-line specific marker *Vasa* (Pepling and Spradling, 2001). Intercellular bridges between cyst cells appear as electron dense regions of the plasma membrane bordering the common interconnecting cytoplasm. In *Drosophila*, these bridges are called ring canals (RC), and are formed in part by F-actin (Pepling et al., 1999; Robinson and Cooley, 1997). Although intercellular bridges have not been recognized in all species, a cyst phase is thought to occur in most metazoans, though its conserved evolutionary function is not understood. The number of interconnected germ cells is variable:

8–32 in mouse, 16 in *Xenopus* and *Drosophila* (Kloc et al., 2004; Matova and Cooley, 2001; Pepling and Spradling, 2001), and much higher in *Caenorabditis elegans* where all nuclei entering meiosis are connected to a common central rachis as part of a unique cyst (Church et al., 1995; Gumienny et al., 1999). Meiosis initiates in the cyst phase but persistence of the cyst with respect to the progression of meiotic events is variable. Cyst breakdown, leading to full cellularization of oocytes, usually occurs early in prophase I, after pachytene in mouse, frog and the nematode, and precedes the vitellogenic phase (Church et al., 1995; Gumienny et al., 1999; Kloc et al., 2004; Pepling and Spradling, 2001). However, the cyst phase in *Drosophila* persists right through to metaphase I arrest of the oocyte, a configuration that is thus far unique in evolution to higher insects (Matova and Cooley, 2001).

The *Drosophila* ovary is composed of 15–20 parallel ovarioles containing progressively maturing egg chambers (King, 1970; Robinson and Cooley, 1997; Spradling, 1993). Each egg chamber contains the growing oocyte and 15 nurse cells, all interconnected by RC. The polyploid nurse nuclei produce most of the cytoplasmic constituents which are

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transported to the oocyte via the RC. Towards the end of vitellogenesis, the syncytial cytoskeleton reorganizes to effect a rapid dumping of cytoplasm from the nurse cells, through the RC, into the oocyte. In mouse and *C. elegans*, a portion of the nuclei composing the cyst enter apoptosis during cyst breakdown, with the majority of their associated cytoplasm transferred to the surviving oocytes (Gumienny et al., 1999; Pepling and Spradling, 2001). This has led to the view that apoptotic germ cells within a cyst play an accessory role in oogenesis. However, in *Xenopus*, all germ cells of the cyst form oocytes (Kloc et al., 2004).

In the present study, we identify a novel oogenic strategy in the Appendicularian, *Oikopleura dioica*, which differs radically from that described in the sister class ascidians and is surprising in a chordate organism. *O. dioica* can be maintained in laboratory

culture and is gaining interest as a model organism because of its phylogenetic position within the closest sister group to vertebrates (Delsuc et al., 2006), its very short life cycle (6.5 days at 15°C) throughout which it remains transparent and its compact 70 Mb genome (Seo et al., 2001). The germline, of unknown origin, becomes apparent at the trunk-tail junction after metamorphosis and increases in size throughout the remainder of the life cycle (Fig. 1). The ovary is composed of a central compartment containing the germline surrounded by a single layer of follicle cells, enclosed by a monolayer epithelium (Ganot et al., 2006). The number of oocytes produced per *O. dioica* female is highly variable in field samples (5 to 420; Fenaux and Gorsky, 1981) though they are of constant size (0.1 mm diameter). Spawning oocytes are arrested in metaphase I and meiosis resumes after fertilization with formation of the polar bodies (Nishino and

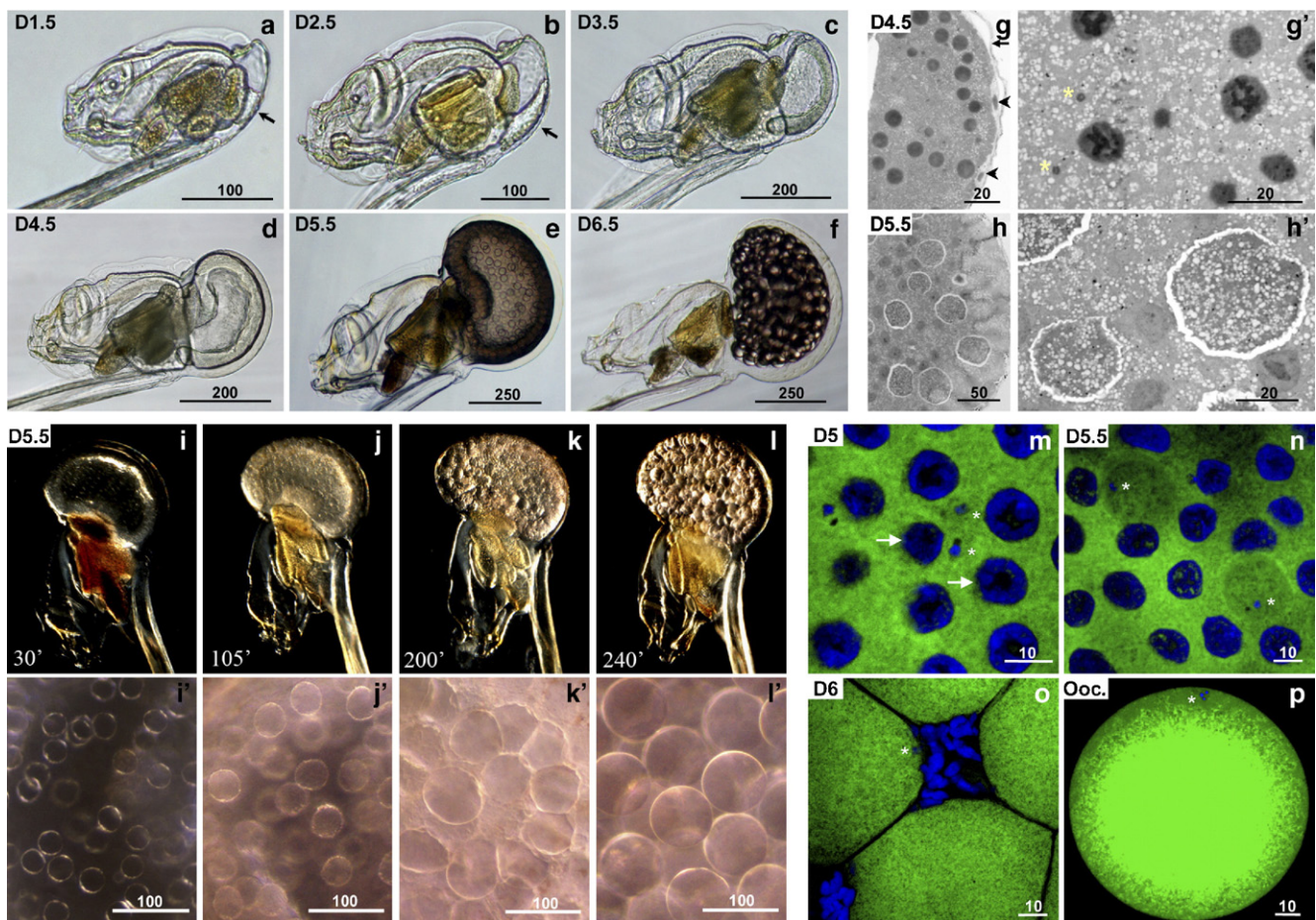


Fig. 1. Ovarian morphology during *Oikopleura dioica* development. (a–f) Light micrographs of *O. dioica* females from day 1.5 to 6.5, oriented anterior (mouth) to left, posterior (gonad) to right, ventral (tail) to bottom. After metamorphosis at day 0.5, the transparent external gonad appears posterior to the trunk (arrows in panels a, b) and grows continuously. At day 5.5, growing oocytes are visible (e) and at day 6.5 (f) mature oocytes fill the ovary volume prior to spawning. (g–h') Plastic sections of *O. dioica* ovaries stained with toluidine blue at two magnifications. (g, g') Day 4.5 ovary prior to oocyte growth: the germ line is one continuous coenocyst with two populations of nuclei, the polyploid nurse nuclei and meiotic nuclei (*). External epithelium (arrow) and peripheral follicle cells (arrowheads) are indicated (g). (h, h') Day 5.5 ovary showing growing oocytes within the coenocyst. (i–l') Time series (min) following an individual female (ovary at top) during oocyte growth and maturation (i–l) with corresponding higher magnification cellular details (i'–l'). A day 5.5 female commencing oocyte growth ($t=0'$) exhibited small, evenly distributed oocytes ($t=30'$) that grew synchronously to rapidly occupy the entire ovary as aggregates ($t=200'$). Shortly after individualized oocytes were apparent ($t=240'$), maturation was completed ($t=360'$) as shown in panel f. Oocyte growth in *O. dioica* requires 6 h on average. (m–p) Arrangement of nurse and meiotic (*) nuclei during oogenesis: DNA, blue; RNA, green. (m) Before oocyte growth, large polyploid nurse nuclei (arrows) shared the same cytoplasm as meiotic nuclei. (n) During oocyte growth, meiotic nuclei were visible inside growing oocytes (reduced RNA staining). (o) Mature oocytes accumulated the vast majority of cytoplasm; nuclei external to oocytes degenerated in small peri-oocytic pockets containing little to no RNA. (p) Spawning oocyte with its cortical metaphase I chromatin organized as condensed pairs of chromosomes. Scale bar units in μm .

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