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Short Communication

The Ovary of the Teleost Fish Xenotoca Eiseni (Goodeidae), where in addition to the Oogenesis Occur Insemination, Fertilization and Gestation

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Abstract

Embryonic development in viviparous teleosts occurs within the ovary as intraovarian gestation that is unique among vertebrates, because all teleosts lack Müllerian ducts from which the oviducts develop in the other vertebrates. Lacking oviducts, viviparous teleosts have evolved intraovarian gestation. Both insemination and fertilization occur in the ovary. The analysis of ovaries of Xenotoca eiseni (Goodeidae) in non-gestation and gestation stages reveals the features of viviparity coincident with intraovarian gestation: fertilization is intrafollicular; during cleavage, the embryos are discharged from the follicle into the lumen. Gestation is intraluminal; sequentially the embryos develop two types of nutrition: lecithotrophy (initially nourishment by yolk) which changes to matrotrophy (nourishment from maternal source) when the embryo develop extensions of the perianal region, the trophotaenia, which absorb the nutrients from the ovarian lumen.

ABBREVIATIONS

H-E: Hematoxylin-Eosin

INTRODUCTION

The ovaries of teleosts are sacular structures with a central lumen (cystovarian type). The internal wall forms irregular folds, call lamellae, that project into the lumen. The lamellae contain stroma that surrounds follicles in different stages of development, in previtellogenesis and vitellogenesis [1-3]. The germinal epithelium borders the ovarian lumen and has oogonia among somatic epithelial cells [4,5]. Therefore, in the cystovarian ovaries of teleosts, ovulation occurs into ovarian lumen instead into the coelom, as occurs in the other vertebrates [6].

An exclusive aspect of the cystovarian condition is the way that the embryos move from the ovarian lumen to the exterior during birth. Because teleosts do not develop Müllerian ducts during the embryogenesis, as occurs in all the rest of vertebrates, teleosts do not have oviducts. As a result, the caudal portion of the ovary, called a gonoduct, connects the ovary to the exterior by a gonopore [7].

These unique features of the ovary have essential adaptations in most viviparous species. These are: a) the sacular ovaries fuse during embryogenesis, forming a single ovary. b) Because of the lack of oviducts, gestation is intraovarian; that is, the ovary performs a gestational role [1,2,8]. Then, the ovary is not only where oogenesis occurs, but it also receives spermatozoa during insemination. The oocytes are fertilized and the embryos remain in the ovary throughout their development.

Viviparous teleosts develop two types of embryonic nutrition during gestation: lecithotrophy and matrotrophy. In the former, nutrients come from the yolk that is stored in the oocyte during oogenesis. In matrotrophy the nutrients are provided by the ovarian tissues during gestation [9,10].

The viviparous species of the family Goodeidae are endemic to the central plateau of Mexico. Their intraovarian gestation is initiated in the follicle where the fertilization occurs. Then, during cleavage the embryos move from the follicle into the ovarian lumen and develop there until birth. This is known as intraluminal gestation [4,6]. Taking into account the complexity of the processes implied in intraovarian gestation and the few species investigated, the goal of this study is to analyze the ovary during non-gestation and gestation stages of the goodeid *Xenotoca eiseni*.

MATERIAL AND METHODS

Adult females *X. eiseni* (total length 8-12cm) (N= 15) were obtained by donation of the Laboratorio de Biologia Acuática, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, México. Females were collected in five reproductive stages, three females during each one: in non-gestation (previtellogenesis and vitellogenesis), and in gestation during early, middle and late gestation (1st, 3rd, and 5th weeks after mating). The specimens were anesthetized and decapitated. The ovary was excised and fixed in Bouin's solution. After fixation, the ovaries were dehydrated and embedded in glycol-methacrylate (JB-4 embedding kit, Polysciences), sectioned at 6μm and stained with hematoxylin-eosin (H-E). Digital photomicrographs were taken using an Olympus camera model C5050Z coupled to an Olympus CX31 microscope.

RESULTS AND DISCUSSION

The ovary of *X. eiseni* is a single, sacular structure (Figure 1A,B). The size of the full-grown oocytes may attain 0.9mm in diameter. The ovarian lumen is divided by a dorso-ventral folded septum into two lateral halves (Figure 1A). The ovarian wall forms

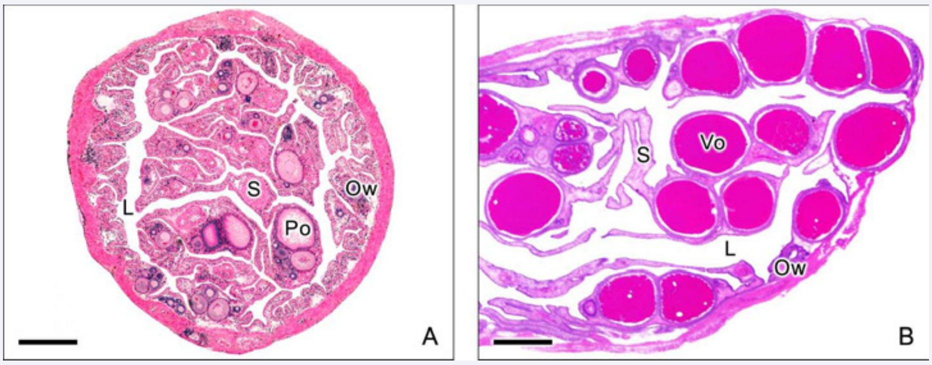

Figure 1 Ovaries of Xenotoca eiseni in non-gestation. A) Transverse section with previtellogenic oocytes (Po), B) Longitudinal section with vitellogenic oocytes (Vo). Ovarian wall (Ow), septum (S), lumen (L). H-E, A bar: 100μm, B bar: 500 μm.

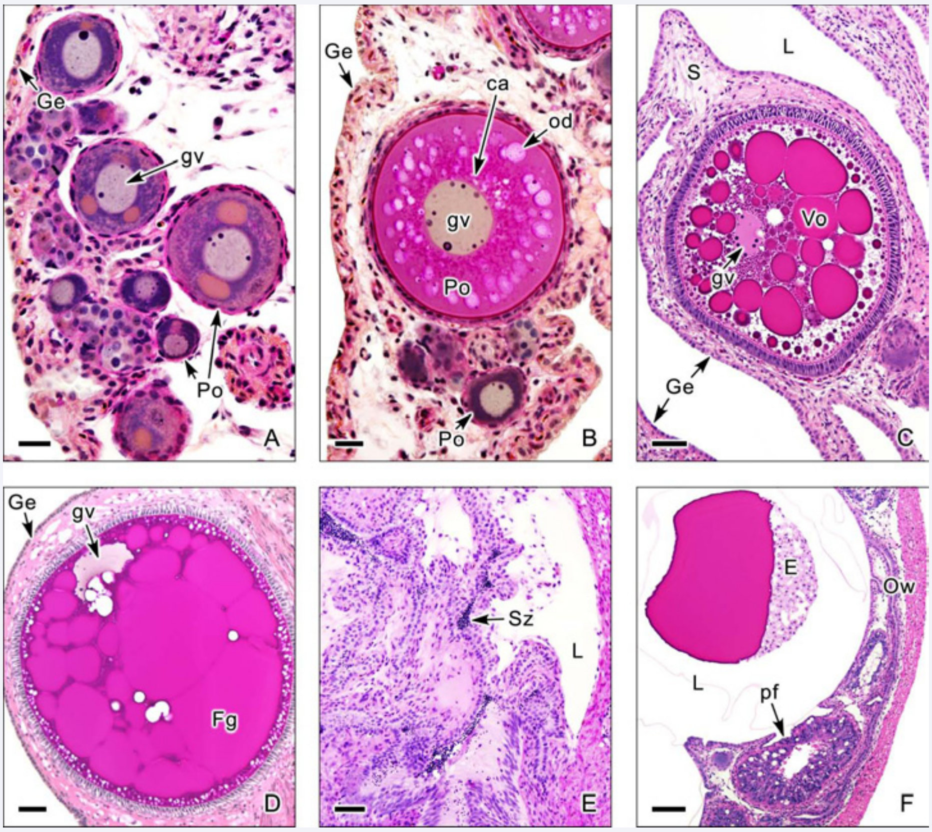

Figure 2 Ovaries of Xenotoca eiseni in non-gestation (A-E), in gestation (F). A,B) Previtellogenic oocytes. C) Vitellogenic oocyte. D) Full-grown oocyte. E) Spermatozoa are in the ovarian lumen. F) Embryo discharged into the lumen, the rest of the follicle forms a postembryonation follicle (pf). Ovarian wall (Ow), septum (S), lumen (L), germinal epithelium (Ge), germinal vesicle (gv), cortical alveoli (ca), oil droplets (od), yolk (y), spermatozoa (Sz), embryo (E) H-E. A,B bars: 20μm, C,D,E bars: 50 μm, F bar: 200 μm.

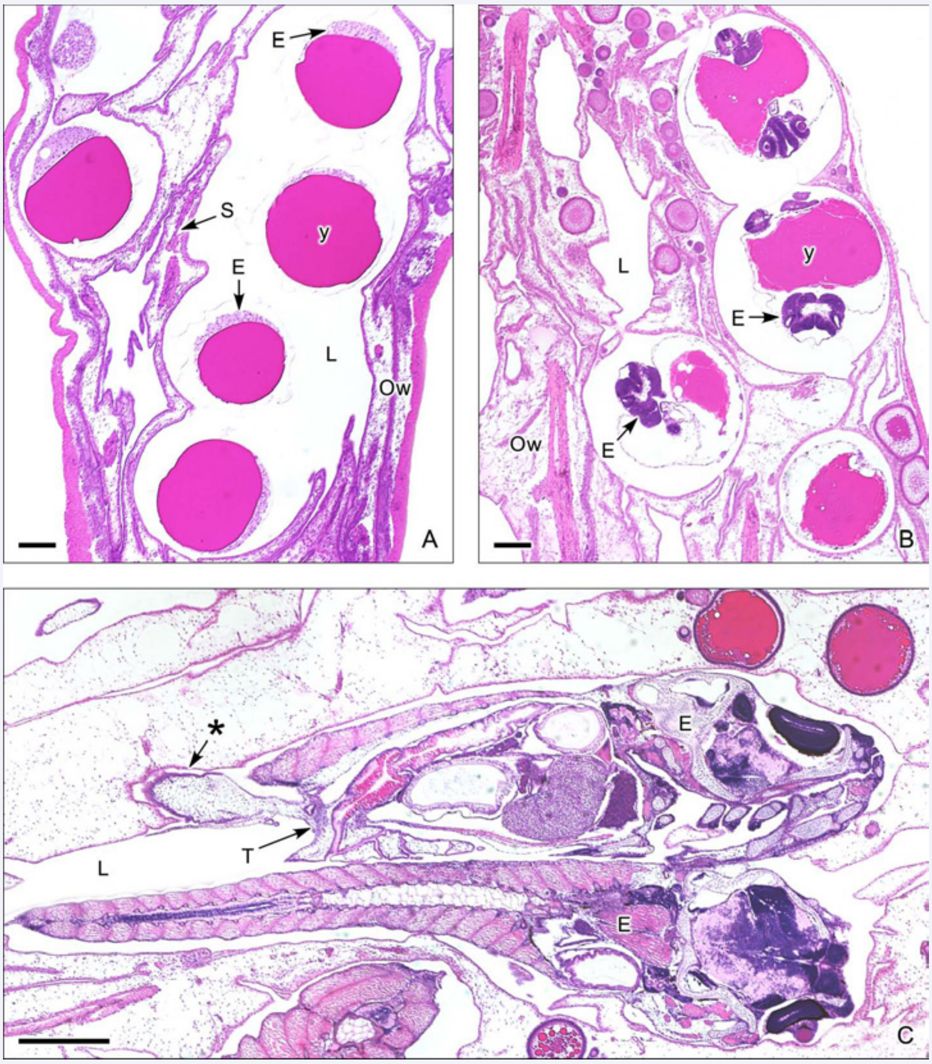

Figure 3 Ovaries of Xenotoca eiseni in gestation. Embryos: A) in cleavage, B) in mid gestation, and C) in late gestation. Trophotaenia formed by extensions of the perianal region, some portion is in apposition to the maternal epithelium, developing a trophotaenial placental (*). Ovarian wall (Ow), lumen (L), yolk (y), embryo (E), trophotaenia (T), H-E. A,B bar: 200μm, C bar: 500 μm.

irregular lamella that project into the lumen (Figure 1A,B). The germinal epithelium borders the lamellae and also the septum (Figure 1A-C) and contains scattered oogonia dispersed between somatic cells. Subjacent to the epithelium there are stroma, smooth muscle and serosa. Within the stroma, previtellogenic and vitellogenic follicles are located (Figure 1A,B). The previtellogenic follicles contain oocytes which include oil droplets (Figure 2A) and cortical alveoli (Figure 2B). The vitellogenic follicles contain growing oocytes with continuing deposition of fluid yolk (Figure 2C,D), and the nucleus (germinal vesicle) moves gradually to the animal pole (Figure 2D) where it is found in full-grown oocytes (Figure 2D). *X. eiseni*, as all goodeids, develops telolecithal oocytes because they contain abundant yolk, as in *Neotoca bilineata* [4], *Ilyodon whitei* and *Goodea atripinnis* [8].

During insemination, spermatozoa enter the ovarian lumen (Figure 2E) and fertilize the oocytes into the follicle. After the fertilization, the developing embryos remain within the follicle for a brief time. During cleavage, the embryos move from the follicle into the lumen (Figure 2F), and development continues as intraluminal gestation [3,6]. The rest of the follicle forms a postembryonation follicle which has similar functions to postovulatory follicles [8] (Figure 2F).

Ovaries of *X. eiseni* in gestation: early (Figure 3A), middle (Figure 3B) and late (Figure 3C), reveal that the yolk is progressively absorbed. Therefore, lecithotrophy is replaced by matrotrophy [9]. Wourms [6] suggested that embryonic nutrition, during the evolution of viviparity, involved a shift from nutritional autonomy utilizing yolk to maternal nutritional dependency. Matrotrophy in goodeids has an essential adaptation due to the development of trophotaenia, ribbon-like structures formed by extensions of the perianal region of the embryo, as in *X. eiseni* (Figure 3C). Trophotaenia have a high absorptive capacity for nutrients that are secreted by the ovarian tissues into the lumen [6,10]. Some portions of these extensions may be in apposition to the maternal epithelium, developing a trophotaenial placenta (Figure 3C). In an excellent analysis of the trophotaeniae of the goodeids *Ameca splendens* and *Goodea atripinnis*, Wourms [6] defines their functional morphology, formation and evolution; and Iida et al., [11] analyze the regression of the trophotaeniae that occurs during late gestation in *X. eiseni*.

CONCLUSIONS

The viviparous goodeid fishes, here represented by *X. eiseni*, have been significantly distinguished in fish reproduction for the essential features of intraovarian gestation, by intraluminal embryonic development, the transition of lecithotrophy to matrotrophy and the development of trophotaeniae.

Considering all of these morphogenetic processes of the ovaries of viviparous teleosts, during oogenesis, fertilization and gestation, we consider that the functional morphology of the ovary in viviparous fishes is unique among vertebrates.

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