Intraovarian Gestation in Viviparous Teleosts: Unique Type of Gestation among Vertebrates

Mari-Carmen Uribe, Gabino De la Rosa-Cruz, Adriana García-Alarcón and Juan Carlos Campuzano-Caballero

Abstract

The intraovarian gestation, occurring in teleosts, makes this type of reproduction a such complex and unique condition among vertebrates. This type of gestation of teleosts is expressed in special morphological and physiological characteristic where occurs the viviparity and it is an essential component in the analysis of the evolutionary process of viviparity in vertebrates. In viviparous teleosts, during embryogenesis, there are not development of Müllerian ducts, which form the oviducts in the rest of vertebrates, as a result, exclusively in teleosts, there are not oviducts and the caudal region of the ovary, the gonoduct, connects the ovary to the exterior. The lack of oviducts defines that the embryos develop into the ovary, as intraovarian gestation. The ovary forms the oocytes which may develop different type of oogenesis, according with the storage of diverse amount of yolk, variation observed corresponding to the species. The viviparous gestation is characterized by the possible intimate contact between maternal and embryonic tissues, process that permits their metabolic interchanges. So, the nutrients obtained by the embryos could be deposited in the oocyte before fertilization, contained in the yolk (lecithotrophy), and may be completed during gestation by additional provisioning from maternal tissues to the embryo (matrotrophy). Then, essential requirements for viviparity in poeciliids and goodeids are characterized by: a) the diversification of oogenesis, with the deposition of different amount of yolk in the oocyte; b) the insemination, by the transfer of sperm to the female gonoduct and their transportation from the gonoduct to the germinal region of the ovary where the follicles develop; c) the intrafollicular fertilization; d) the intraovarian gestation with the development of embryos in intrafollicular gestation (as in poeciliids), or intraluminal gestation (as in goodeids); and, e) the origin of embryonic nutrition may be by lecithotrophy and matrotrophy. The focus of this revision compares the general and specific structural characteristics of the viviparity occurring into the intraovarian gestation in teleosts, defining this reproductive strategy, illustrated in this review with histological material in a poeciliid, of the species *Poecilia latipinna* (Lesueur, 1821) (Poeciliidae), and in a goodeid, of the species *Xenotoca eiseni* (Rutter, 1896) (Goodeidae).
Keywords: oogenesis, gonoduct, intrafollicular gestation, intraluminal gestation, lecithotrophy, matrotrophy

1. Introduction

Viviparity, the marvelous and complex reproductive strategy in which the mother retains developing eggs inside their body and give birth to a living young, occurs in all the Classes of vertebrates, except in birds. Viviparity among vertebrates makes the evolutionary first appearance in fishes, becoming essential in the understanding of this reproductive strategy [1–4]. The viviparity develops an ample diversity of features along the evolution of this type of reproduction in vertebrates, this is the case of teleosts of the families Poeciliidae and Goodeidae. The adaptations for viviparity in these species developed strategies that have been successful in a wide variety of aquatic environments [3, 5, 6]. In teleosts, during embryogenesis, there are not development of Müllerian ducts, which form the oviducts in the rest of vertebrates, as a result, exclusively in these fishes, there are not oviducts, consequently there is not uterus. Therefore, the posterior zone of the ovary of teleosts, called gonoduct, characterized by the absence of germinal cells, connects the rest of the ovary to the exterior, opening at the genital pore. The lumen of the germinal region of the ovary is continuous with the lumen of the gonoduct [1–3, 7–10]. Because of the lack of oviducts in viviparous teleosts, the development of the embryos occurs into de ovary, as an intraovarian gestation, unique in vertebrates, instead of into the uterus as occurs in the rest of viviparous vertebrates. This ovarian structure defines the characteristics of the teleosts viviparity as occurs in poeciliids and goodeids. The characteristics of the ovary during non-gestation and gestation stages are presented and compared in this study, taking as models two species: the poeciliid *Poecilia latipinna* (Lesueur, 1821), and the goodeid *Xenotoca eiseni* (Rutter, 1896). During non-gestation, ovaries during previtellogenesis and vitellogenesis where selected; and, during gestation, ovaries in early, middle, and advanced gestation where selected. The ovaries were prepared for histological analysis, stained with Hematoxiline-Eosine and the image 3A is PAS [11]. Digital photomicrographs were taken using an Olympus digital camera (model C5050Z) coupled to an Olympus CX31 microscope.

The gonadal differentiation includes the initial development of two ovaries which fuse forming a single and saccular ovary with a central lumen [1, 2]. The lack of Müllerian ducts determines the lack of oviducal development. Consequently, the female reproductive system is formed only by the ovary where the gonoduct, a non-germinal caudal portion of the ovary, connects it with the exterior [8–10]. In agreement with these structural characteristics, gestation occurs in the ovary. The embryonic development in poeciliids is intrafollicular therefore, there is not ovulation, and in goodeids is intraluminal, being the embryos discharged from the follicle to the ovarian lumen just after fertilization.

Poeciliids produce eggs generally larger than goodeids. The eggs of the most of poeciliid species attains approximately 2.0–2.5 mm in diameter, meanwhile the eggs of the most of goodeid species attains approximately 0.5–1.0 mm in diameter. Similar data for species of both families are related to time of gestation period, approximately 45–60 days of gestation, and the total length of embryos at birth about 13-20 mm total length. Then, the larger eggs of poeciliid eggs compared with smaller eggs of goodeid eggs, but similar size in the newborns indicates the more intense lecithotrophy in poeciliids compared with more intense matrotrophy in goodeids. [1–3, 6]. Consequently, goodeid embryos required to absorb more nutrients derived from maternal tissues during gestation.
2. Structure of the ovary in poeciliids and goodeids

As in most viviparous teleosts, in all poeciliids and goodeids, such as *P. latipinna* and *X. eiseni*, the ovary is a single organ, longitudinally situated. The single ovary presents a saccular structure, with a central lumen, corresponding to the cyst-ovarian type. The single ovary is the result of the fusion of both ovaries during embryological development [2, 3, 12, 13]. The ovary is surrounded by the coelom. The ovary is located dorsally to the digestive tract and remains attached to the dorsal wall of the body by the mesovarium. The ovarian wall contains four tissue layers, they are: a) the germinal epithelium which lines the ovarian lumen; b) the stroma, subjacent to the epithelium, formed by loose vascularized connective tissue, containing follicles in different stages of development; c) smooth muscle layers in circular and longitudinal disposition; and d) serosa, formed by scarce connective tissue and mesothelium at the periphery [7, 13–17]. The ovarian mucosa forms irregular folds, that extend into the ovarian lumen, called lamellae. The lamellae are lined by germinal epithelium, where follicles in diverse stages of oogenesis may be located. The germinal epithelium contains oogonia, situated among somatic epithelial cells [3, 13, 17, 18]. The internal position of the germinal epithelium in the saccular ovary defines that the ovulation in oviparous teleosts occurs into the lumen, instead of into the coelom as happens in all other vertebrates [2, 3, 13, 16, 19].

The ovary of *P. latipinna*, and *X. eiseni*, is essentially characterized by the occurrence of the oogenesis, complex and vital process of the female germinal cells, as in all animals, during their development to mature oocytes [20]. The oogenesis in viviparous teleosts, is similar to that described in oviparous teleosts, involving cyclical sequence of morphophysiological changes in the differentiation of oogonia into full-grown oocytes. According to the annual cycles, the ovary may contain only early stages of oogenesis (previtellogenesis) (Figure 1A and 2A), or late stages of oogenesis (vitellogenesis) (Figure 1B and 2B). Several authors analyze this process [7, 14–16, 21–24]. Oogonia is the earliest stage of germ cells which grow from an initial diameter of approximately 10 μm. Oogonia initiate meiosis becoming oocytes which are surrounded by follicular cells, developing the primordial follicles. This process comprises two main stages in sequence: previtellogenesis (Figure 1A, C, D and 2A, C, D), and vitellogenesis (Figure 3A–D and 4A–D). During previtellogenesis, the nucleus of the oocyte, call germinal vesicle, has a nucleolus which proliferates to multiple nucleoli, and the ooplasm initiates the growths involving a great increase in the number of organelles associated with synthetic activities, as ribosomes, endoplasmic reticulum, mitochondria, and Golgi apparatus, becoming basophilic for the staining affinity of the ooplasm. Posteriorly, during the vitellogenesis, the oocyte growth considerably when accumulates lipid globules and yolk, becoming acidophilic for the staining affinity of the yolk. Yolk is the fundamental and more abundant material stored during oogenesis for the metabolic activities required during the embryonic development. In addition to yolk, glycogen granules and lipid globules are also stored in the oocyte, forming an essential complex for embryonic nutrition. In the full-grown oocyte, the germinal vesicle moves towards the animal pole. In both, goodeids and poeciliids, during oocyte maturation the hydration of yolk occurs and becomes fluid and homogeneous, and some lipid globules may remain around the oocyte periphery [5, 7, 13].

There is a clear difference between the egg size diameter of mature eggs of poeciliids and goodeids, being larger the eggs of poeciliids. In most poeciliid species there is a mean diameter of mature eggs of 1.5 mm to 2.5 mm [6, 25–27]. Even there are some poeciliids with smaller oocytes as *Heterandria formosa*, which mature
Figure 1.
Ovarian structure of *Poecilia latipinna*, comparing ovaries during non-gestation with previtellogenic oocytes (A) and vitellogenic oocytes (B). A) Saccular ovary with a central lumen. Ovary during non-gestation with numerous follicles during different stages of previtellogenesis seen by the change in the oocyte diameter. In some oocytes, the nucleus (germinal vesicle) is seen. The follicular cells surround the oocytes. In the caudal region of the ovary the initial portion of the gonoduct is seen. B) Saccular ovary with a central lumen. Ovary during non-gestation with follicles during late vitellogenesis containing abundant yolk fluid and homogeneous. Lipid globules are seen at the periphery. The follicular cells surround the oocytes. C) Follicles during different stages of previtellogenesis, follicular cells surround the oocytes, a group of oogonia is seen. The lumen is surrounded by the germinal epithelium. D) Two follicles in advanced stage of previtellogenesis, the basophilia diminishes with the growth of the oocyte. (fe) follicular epithelium, (ge) germinal epithelium, (gv) germinal vesicle, (go) gonoduct, (L) ovarian lumen, (lg) lipid globules, (Og) oogonia, (Oo) oocytes, (Y) yolk. Staining technique: A-D: Hematoxiline-Eosine.
Figure 2.
Ovarian structure of *Xenotoca eiseni*, comparing ovaries during non-gestation with previtellogenic oocytes (A) and vitellogenic oocytes (B). A) Saccular ovary with a central lumen. Ovary during non-gestation with follicles during different stages of previtellogenesis seen by the change in the oocyte diameter. B) Saccular ovary with a central lumen. Ovary during non-gestation with follicles during late vitellogenesis containing abundant yolk. In some oocytes, the nucleus (germinal vesicle) is seen. The follicular cells surround the oocytes. C) Follicles with oocytes in different stages of previtellogenesis, follicular cells surround the oocytes. The lumen is surrounded by the germinal epithelium. D) Detail of oocytes in early stages of previtellogenesis. The nucleus (germinal vesicle) is seen. The follicular cells surround the oocytes. (fe) follicular epithelium, (ge) germinal epithelium, (gv) germinal vesicle, (L) ovarian lumen, (Oo) oocytes, (Y) yolk. Staining technique: A-D: Hematoxiline-Eosine.
The oocyte attains an egg diameter of 0.4 mm, considered the smallest egg of poeciliids [28]. The species *P. latipinna* forms mature eggs with a mean diameter of 2.2 mm [26]. In most goodeid the mature egg has a mean diameter of 0.6 mm to 1.0 mm., the species *X. eiseni* forms mature eggs with a mean diameter of about 0.8 mm in diameter [29].

**Figure 3.**

Ovary of *Poecilia latipinna*. A) Ovary during non-gestation with follicles during the initial vitellogenesis, with yolk platelets at the periphery. Lipid globules are seen among the yolk. The acidophilia is clear by the presence of the yolk. The ovarian lumen is surrounded by the germinal epithelium. B) Follicle in advanced stage of vitellogenesis, the yolk is initially becoming fluid and homogeneous. Abundant lipid globules are seen. C) Portion of a vitellogenic oocyte, with lipid globules at the periphery, the yolk is fluid and homogeneous. The follicular cells surround the oocytes. Compare this vitellogenic oocyte with the previtellogenic oocyte seen in the upper part of the image. D) Late vitellogenic oocyte, the yolk is completely fluid and homogeneous, some lipid globules may be seen around the oocyte periphery. (fe) follicular epithelium, (ge) germinal epithelium, (gv) germinal vesicle, (L) ovarian lumen, (lg) lipid globules, (Oo) oocytes, (Y) yolk. Staining technique: A: PAS; B-D: Hematoxilin-Eosine.
3. Fertilization

Viviparity is basically related to the evolution of reproductive behavior, insemination and fertilization are essential requirements for viviparity. In viviparous species, as poeciliids and goodeids, the internal fertilization involves the insemination, with...
the entrance of spermatozoa to the female reproductive system, through the transfer of sperm from the male to the female gonoduct, and the sequence of the entrance of the sperms, from the gonoduct to the germinal zone of the ovary, where occurs the internal fertilization [1, 19, 30–32]. The secretory activity of the ovarian epithelium, having a trophic function for the spermatozoa, contributes for their survival during the appropriate time for the fertilization. In *P. latipinna*, and *X. eiseni*, the spermatozoa may be seen in the ovarian lumen (Figure 5A and 6A), many of them show their heads in contact with the apical end of the germinal epithelial cells.

Insemination in viviparity may allow the temporal separation of mating and fertilization, and consequently, the temporal diversification of the time
between insemination and birth, by the possibility of sperm storage in the ovary. Additionally, the sperm storage permits that, with one insemination, several clutches of eggs maturing on several occasions, may be fecundated [31].

In most viviparous teleosts, as poeciliids and goodeids, fertilization occurs inside the follicle, as an intrafollicular fertilization, therefore, there is not ovulation. During the fertilization, sperm must penetrate the follicular wall to reaches the oocyte membrane [31, 33–35].
4. Intrafollicular and intraluminal gestation in poeciliids and goodeids

After the intrafollicular fertilization the embryogenesis may follow two different ways of gestation: a) intrafollicular gestation, where the embryos remain in the follicle during their development and move into the ovarian lumen immediately before birth, as occurs in poeciliids; or b) intraluminal gestation, in which the embryos, during early development as blastula, move from the follicle to the ovarian lumen where gestation continues until birth, as occurs in goodeids, in this type of gestation the embryos in the lumen are surrounded by a fluid, called histotrophe, secreted by the

Figure 7. Ovary of Poecilia latipinna in intrafollicular gestation. A) Ovary during gestation with an embryo in middle stage of development. Lipid globules are seen at the periphery. Around the yolk is seen the yolk sac. The follicular epithelium surrounds the follicle in gestation. Oocytes are seen in the ovarian wall. B) Periphery of the yolk, where it is seen the vascularized yolk sac with blood vessels. Lipid globules are seen. The follicular epithelium surrounds the follicle in gestation. C) an embryo during advanced stage of gestation, the amount of yolk diminishes with the growth of the embryo. Lipid globules are seen. The follicular epithelium surrounds the follicle in gestation. (bv) blood vessels, (E) embryo, (fe) follicular epithelium, (L) ovarian lumen, (lg) lipid globules, (Oo) oocytes, (Y) yolk, (Ys) yolk sac. Staining technique: A-C, Hematoxilin-Eosine.
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ovarian epithelium to the lumen [1, 29, 30, 36, 37]. Thus, the intrafollicular gestation is the case of the poeciliid P. latipinna, and the intraluminal gestation is the case of the goodeid X. eiseni. Embryos of P. latipinna in early intrafollicular gestation (Figure 5B and C) and embryos of X. eiseni, in early intraluminal gestation (Figure 6B–D), are seen. Embryos of P. latipinna in late intrafollicular gestation (Figure 7 A–C) and embryos of X. eiseni, in late intraluminal gestation (Figure 8A–C), are seen.

Figure 8.
Ovary of Xenotoca eiseni in intraluminal gestation. A) Ovary during gestation with embryos in the lumen during middle stage of development, with early development of eyes. Reduced yolk in the ventral side of the embryo. Oocytes are seen in the ovarian wall. B) Ovary with embryos in the lumen during advanced stage of development. There is not yolk. C) Ovary with embryos during advanced stage of gestation. The trophotaeniae is seen as extensions of the intestine to the ovarian lumen. (E) Embryo, (L) ovarian lumen, (Oo) oocytes, (T) trophotaeniae (Y) yolk. Staining technique: A-C: Hematoxiline-Eosine.
Consequently, both types of gestation, intrafollicular and intraluminal, define different relationships between the tissues of the embryos and the mother and successively, diverse adaptations for metabolic interchanges between them, reflected mainly in the type of embryonic nutrition. Nutrition during gestation in viviparous species reflects essential strategies which impact in the evolution of vertebrate viviparity, as occurs in goodeids and poeciliids [19, 38, 39].

In recognition of vertebrate diversity, we follow Blackburn & Starck [40] in using the term “embryo” in the broad sense, to include all types of developing offspring in gestation.

5. Embryonic nutrition by lecithotrophy and matrotrophy

The maternal–embryonic relationships include trophic, osmoregulatory, excretory, respiratory, endocrinological, and immunological processes [4, 36, 37, 40]. These interchanges are essentially related to the diversity of mechanisms of embryonic nutrition. During intraovarian gestation of poeciliids and goodeids, two types of embryonic nutrition may occur: a) lecithotrophy, wherein the nutrients are provided by the yolk stored in the oocyte during oogenesis; and, b) matrotrophy, where the nutrients are transferred by maternal tissues to the embryo during gestation. Both types of nutrition are not mutually excluding, may occur both with different degree of nutrient transfer. These strategies require a modification in the timing of maternal resource offered to the embryo, these are: during oogenesis, previously to fertilization, in lecithotrophy, and posteriorly to fertilization, in matrotrophy. Several studies analyze the adaptations from lecithotrophy to matrotrophy [4, 19, 27, 29, 38, 40–44].

In lecithotrophic species, the yolk develops a big and vascularized yolk sac around the yolk, in the ventral part of the embryo (Figure 7A and B). The yolk sac has a simple epithelium and a plexus with abundant capillaries, structures that allow the reception of the nutrients from the yolk and their distribution to the rest of the embryonic body, throughout the circulation. During gestation, the yolk sac progressively diminishes (Figure 7C), as the yolk is used for the nutrition of the embryo [19, 45, 46].

The viviparity generates the opportunity for the embryo to acquire resources from the mother, developing specialized structures for interchanges, as it is the development of placental structures [27, 42, 47]. In the intrafollicular gestation, maternal tissues (follicular epithelium and the subjacent net of capillaries), and embryonic structures establish the maternal–embryonic relationships during gestation [3, 19].

According to the differences of amount of yolk, the species having eggs with abundant yolk are lecithotrophic, even some transfer of maternal nutrients may also occur through the contact of the maternal blood vessels subjacent to the follicular epithelium, which surrounds the embryo in development, as occurs in poeciliids, as P. latipinna (Figure 5B and C). In contrast, the species having eggs with scarce yolk deposited during oogenesis, observed during early gestation in goodeids as X. eiseni (Figure 6B–D and 8A), but, when the scarce yolk is early consumed, and the embryo needs nutrients from the mother for the continuation of the development are matrotrophic (Figure 8B and C).

Lecithotrophy has been revealed to be better adapted energetically to seasonally unpredictable habitats, whereas matrotrophy requires a predictable food supply during gestation. Therefore, matrotrophy requires stable conditions throughout gestation for a constant transfer of nutrients from the mother to the embryos. Then, the condition of the habitat determines the convenience of lecithotrophy or matrotrophy [42, 47–49].
Early in the embryogenesis of goodeids, when the yolk is completely consumed (Figure 8B and C), the embryonic growth is progressively dependent of maternal nutrients through matrotrophy, initially by the nutrients dissolved in the histotrophe and then, by the transfer of nutrients via the development of complex and diverse placental structures where occurs the apposition of embryonic and maternal tissues [29, 36, 39, 43, 50–52]. Several embryonic structures have been considered for the transfer of nutrients from the histotrophe such as: the skin, the gills, the digestive tract through the mouth, and the characteristic structure of goodeids, the trophotaeniae [1, 7, 29, 39, 52–54]. The trophotaeniae is seen as extensions of the intestine to the ovarian lumen (Figure 8C). Additionally, transfer of nutrients occurs by placental structures, such as: the apposition of trophotaeniae to maternal epithelium, or by branquial placenta, a structure formed when folds of ovarian tissue enter the embryonic branchial chamber developing apposition of the ovarian folds to the embryonic branquial epithelium [49, 52, 55].

Embryos developing in the ovarian lumen, as X. eiseni (Figure 6C, D and 8A–C), are bathed by histotrophe, a fluid rich in nutrients containing abundant proteins derived from the maternal blood, secreted by the ovarian tissues, and discharged in the lumen [29, 55]. The absorption of these nutrients is reached by goodeid embryos through long and vascularized extensions of the hindgut that grow outside of the embryo into the ovarian lumen developing extraordinary absorptive structures call trophotaeniae (Figure 8C). Trophotaeniae is also involved in gas exchange and develop process of immunity [19, 29, 30]. This capacity of absorption is evidenced by the morphological features of the trophotaeniae, as the surrounding columnar epithelium with apical brush-border and the abundant vascularization subjacent to the epithelium [29]. Then through the epithelium, the blood vessels of the trophotaeniae transport the contains from the histotrophe to the embryo. Numerous morphological and experimental studies of the trophotaeniae analyzed the transfer of nutrient to the embryonic body, as: [29, 39, 50, 52–54]. Ecdysis of the trophotaeniae occurs at birth; when the postnatal phase initiates the oral nutrition [19, 30, 36, 53].

In poeciliids during birth, the embryos are going from the follicle to the ovarian lumen and then through the gonoduct to the exterior. In goodeids during birth, the embryos are already in the ovarian lumen, then through the gonoduct they move to the exterior.

6. Conclusions

The structure of the ovary and the lack of oviducts of teleosts define the characteristics of the viviparity with the intraovarian gestation, as it was presented morphologically in the sequence of Figures of ovarian histology of the poeciliid P. latipinna, and the goodeid X. eiseni in this analysis.

The ovary of viviparous teleosts is not only the organ where occurs the oogenesis, but also it receives the spermatozoa during insemination, occurs the fertilization of oocytes and the embryos remain throughout their development until birth, making the intraovarian gestation of viviparous teleosts a such complex and unique type of gestation in vertebrates.

The oogenesis is similar to that described in oviparous teleosts, since the formation of the primordial follicle, integrated by the oocyte surrounded by the follicular epithelium, and through previtellogenesis and vitellogenesis. In accordance with the species, as it is seen in poeciliids and goodeids, the oogenesis organizes oocytes with different diameters corresponding to the amount of yolk.
The intraovarian gestation may be as: a) intrafollicular, where the embryos remain in the follicle during their development and move into the ovarian lumen immediately before birth, or b) intraluminal, in which the embryos, during early development move from the follicle to the ovarian lumen where gestation continues until birth.

The origin of embryonic nutrition occurs by lecithotrophy and matrotrophy developing active structures in the transfer of nutrients to the blood vessels of the embryo. The lecithotrophy, occurring in the intrafollicular gestation of *P. latipinna*, develops the yolk sac, which decrease progressively during gestation. The matrotrophy occurring in the intraluminal gestation of *X. eiseni*, allows the provision of nutrients from the histotrophe, and develop the trophotaeniae and the branchial placenta.

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