Chapter

A Review of the Macroscopic, Microscopic, and Ultramicroscopic Characteristics of Some Key Oocyte Developmental Processes in Fish Species

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Abstract

Studies involving the reproductive biology of fish have several possibilities of approach, such as the understanding of gonadal development, oocyte development, and the reproductive cycle of the species. In addition, analyses of gonadal morphology can be made at macro-, micro-, and ultramicroscopic levels. This knowledge helps to define factors that determine the different stages of gonadal development, as well as the "triggers" that initiate the reproductive process. In females, the growth and maturation of the ovarian follicles depend on a carefully elaborated communication between the follicular cells and the oocyte and a precisely organized contractile system. Changes in these systems appear to be related to apoptotic cells. This extensive remodeling of gonadal tissue, due to cell proliferation and differentiation, promotes also changes in the extracellular matrix. With this in mind, we provide herein a complementary and in-depth information on cell-cell and cell-matrix interactions related to the process of oocyte development in fish species. This information, together with the existing structural and ultrastructural descriptions of ovaries of different species, will enable a better understanding of the reproductive processes for the group of fish.

Keywords: fish species, reproductive biology, gonadal and oocyte development, cell-cell interactions, cell-matrix interactions

1. Introduction

The knowledge on the reproductive characteristics of fish is fundamental to understand the adaptations developed to maximize the reproductive success in a given environment, considering the life history aspects of each species [1]. Studies involving the reproductive biology of fish have several possibilities of approach, such as the understanding of gonadal development and the reproductive cycle of the species. Analyses of gonadal morphology are important for the understanding of the biology of the species and have been widely applied in

Teleostei, as in recent studies on spermatogenesis [2–5], folliculogenesis [6–8], reproductive cycle [8–12], and fecundity [13].

Studies have been carried out to describe and classify the stages of gonadal development and reproductive stages of fish in the Neotropical region. One of the most classic and used bibliographic sources has been Vazzoler [14]. However, other proposals for description have already been made by Grier and Taylor [15], Grier [16], and Lo Nostro et al. [17], which detail the continuity and discontinuity of the germinal epithelium and the cell types present in the gonads. Recently, Brown-Peterson et al. [18] developed a simpler terminology to facilitate the communication and comparison of studies on the reproductive biology of fish. Still in order to make the nomenclature more comprehensive, the stages of oocyte development were simplified by Quagio-Grassiotto et al. [19], and the development of stages of atresia, which are characterized as involutive processes, follows according to Miranda et al. [20].

Gonadal development can be analyzed macroscopically, and changes in shape, size, color, and texture of the gonads have been used as parameters for the classification of maturation status in many studies of ecology and reproductive dynamics[14, 21]. However, the most used analysis has been of the microscopic characters, since it allows a more detailed and precise description of the transitions and morphological and structural transformations that happen during gonadal development [8, 22, 23]. Thus, regarding the microscopic aspects of the gonad, it is verified that [24]:

- Spermatogenesis shows stages of development that include spermatogonia, spermatocytes, spermatids, and spermatozoa.

- Oogenesis usually shows the following progression: oogonia, primary growth oocytes, a previtellogenic stage in which oocytes grow larger and often have cortical alveolar vesicles, an extensive vitellogenic phase, oocyte maturation, and ovulation.

The oocyte development in a mature egg is a complex process modulated by numerous environmental and endocrine factors [25], and understanding the morphological characteristics of oocytes is important to interpret the dynamics of oogenesis [26]. Among the oocyte processes, folliculogenesis results in the removal of the primary oocyte from oogonium nests and consequent formation of ovarian follicles [27]. Descriptions for the germinal epithelium made by Grier [28] conceptualized "follicular complex" as the functional unit of the ovary. This complex is formed by two compartments separated by a basement membrane. One compartment is the follicle, which consists of the oocyte surrounded by follicular cells and originated from the germinal epithelium. The second compartment is the theca, made up of undifferentiated ovarian stromal cells.

In the previtellogenic oocyte phase, multiple nucleoli are observed, as described by Grier et al. [29]. These oocytes are also called perinucleolar oocytes, when the nucleoli migrate to the nuclear periphery. There is also the formation of the zona pellucida, a complex structure consisting generally of two layers crossed by pores or channels containing the oocyte microvilli and/or follicular cell extensions. The zona pellucida reflects adaptations to different ecological conditions in which the eggs develop [30], whose inner layer protects the egg from mechanical damage and whose outer layer protects it from microorganisms.

Another cell characteristic that is used to describe the stages of oocyte development is the presence of nüages, Balbiani corpuscles, and cortical alveoli. The nüages are originated by the transfer from the nucleus to the cytoplasm of large amounts of heterogeneous and ribosomal RNA synthesized [31] and associated with proteins. Balbiani corpuscles or yolk nuclei, described by Hubbard [32], were recognized

as clusters of organelles located near the nucleus, which proliferate intensely and spread throughout the cytoplasm. And, the cortical alveoli, as observed by Grier et al. [29], are vesicles filled with glycoproteins, formed by depressions of the oocyte membrane that become progressively larger, marking the final stage of primary or previtellogenic growth.

The described changes are followed by an expressive growth of the oocyte during vitellogenesis, in which the oocyte accumulates the nutritive reserves necessary for the development of the embryo. The oocyte also accumulates RNA and completes the differentiation of its cellular and noncellular envelopes. During this time, the oocyte interrupts the meiosis at the end of the prophase and in the diplotene stage. Maturation processes are characterized by the reduction or halting of endocytosis, resumption of meiosis, breakdown of the germinal vesicle, formation of a monolayer of cortical alveoli under the plasma oocyte membrane, and dissolution of yolk platelets; pelagic oocytes still undergo hydration [6].

The understanding of cellular modifications is used to describe the reproductive cycle. This allows the recognition of the reproduction period and the gonadal morphological changes that occur. Descriptions of the reproductive cycle were initially elaborated by Yamamoto [33] and Agostinho et al. [34, 35], revalidated by Vazzoler [14], and later used by many authors. Next, Nuñez and Duponchelle [10] defined five stages of ovarian development with greater cellular detail and other four stages of testicular development based on macro- and microscopic characteristics. The last descriptions made by Lowerre-Barbieri et al. [24] and Quagio-Grassiotto et al. [19] on oocyte development, coupled with the stages of the reproductive cycle described by Brown-Peterson et al. [18], brought a proposal to homogenize the terms used and that has been applied in more recent studies. Research on the reproductive cycle of a given species helps to define determinant phases of gonadal development, as well as the "triggers" that initiate the process of cell proliferation and differentiation in the formation of gametes [14, 36–38].

2. Important cellular morphological modifications during the oocyte development process

2.1 Cellular junctions and your distribution throughout the oocyte development

The growth and maturation of the ovarian follicles depend on carefully crafted communication between the somatic cells of the follicle and the oocyte. This association between somatic cell and germ cell in the ovaries of various vertebrate and invertebrate species is established through intercellular junctions [39–43]. In vertebrate ovarian follicles, direct cytoplasmic connections between the oocyte and follicular cells of the granulosa layer associated with it are established early in the oocyte development. In fish, amphibians, and mammals, these cytoplasmic connections are established at the points of contact between the oocyte microvilli and follicular cells or between follicular cell microvilli and oocyte, via specialized membrane junctions known as GAP junctions [44–47].

GAP junctions are intermembrane channel aggregates between adjacent cells composed by connexin proteins [48]. These junctions are considered homologous when they connect follicular cells to follicular cells and heterologous when they connect follicular cells to the oocyte [49]. Recent observations suggest that the functional coupling of GAP junctions, especially homologous ones, is necessary for the occurrence of the oocyte maturation process [50]. A possible role for the heterologous GAP junctions is the transfer of cAMP (PKA activator) from the follicular cells to the oocyte in order to induce the production or activity of membrane receptors

for the maturation-inducing hormone, or MIH [50], indirectly participating in the oocyte maturation process. GAP junctions may also be involved in specifying the pattern of polarity in the oocytes of various animal groups, so this junctional route can be used to pass intercellular signals from follicular cells to the oocyte to determine oocyte symmetry [51].

As previously reported, the fish oocyte is enveloped by the zona pellucida (microvillus area), by the follicular cells and by the basement membrane. Thus, from a morphological and functional point of view, it is important to know if there are any tight junctions between adjacent follicular cells, since these joints promote barriers for the passage of fluids through the extracellular space between adjacent cell membranes and maintain tissue and cell integrity [45, 52–54]. The main components of the intercellular junctions are the tight junctions [55, 56], which are composed of different transmembrane proteins that promote a homophilic interaction. The cytoplasmic domain of the transmembrane adhesion molecules connects the binding proteins which, in turn, anchor the cytoskeletal adhesion complex. Of these molecules, occludins and claudins are the most extensively studied. Although occludin is a highly conserved molecule, claudins comprise a family of more than 20 different proteins, some of which are expressed in a tissue-specific manner [57–59].

As claudins, cadherins are a transmembrane superfamily of proteins that contain several homologous members, exhibiting tissue diversity and distinct binding specificities [60–62], with a highly conserved cytoplasmic domain [63, 64]. These molecules mediate cell-cell contact at adhesion junctions also anchored in the cytoskeleton, thus playing an important role in the separation, positioning and control of cell movements, and in morphogenesis [65–67]. In a study with *Danio rerio*, E-cadherin homologous proteins were identified, and their synthesis and storage during oogenesis were verified [62]. Also, the establishment of heterotypic junctions linking the oocyte to follicular cells throughout folliculogenesis and cooperating in the determination of follicle architecture was observed [62]. When oocytes progress in vitellogenesis, the localization of adhesion proteins in the oocyte becomes restricted to a more specific pattern, which reflects the points of contact between the oocyte and the follicle cells and their adjustment to changes in the oocyte cytoskeleton throughout this phase [62].

2.2 Distribution and structuration of the cytoskeleton throughout the oocyte development

All intracytoplasmic and cortical events in oocytes involve a precisely organized and collaborative contractile system and a stable support matrix [68]. The cytoskeleton of the oocytes and embryos is implicated in key developmental events, such as creation and maintenance of axial polarity, cytoplasmic reorganization, cell division, change of surface architecture, morphogenetic motions, and internal arrangement of organelles [69]. It seems very likely that cytoskeletal structures are responsible for spatial distribution of yolk, cortical and pigment granules, lipid droplets, or mitochondria [68, 70]. Thus, the spatial organization of cytoskeletal filaments may be important for the preservation of oocyte viability [71].

Among the different proteins expressed in the cytoskeleton, the intermediate filament proteins are exceptionally complex [72, 73], especially in the class of cytokeratins. This is a class of proteins typical and specifically induced in cells compromised for epithelial differentiation [72, 74, 75], and their identification in oocytes and eggs presents an interesting contrast when comparing to other cytoskeletal proteins in germ cells. Cytokeratins are not synthesized in previtellogenic oocytes but are expressed and accumulated in the vitellogenic stage. These filament proteins are first detectable in the cortex of oocytes in later stages of previtellogenesis; at

the beginning of vitellogenesis, they are distributed primarily in the region closest to the nucleus and appear to become cortical again in mature oocytes [76]. Intermediate filaments of cytokeratin contribute to the complex structure of the oocyte and egg cortex, which is also rich in other cytoskeletal filaments such as actin filaments and microtubules [68, 77–79].

The microtubule matrix seems to be a very important component in the immature oocyte cortex in fish. The function of the cortical matrix of microtubules in oocytes remains undetermined but may be related to the mechanical stiffness that has been attributed to the cortex [80]. Even the basic mechanism of germinal vesicle migration and its mechanical anchoring in the region of the animal pole occur from the depolarization of the microtubules, leading to a consequent change in the position of the germinal vesicle [80, 81].

Evident changes occur in the distribution and localization of tubulin-containing structures in growing oocytes. In previtellogenic oocytes, a great amount of tubulin is concentrated in the Balbiani corpuscle [82–85]. During vitellogenesis, mitochondria are displaced from the Balbiani corpuscle to the surface of the cell, while others remain around the nucleus [82, 86], and this movement seems to be related to the reorganization of tubulin [87]. With the disintegration of the Balbiani corpuscle, due to the anterior displacement of membranous organelles, the released space is gradually filled with yolk, i.e., the yolk granules are in a tubulin-positive region. As vitellogenesis progresses, rearrangement of cell growth and its contents occurs with the movement of endosomes to transport yolk through the microtubules [87].

The proper organization and assembly of the cytoskeleton microtubule is an integral phenomenon, which is related to the expression of cellular asymmetry. Particularly in oocytes, the microtubules exhibit a unique paradigm as forming an eccentric meiotic spindle which, consequently, gives rise to asymmetric cytokinesis to form the first and second polar bodies. Its existence and function are dynamically regulated throughout the process of cell division, particularly during the S and M phases of the cell cycle [88].

Another element that contributes to the oocyte asymmetry is the actin cytoskeleton. In oocytes, the actin filaments are not randomly distributed within the cell [89]. In germ cells, as in many other cells, two types of actin are present: filamentous (F-actin) and non-filamentous (G-actin) actins [90]. Actin polymerization-depolymerization process is essential for the translocation of many organelles, as mitochondria [91], Golgi system [92], and cortical granules [93, 94], as well as for the regulation of ion channel activity [95]. In addition, a certain proportion of F-actin and G-actin is required for the normal course of meiotic and mitotic divisions [96].

In many cells, a significant part of these filaments is in the area of the cellular cortex, so it has been proposed that they take part in the transduction of transmembrane information signals, including hormonal signaling [97, 98]. Still in the oocyte cortex, the cortex-specific F-actin layer is peculiarly absent in the space between the germinal vesicle and the plasma membrane at the animal pole. In fact, it is through this "corridor" that the two polar bodies are extruded in the posterior phase of meiosis [99, 100].

The formation of actin bundles in the oocyte cortex is one of the first morphological markers of induction to maturation [99]. The role of actin microfilaments in oocyte maturation seems to be related to the translocation of the endoplasmic reticulum structures to the germinal vesicle area and to the coordination of the cortical granules in the plasma membrane zone [93, 101]. Even during follicular atresia, the actin cytoskeleton undergoes changes associated with the yolk degradation, while it remains preserved in follicular cells. Thus, maintenance of the actin cytoskeleton may be a sign of survival for follicular cells during early and/or advanced atresia processes [102]. Cytoskeleton changes have been extensively reported in apoptotic cells, among which changes in cell shape and anchorage are dependent on the reorganization of actin filaments and focal adhesion contacts [103].

3. Morphological characteristics related to ovarian reorganization

3.1 Processes of atresia and cellular proliferation

Atresia is a degenerative process by which the ovarian follicles lose their integrity and are eliminated [104]. It is a common process in vertebrate ovaries under natural and/or experimental conditions [105] and can be induced by a series of exogenous and endogenous factors [106–109]. Oocyte degeneration, or follicular atresia, is a process that may occur before spawning, in oocytes that have not reached maturity and thereafter in oocytes that are no longer ovulated [110, 111]. In fish, atresia is involved in normal ovary growth [112, 113] and postovulatory regression [114–116], especially in females that are not able to perform maturation or ovulation after the vitellogenesis process [117].

Fish, in general, exhibits a reproductive periodicity, and, therefore, oocytes at various stages of development may be resorbed with the resultant formation of an atretic body. Considering the foregoing, Rajalakshmi [118] made a classification of the atretic processes taking into account the following stages: (1) "immature oocyte atresia" begins with the distortion of the cell shape, followed by loss of cytoplasmic homogeneity and reabsorption of the structure (in this type of atresia, the follicular cells do not exhibit any activity so the reabsorption of oocytes without yolk seems to be a relatively simple process); (2) "mature oocyte atresia" begins with the loss of the soft outline of the zona pellucida and dissociation of the follicular cells, which will then present phagocytic characteristic (i.e., enzymatic activity of acid phosphatase that will liquefy the yolk), followed by a slow dissolution of the zona pellucida and culminating in total resorption of the follicle; (3) "postovulatory complex atresia" begins with the distortion of the follicular cell shape, followed by loss of cell boundaries and formation of a syncytial structure, and finally the follicle shrink, with consequent degenerative changes.

The morphological characteristics of the atretic bodies and their stages of involution, independent of cellular development stage, were summarized in the study of Miranda et al. [20], as (1) initial atresia, with the disintegration of the oocyte nucleus, fragmentation of the zona pellucida, and follicular cell hypertrophy; (2) intermediate atresia, with follicular cells presenting phagocytic characteristics and ingesting the yolk; (3) advanced atresia, with numerous myelinic figures in the cytoplasm of follicular cells; and (4) final atresia, with the reduction in the number of follicular and theca cells and presence of granules of lipofuscin and granulocytes near the atretic follicle. With the current emergence of the theme of cell death pathways, studies about ovarian involutive processes in fish were brought to the spotlight again with new descriptions being made [102, 108, 116, 119–124] that add and/or corroborate those morphological characteristics already proposed by Miranda et al. [20].

In fish, mammals and, presumably, other vertebrates, the molecular mechanism responsible for ovarian follicular atresia is cell death by apoptosis [102, 124, 125]. Apoptosis, or programmed cell death, is a physiological process controlled by various hormones and growth factors. This is an evolutionarily conserved process, involved in remodeling, differentiation, and tissue degeneration in a variety of cell types [125]. It is characterized by biochemical and morphological changes such as chromatin condensation, DNA fragmentation, and the formation of apoptotic bodies [126]. The main effector proteins in apoptosis are the caspases, a family of highly conserved cysteine proteases [127, 128]. Among the caspases, caspase-3 is the major effector one, including in the ovarian tissue in which it is expressed in the follicular cells of atretic follicles of fish and mammals [102, 124, 129].

In addition to apoptosis, Thomé et al. [130] presented a new route to cell death—the autophagy. This route differs from apoptosis by the purpose of the processes:

apoptosis is the programmed cell death, and autophagy is a stress adaptation to prevent cell death. The functional relationship between apoptosis and autophagy is complex. In some cases, autophagy is a form of adaptation to suppress apoptosis, whereas, in other cases, autophagy constitutes an alternative pathway of cellular elimination called autophagic or type II cell death [131–133]. It has been understood that apoptosis is the main mechanism involved in the involution of postovulatory follicles [116, 121], while autophagy contributes to the regression of atretic follicles [20, 130]. Even though the limits and interrelationships between these two processes have not yet been well established, recent studies have shown that there may be a crosstalk between autophagy and apoptosis pathways in the ovarian involution processes. A fine balance between the signs for survival and cell death appears to be essential for determining the fate of follicular cells, particularly in follicular atresia [102, 124].

During follicular development, a low rate of follicular cell apoptosis can be considered as a physiological event for the control of the appropriate number of cells and elimination of the undesirable ones [134]. However, high apoptosis values can be observed under unfavorable conditions, compromising follicular viability [135]. Thus, organic homeostasis is dependent on the balance between cell proliferation, differentiation, and death, so populations of rapidly proliferating cells usually have high rates of cell death by apoptosis [125, 136].

The mechanism of cell proliferation is a highly regulated process that seems to be essential for the maintenance of ovarian homeostasis [137], and yet the hormonal mechanism controlling oocyte proliferation and recruitment of oocytes is not understood completely for any vertebrate [6]. In contrast to mammals, oogonia continue to proliferate in adult female fish [138], thus renewing stocks of young oocytes and follicles [139, 140]. The pre-follicular and follicular cells begin to proliferate when in the folliculogenesis phase, to support the oocyte growth [19]. However, ovarian mitosis in fish is usually observed at the end of each reproductive cycle [137], when ovarian tissues are reorganized [141, 142]. Throughout ovigerous lamellae in adult females, germ cell proliferation and the formation of germline cysts result in extensions of the germinal epithelium that are segregated from the connective tissue by a basement membrane [19]. These extensions of the germinal epithelium are known as oogonium nests [28, 143] and mark the beginning of the reproductive cycle again.

3.2 Extracellular matrix and its changes through the reproductive cycle

During the reproductive cycle, ovarian tissue is constantly remodeled, with extensive cell proliferation and differentiation, as well as extracellular matrix changes from early follicular development to tissue involution after ovulation [144]. Among the processes and factors involved in tissue remodeling are apoptosis, changes in hormone levels, and degradation of the extracellular matrix in contact with cells [134].

The extracellular matrix is an insoluble network of several structural and functional macromolecules found in connective tissues and basement membranes [145]. It is both a barrier that separates the organism into tissue compartments and a substrate for cell adhesion [146]. In addition to these structural functions, the extracellular matrix is an essential regulator of cellular physiology, predominantly in cell survival, cell cycle, cell migration, and morphogenesis [147].

A coordinated interaction of signals is necessary to regulate the proliferation, differentiation, adhesion, and migration of specific cell types for the development and organization of structural tissues [148]. During the normal development of an organ or in pathological modifications, the matrix undergoes intense changes in its composition. This process, called matrix remodeling, is involved in many

physiological processes, such as activation of immune cells [149], wound healing [150, 151], embryogenesis [152, 153], or reproductive cycle [154].

The extracellular matrix-cell interactions influence gene regulation, cytoskeletal structure, differentiation, and many aspects of cell growth [155]. Changes in the expression of components that make up the extracellular matrix accompany follicular growth, ovulation, and involution of postovulatory follicles, which in its turn may influence follicular maturation, cell survival, and steroidogenesis [134, 156, 157]. Studies with mammals demonstrate that gonadal support cells synthesize a variety of components comprising the extracellular matrix and the basement membrane, such as collagen, laminin, keratin, fibronectin, lectin, and fibril chains [158, 159].

The balance between the degradation and regeneration of the extracellular matrix in ovarian tissues is maintained, in part, by the action of extracellular proteolytic enzymes that are secreted by the local cells. Most of these enzymes are matrix metalloproteinases (MMPs), which depend on the Ca^{+2} or Zn^{+2} binding to their activity [160]. During oogenesis, great changes in the extracellular environment of the ovary were largely attributed to the action of MMPs [144]. MMPs play an important role in the ovulation process in different groups of vertebrates, acting on follicular rupture, basement membrane fragmentation, and follicular connective fibers [144, 161, 162].

The integrity of the basement membrane is also evidenced by the continuous marking of laminin-β2 and type IV collagen, which allows the development of ovarian follicles [159, 163]. On the other hand, the discontinuous labeling of laminin-β2 and type IV collagen in the basal membrane of postovulatory follicles indicates that basement membrane degradation occurs due to the breakdown of these major components [134]. The loss of the basement membrane integrity may contribute to the increase of follicular cell apoptosis, suggesting its influence on the survival of postovulatory follicle cells [116].

Fibronectin and laminin have been shown to be extracellular matrix proteins synthesized by follicular cells [164, 165]. The presence of fibronectin on the surface of postovulatory follicle cells is due to the need of interaction between their domains with type IV collagen and cell surface integrin, and it is important for the maintenance of cell adhesion in the extracellular matrix [159]. According to Iwahashi et al. [166], the type IV collagen detected in the connective tissue among theca cells may be involved in the organization of extracellular fibronectin. This interaction between type IV collagen and fibronectin may act on cell migration that occurs during the late remodeling of postovulatory follicles [134].

Thus, the structure and composition of the extracellular matrix play an important role during follicular development and post-spawning involution in teleost fish. The basement membrane integrity is important for follicular cell survival, and the loss of integrity contributes to increased follicular apoptosis. In addition, MMP-9 may be involved in the final oocyte maturation and regression of postovulatory follicles [134]. Therefore, it follows that different combinations and proportions in the assembly of extracellular matrix components, together with the presentation of a large variety of proteoglycans at various times during the development and maturation of the gonads, can orchestrate distinct gene expression programs and culminate in more diverse tissue variations and adaptations [148].

4. Conclusions

Studies in gametogenesis help to understand the ecological, adaptive, and evolutionary relationships in the groups of species, especially when the oocyte structures are analyzed in an ultrastructural level. This is even more important when we

consider that there are few fish species that present descriptions with adequate morphological and/or functional detail. Most of the studies do not evaluate the reproductive characteristics with the necessary histological and ultrastructural details, which can lead to incomplete interpretations of the reproductive characteristics of the species. Likewise, studies involving organelles and their distribution throughout the reproductive cycle and cellular development in fish species are punctual or restricted to a developmental stage. The understanding of these processes is then due to the sum of several studies at different stages of development, but they do not necessarily represent the same environmental, behavioral, and population pressures that are being addressed to the individuals of a given species. Thus, the continuous study of these variables throughout the reproductive cycle of key species may allow more real parameters on the dynamics of the intracellular structures in germ cells and follicular cells, as well as the extracellular matrix. All of the above is even more relevant when applied to such a diverse group, as fish, that have great ecological, social, and economic importance.

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Conflict of interest

The author declares that there is no conflict of interest regarding the publication of this chapter.

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