Review Article

Changes in Nucleus and Cytoplast During Oocyte Maturation: Involvement in Embryo Production

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Abstract | Embryo production steps either *in vivo* or *in vitro* include oocyte meiotic maturation, fertilization and culture processes. Oocyte maturation is the first step for *in vivo* or *in vitro* embryo production. Oocyte maturation appears to be a simple step, but it is a very complex process. Maturation of oocytes include several changes at the cytoplasmic and nuclear levels that makes the oocytes able to undergo fertilization, pre-implantation and post-implantation embryo development. Oocyte meiotic maturation *in vivo* starts after LH hormone surge whereas it starts *in vitro* upon release of oocyte from the ovarian follicle. Rodent oocyte maturation lasts 15-17hr. whereas that of ruminant oocyte lasts 24hr. Several factors affect on oocytes maturation either *in vitro* or *in vivo* and therefore affect development of the resulting embryos. Because of the significance of oocyte maturation stage on further embryonic development, this review aims to discuss the knowledge of oocyte maturation and its effect on further development of embryos *in vivo* and *in vitro*.

Keywords | Oocytes, Cumulus cells, Cytoplast, Nucleus, Embryos

Received | July 04, 2022; **Accepted** | August 10, 2022; **Published** | September 05, 2022
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Citation | Al Zeidi R, Al Masruri H, Al Mufarji A, Mohammed AA, Mohammed H (2022). Changes in nucleus and cytoplast during oocyte maturation: involvement in embryo production. Adv. Anim. Vet. Sci. 10(9): 2081-2089.
DOI | http://dx.doi.org/10.17582/journal.aavs/2022/10.9.2081.2089
ISSN (Online) | 2307-8316

INTRODUCTION

Ovarian primordial follicles' growth to the preovulatory follicles is dependent on multiple intra-follicular and extra-follicular factors including stage-specific growth as growth and differentiation factor-9 (GDF-9) or basic fibroblast growth factor (bFGF) (Tang et al., 2012) and hormonal factors (Baerwald and Pierson, 2020; O'Connell and Pepling, 2021). Ovarian follicle development occurs during prenatal and postnatal periods through initial and cyclic recruitments (Campbell et al., 1995; 2003). Initial recruitment characterizes dormant primordial follicles' recruitment continuously to the growing follicles' pool whereas cyclic recruitment characterizes antral follicles' recruitment per estrous cycle (Figure 1; Mohammed, 2006). At the onset of each estrous cycle, there is a group of early antral follicles developed to one or more ovulatory follicle(s) continuously through follicles' selection and dominance. Recent interest has grown in the use of aspirated oocytes from antral ovarian follicles of live animals or slaughter-house ovaries for embryo production *in vitro* (Figure 2; Mohammed, 2006) (Mohammed, 2006; Mohammed, 2008; Mohammed, 2014a; Mohammed, 2014b; Mohammed et al., 2019; Ferré et al., 2020; Tian et al.,

2021), which could be used for different purposes.

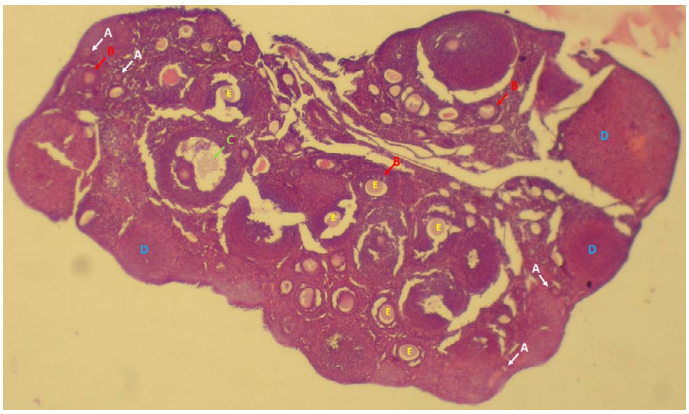

Figure 1: Ovarian follicle structures in mice; pre-antral follicles (A), antral follicles (B), preovulatory follicles (C), corpora lutea (D) and oocytes inside the follicles (E).

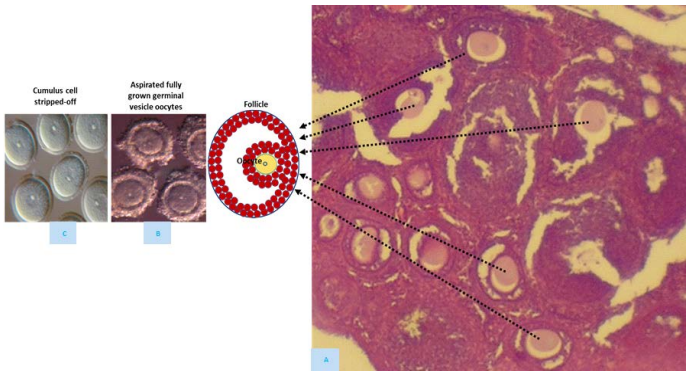

Figure 2: Aspiration of oocytes from follicles (A), antral follicle (B), the collected cumulus-enclosed germinal vesicle oocytes (C) stripped-off cumulus cells from the cumulus-enclosed germinal vesicle oocytes (D) in mice.

Follicle stimulating hormone (FSH), equine chorionic gonadotropin (eCG), luteinizing hormone (LH) and human chronic gonadotropin (hCG) were used for regulating ovarian follicle growth and ovulation *in vivo* (Mohammed et al., 2005; Mohammed et al., 2012a; Mohammed et al., 2012b; Mohammed et al., 2019; Koloda et al., 2022). In addition, culture conditions including gases, culture media and additives to culture media were used *in vitro* for regulating ovarian follicles' growth and development and oocytes' maturation (Mohammed et al., 2005; Mohammed et al., 2020; Salhab et al., 2011; Bahrami and Cottee, 2022). Collectively, the embryos' developmental competence resulting from oocytes *in vivo* matured is higher than those resulting from oocytes *in vitro* matured, reflecting the inefficiency of maturation culture conditions. Because of the significance of oocyte maturation stage on further embryonic development, this review aims to discuss the knowledge of oocyte maturation and its effect on further development of embryos *in vivo* and *in vitro* in addition to the meiotic maturation and development of reconstructed GV cytoplasts.

Growing and Fully-Grown Germinal Vesicle Oocytes

Nuclei of germinal vesicle oocytes are stopped in the diplotene of 1st meiotic prophase stages (Zhang, 2018; Llano et al., 2022; Mohammed et al., 2022). Germinal vesicle oocytes are in a long G2 stage because the last DNA replication round occurred at the 12th to 13th days of fetal stage in mice (Lima-de-Faria and Borum, 1962). Germinal vesicle oocyte must grow and develop to be able to undergo meiotic maturation.

A complex bidirectional attachment between the enclosing cumulus cells and germ cell occurs during oocyte growth and differentiation (Eppig, 1991; Eppig, 2001; Doherty et al., 2022). Oocyte within primordial follicle stage is stopped at prophase of 1st meiotic stages and enclosed by a single layer-squamous cells. Follicles' growth and their containing oocytes are regulated through paracrine factors secreted from both the surrounding cells and germ cell of juvenelle ovary (Eppig et al., 1997). Formation of antral follicles in mice occurs after birth approximately at day 14th. Only a small proportion of oocytes at day 14th of age is competent to resume meiosis. At day 22nd after birth, oocytes aspirated from the large antral follicles have acquired the ability of meiotic maturation and pre-implantation embryonic development (Eppig and Schroeder, 1989).

During oocyte growth, meiotic competence is acquired progressively in mice (Eppig et al., 1994; Němcová et al., 2019; Caballero et al., 2020) and necessitates an accumulation of cell cycle regulatory molecules including $p34^{cdc2}$ and cyclin B (Polanski et al., 1998; Viveiros and De La Fuente, 2019). In addition, meiotic resumption is also associated with further translational and post translational modification of mitotic kinases (Mitra and Schultz, 1996; de Vantery et al., 1997). The growing oocyte undergoes dynamic changes in chromatin and microtubule configurations (Mattson and Albertini, 1990). The nuclear morphology undergoes dynamic modification from a decondensed chromatin configuration (not surrounded nucleolus; NSN) to a condensed chromatin around the nucleolus (surrounded nucleolus; SN) (Wickramasinghe et al., 1991). Both SN and NSN chromatin configurations are found in the fully grown germinal vesicle oocytes (Zuccotti et al., 1995). Synthesis and storage of transcripts during oocytes' growth are essential constructs in oocytes for further embryo development before transcriptional repression takes place at germinal vesicle stage.

Gonadotropins stimulation to mature females resulted in increase of oocytes with the SN configuration (Bouniol-Baly et al., 1999). Gonadotropin stimulation *in vitro* increased the proportion of SN oocytes that have compact enclosed-cumulus cells whereas those oocytes with loosely

or denuded cumulus cells upon stimulation have a similar proportion of NSN and SN configurations (De La Fuente and Eppig, 2001).

Oocyte communication with surrounding cumulus cells is probably essential for both oocyte growth and acquisition of meiotic competency (Eppig et al., 1997). However, both $p34^{cdc2}$ and cyclin B components accumulate in cumulus-enclosed and denuded germinal vesicle oocytes (Chesnel and Eppig, 1995). In addition, neither oocyte growth nor oocyte competence to undergo germinal vesicle breakdown (GVBD) occurs at the same rate in cumulus-enclosed and denuded germinal vesicle oocytes. This suggests that meiotic competence is regulated by an oocyte-intrinsic program and granulosa cells (Chesnel and Eppig, 1995).

Meiotic Maturation of Germinal Vesicle Oocytes

Meiosis occurs in mammalian germ cell up to the diplotene stage during the fetal period. Germinal vesicle oocyte remains blocked at the diplotene stage of the 1st meiotic division in growing and dominant ovarian follicles. The germinal vesicle oocytes resume meiosis after removing from the antral follicles or LH surge (Pincus and Enzmann, 1935; Dieleman et al., 1983). Meiosis resumption *in vivo* is initiated by LH surge and occurs only in fully-grown germinal vesicle oocyte of pre-ovulatory follicle. The oocyte is surrounded before LH surge by layers of compact cumulus-enclosed cells, numerous projections of cells penetrate the zona pellucida and end on the oocyte oolemma with gap junctions. Disruption of these junctions occurs shortly after the LH hormone surge. Between the period of LH surge and ovulation, the fully grown germinal vesicle oocyte of pre-ovulatory follicle undergoes several changes in its GV nucleus and cytoplast known as oocyte maturation. The first sign of resumption of meiotic maturation is GVBD, which occurred approximately 2h of starting maturation in mouse oocytes (Gao et al., 2002; Mohammed et al., 2008; Mohammed et al., 2010; Mohammed et al., 2019; Mohammed and Farghaly, 2018), and thereafter the chromosomes condense, microtubules pull the chromosomes to form the metaphase I (MI) plate. The 2nd meiotic division occurs immediately without chromosome replication and the oocyte reaches the MII stage. The oocytes remain arrested at the MII stage until fertilization occur and the oocyte complete the second meiotic division.

Cytoplasmic maturation involves transformations that prepare oocyte to support fertilization and development of resulting embryo. Both nuclear and cytoplasmic maturation are needed for subsequent embryo cleavages and development (Chang et al., 2005). Cytoplasmic and nuclear maturation are required after fertilization to block polyspermy, to decondense fertilized spermatozoa and to form male and female pronuclei. The cytoplasmic maturation changes include organelles redistribution and mitochondrial migration to a perinuclear position. The nuclear maturation includes the changes from GV to MII stage. Furthermore, ultrastructural changes occurred including changes in maturation-promoting factor (MPF), mitogen-activated protein kinase (MAP kinase) and cyclic adenosine monophosphate (cAMP) levels.

Maturation-Promoting Factor

Meiosis resumption in oocyte is regulated by MPF. MPF is composed of two subunits: $p34^{cdc2}$ and cyclin B (Gautier et al., 1988). $p34^{cdc2}$ is the catalytic component and cyclin B is the regulatory component. Activity of MPF appears shortly before GVBD, maintains at high level during MI stage, decreases prior to the 1st polar body extrusion, and rises again throughout the metaphase II stage (Campbell et al., 1996).

Maturation-promoting factor seems to be the universal regulator of meiotic cell cycles (Wu et al., 1997). MPF phosphorylates number of proteins. MPF is believed to be responsible for GVBD, chromatin condensation and microtubular relocation (Verde et al., 1992). The oocytes then acquire the ability to form a MI plate and a spindle. The next step is progression to the second metaphase plate and 1st polar body extrusion. The last meiotic event is arrest at the MII stage through cytostatic factor (CSF) (Masui and Markert, 1971). Inactivation of MPF by degradation of the cyclin component occur after sperm or parthenogenic activation to meiosis resume (Murray, 1992).

Mitogen-Activated Protein Kinases

Mitogen-activated protein kinases (MAPKs) are known to be involved in maturation processes of oocytes. Two isoforms of mitogen-activated protein kinases (MAPKs) in mammalian oocytes are presented including ERK1 and ERK2 (Sun et al., 1999). MAPKs appears activated after GVBD in mouse oocytes (Gavin et al., 1994). MAPKs activity during oocyte maturation is associated with cytoplasmic events including regulation of microtubule dynamics, spindle assembly and chromosomal condensation (Dedieu et al., 1996).

Regulating growth and development of ovarian follicles *in vivo* and *in vitro* is considered the most important process for successful reproductive performance. The great importance extends to oocyte maturation where essential cytoplasmic and nuclear changes occurs for successful fertilization and further developmental competence of embryos. The potential regulation of ovarian follicles and oocytes' maturation *in vitro* and *in vivo* occur through nutrition and feed additives, hormonal supplementation, conditions

of *in vitro* culture system including gases, culture media, additive to culture media including fetal calf serum, cumulus cells and follicular fluid (FF), hormones and amino acids (Liu and Foote 1995; Mohammed et al., 2005; Ge et al., 2008; Lee et al., 2018). The importance of oocyte maturation confirmed through gene expression, fertilization, timing of embryo cleavage, stage of embryo development and offspring obtained after transfer to the surrogate mothers. The higher the oocyte maturation the higher embryo development and offspring obtained after transfer. Therefore, the success in oocyte maturation would be helpful in assisted reproductive techniques. Further studies are still required to make development of oocyte matured *in vitro* comparable to oocytes matured *in vivo*.

Factors Affecting Oocyte Maturation

Oocyte maturation is the most important step for pre- and post-implantation development of embryos (Mohammed et al., 2005). The *in vitro* maturation of mouse oocyte needs approximately 15-17 hr. (Mohammed and Farghaly, 2018; Mohammed et al., 2008; Mohammed et al., 2010; Mohammed et al., 2019). The cytoplasmic and nuclear changes that occur during maturation of oocyte are important for successful fertilization and embryo development (Mohammed, 2014a; Mohammed et al., 2014b; Mohammed and Farghaly, 2018; Mohammed et al., 2019a; Saini et al., 2022). Changes of maturation promoting and cytostatic factors in addition to two asymmetrical meiotic divisions resulting in a single oocyte and polar bodies for oocyte maturation.

The oocyte resumes meiotic division to the metaphase II (MII) stage *in vivo* after the LH hormone surge and *in vitro* when it removes from antral ovarian follicle and cultured in favorable medium within 5.0% CO2 incubator (Grabarek et al., 2004; Mohammed 2006). Development of *in vivo* matured oocytes to embryos is higher than *in vitro* matured ones (Margalit et al., 2019; Sakaguchi and Nagano, 2020). This might be attributed to insufficient nucleus and/or cytoplasmic maturity (Blondin et al., 1997).

Follicle size (Gordon, 2003; Patton et al., 2021), nutrition and feed additives (Cavalieri et al., 2018; Mohammed, 2018; Mohammed, 2019; Mohammed and Al-Hozab, 2020; Pournaghi et al., 2021; Gutiérrez-Añez et al., 2021; Saini et al., 2022), the media for maturation and their enrichments (follicular fluid, bovine serum albumin, amino acids and hormones: Mohammed, 2006; Mohammed et al., 2005; de Senna Costa et al., 2022), incubator conditions (humidity, CO2 and oxygen concentrations) were found to affect oocyte maturation (Kang et al., 2021; Yousefian et al., 2021).

Enrichment of maturation media with cumulus cells (Al Zeidi et al., 2022), growth factors and hormones (Bunel et al., 2020; Ko et al., 2021; Kumar et al., 2020; Wolff et al., 2022), and other factors (Martínez-Quezada et al., 2021; Zabihi et al., 2021; Saini et al., 2022; Chelenga et al., 2022) improves oocyte maturation and embryo development thereafter (Gordon 2003; Baruffi et al., 2004; Somfai et al., 2012). In addition, super-stimulation of ovarian follicles via gonadotropin injections resulted in changes in small, medium, and large follicles according to the number and dose of gonadotropin injections and side of the ovary (Abdelnaby et al., 2021). FSH stimulates transcription and translation in ovarian granulosa cells, which are essential for female reproductive endocrine regulation (Dai et al., 2021). Collectively, it could be concluded that the *in vivo* and *in vitro* conditions or factors effect on oocytes' maturation and their developmental competence to embryos and fetus.

Germinal Vesicle Cytoplast For Creation "Artificial Gamete"

Fully-grown germinal vesicle (GV) cytoplasts could be divided through two consecutive meiotic divisions; first and second meiotic divisions if cultured *in vitro*. The hypothesis that the GV cytoplasts are able to divide G0/G1 or G2/M nucleus through first and second meiotic divisions, respectively (Mohammed, 2006; Mohammed, 2014a; Mohammed et al., 2014b; Mohammed et al., 2010; Mohammed et al., 2019a; Mohammed et al., 2022; Al Zeidi et al., 2022). Therefore, GV nuclei, male germ cells, embryonic and somatic cells at G0/G1 or G2/M stage might divide correctly in the GV cytoplasts through 1st and 2nd meiotic divisions, respectively to solve the problem of infertility as ageing-associated chromosome misalignment in meiosis of oocytes from the aged mice or studying reprogramming of the introduced nuclei or nucleolar dysfunction (Fulka et al., 2004; Mohammed et al., 2022; Al Zeidi et al., 2022). In case of male infertility due to complete absence of the germline, GV cytoplast could be reconstructed with germ cell of male in order to create "artificial oocyte" containing the male haploid genome of the fused germ cell after *in vitro* maturation.

Unfortunately, the few trials so far concerning the GV cytoplast reconstructed with embryonic/somatic nuclei resulted in abnormalities in maturation compared to normal maturation if the GV cytoplast reconstructed with GV nucleus (Figures 3, 4 & 5; Mohammed, 2006). One of the first studies in which GV oocytes were reconstructed with G_0/G_1 somatic nucleus performed by Kubelka and Moor et al. (1997) and Fulka et al. (2002). These studies failed to obtain 1st meiotic maturation of cell-oocyte complex. However, Polanski et al. (2005) reported meiotic maturation of G0/G1 cumulus cells after their transfer into GV cytoplasts. Reports thereafter described the meiotic mat

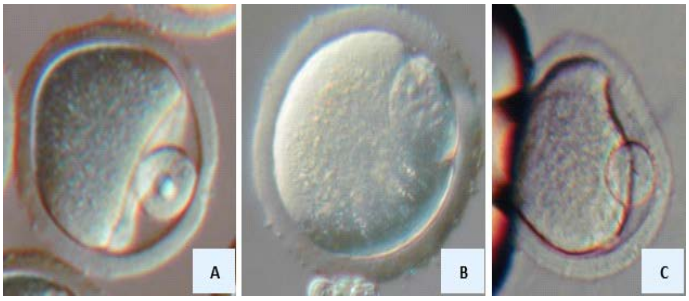

Figure 3: Germinal vesicle cytoplast used for germinal vesicle (A) embryonic (B) and somatic (C) nuclear transfer

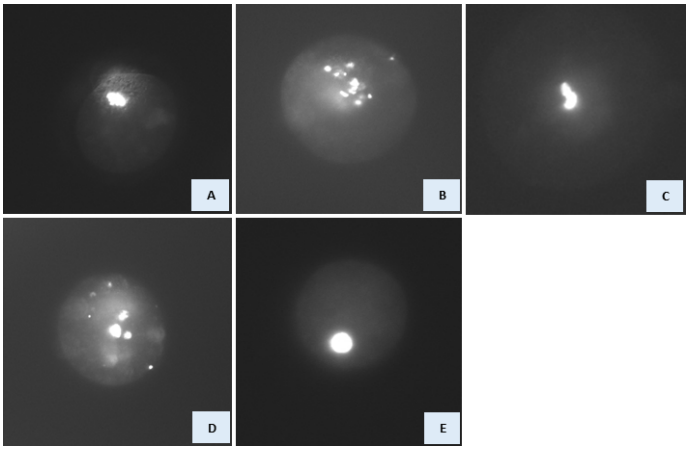

Figure 4: Nuclear morphology at the expected MI stage of GV cytoplasts reconstructed with GV, embryonic and somatic nuclei. DNA was stained with Hoechst 33342. A) GV cytoplast reconstructed with GV nucleus. Various abnormal nuclear morphology was observed in manipulated GV cytoplast reconstructed with embryonic/somatic at the expected MI stage. These include: condensed, scattered chromosomes (B), partially condensed chromosomes (C), formation of micronuclei and «pycnotic» nuclei (D), and interphase-like nuclei (E).

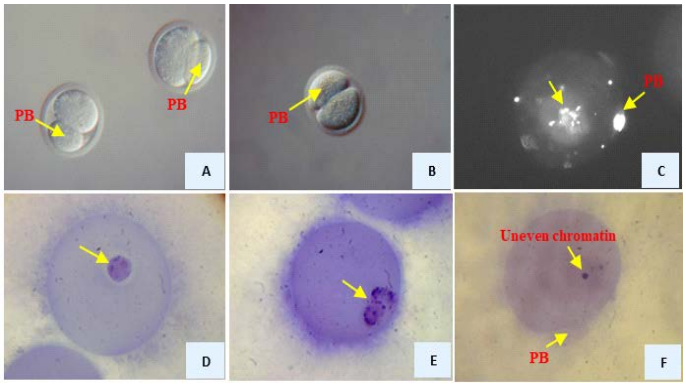

Figure 5: Reconstructed GV oocytes with somatic cells after 17 hr. of maturation. Extruded large-sized PBs (A, B), DNA was stained with Hoechst 33342 where the oocyte had scattered chromosomes (C), DNA was stained haematoxyline where the oocyte had interphase-like nucleus (D), the oocyte had partially condensed chromosomes (E) the oocyte had uneven distribution of chromatin (micronuclei)

uration of the enucleated GV oocytes after nuclear transfer of G2/M stage embryonic or somatic (Grabarek et al., 2004; Chang et al., 2004; Mohammed 2006; Mohammed et al., 2008; Mohammed et al., 2010; Mohammed et al., 2019a; Mohammed et al., 2022) cell nuclei. The previous results demonstrated that meiotic maturation of GV cytoplasts reconstructed with embryonic/somatic cells (G0/G1 or G2/M stage) were associated with abnormalities in earlier extrusion of 1st polar body, chromosomal alignment over spindle and condensation, and cytokinesis (Figures 4 and 5; Mohammed 2006). Our trials to overcome and to explore such abnormalities have been reported (Mohammed 2006; Mohammed et al., 2022; Al Zeidi et al., 2022). Such previous trials improved the competence of enucleated GV cytoplast after embryonic/somatic nuclear transfer followed by maturation and activation/fertilization. The proper pronuclei of the introduced embryonic/somatic nucleus were formed in addition to the male pronucleus in case of fertilization. The zygotes proceed development to the blastocyst and hatching/hatched stage. This was occurred through a technique called "selective enucleation" of GV oocyte surrounding with cumulus cells. In this technique. the nucleolus and nuclear sap were left in the GV cytoplast in addition to cumulus attachment with zona pellucida. Such selective enucleation technique reached the reconstructed GV cytoplasts to the embryonic stages of blastocysts and hatched blastocysts compared to complete enucleation of denuded GV oocyte. The germinal vesicle cytoplasts obtained with technique called "complete enucleation" where the whole GV nucleus removed upon enucleation.

Over reconstruction with embryonic/somatic nuclei, the GV cytoplasts were blocked at one cell-stage embryos. Hence, further studies are still needed required for improvement embryos development, which obtained through GV cytoplast reconstructed with embryonic somatic nuclei in addition to obtaining offspring over embryo transfer to surrogate mothers.

CONCLUSION

Regulating ovarian follicles' growth and development either *in vitro* or *in vivo* is considered necessitate process for successful reproductive performance. The great importance extends to oocyte maturation where essential cytoplasmic and nuclear changes occurs for subsequent fertilization and development of the resulting embryos. The potential regulation of maturation of ovarian follicles and oocytes either *in vitro* or *in vivo* occurs through nutrition and feed additives, hormonal supplementation, conditions of *in vitro* culture system including gases, culture media, additive to culture media including fetal calf serum, cumulus cells and follicular fluid (FF), hormones and amino acids.

The importance of oocyte maturation confirmed through gene expression, fertilization, timing of embryo cleavage, stage of embryo development and offspring obtained after transfer to the surrogate mothers. The higher the oocyte maturation the higher embryo development and offspring obtained after transfer. Therefore, the success in oocyte maturation would be helpful in assisted reproductive techniques. Further studies are still required to make development of oocyte matured *in vitro* comparable to oocytes matured *in vivo*.

ACKNOWLEDGEMENTS

This work was supported through the Annual Funding track by the Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Saudi Arabia [GRANT 1015].

CONFLICT OF INTEREST

There is no conflict of interest for authors to declare.

AUTHORS CONTRIBUTION

Mohammed wrote and submit manuscript. Al Mufarji, Haitham Al Masruri, Rashid Al Zeidi, and Al-Hassan Mohammed collected references and prepared figures.

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