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Histology of the ovary of *Chinchilla lanigera* in captivity

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ABSTRACT

Chinchilla, the lanigera variety in particular, is one of the most valuable rodents in the fur industry. The chinchilla ovary is morphologically similar to that of other South American hystricognath rodents, especially as regards its anatomy and, to a lesser degree, its histology.

The presence of numerous primary follicles throughout the annual cycle suggests that a few of them are recruited to initiate growth and differentiation during folliculogenesis. Primary follicles with two or more oocytes are common; this is not the case with follicles at more advanced stages, suggesting that they do not develop.

Only one or two large corpora lutea (CL) and three to five small or accessories CL were observed but no corpora albicans. The presence of accessory CL may reflect the importance of continuous hormonal production to support prolonged gestation. Atretic CL were also present, showing signs of degeneration in luteal cells. The interstitial cells distributed throughout the cortex were the main histological feature shared with other species, as stated in previous reports. Antral atresia was observed in all sizes of antral follicles while basal atresia was confined exclusively to smaller follicles.

1. Introduction

Chinchilla, together with squirrel, beaver, mouse and rat, belongs to the order Rodentia which, with its almost 2000 species, constitutes the most numerous order of mammals. A nocturnal rodent, native to South America, chinchilla (*Chinchilla lanigera* and *Chinchilla brevicaudata*) belongs to the suborder Hystricomorpha, whose members have a similar reproductive pattern. They are fully developed at birth, fully furred and with open eyes. Their gestation period is longer than that of other rodents (111 days) and they usually have 1 or 2 young per litter.

Chinchillas, seasonal polyestrous animals whose reproductive period ranges from November to May in the northern hemisphere and approximately from April to October in the southern hemisphere, are native to the Andes Mountains and inhabit the Andean plateau from southern Peru and western Bolivia to northwestern Chile and Argentina. Wild chinchillas are mainly vegetarian, live in rocky caves, and develop thick fur because of the cold climate. They always live in colonies, as they are social animals. Their fur is highly appreciated, which has led to indiscriminate hunting resulting in a dramatic decrease in the wild population. The maximum lifespan of wild chinchillas is 6 years. In captivity, it ranges from 12 to 15 years, a difference attributable to factors such as the greater amount of available food and the absence of predators. Because of the characteristics of its fur, chinchilla is one of the most valuable rodents in the fur industry, so that at present most chinchilla specimens are farm raised, especially those of the lanigera variety.

Studies of the anatomy of chinchillas of include detailed descriptions of their external morphology and reproductive cycle (Hillyer et al., 1997; Jimenez, 1990). Weir (1966,

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1974) conducted the analysis and description of the chinchilla reproductive system, this being the only existing study up to the present.

An important problem in the intensive breeding of chinchillas is their low reproductive rate and the lack of knowledge of their reproductive biology. The aim of the present study was to provide a histological description of the ovary, during the sexual maturity of adult *C. lanigera* in captivity.

2. Materials and methods

2.1. Animals

We worked with fourteen sexually mature females of *C. lanigera* weighing 750–800 g. All animals were maintained under a 12-h light–dark cycle (lights on from 07:00 to 19:00) at a constant temperature of $22 \pm 1\,^{\circ}C$, with food and water *ad libitum*. The animals were sacrificed by cervical dislocation and immediately taken to the laboratory in thermal containers to maintain constant temperature. Both ovaries were extracted and immersed in a fixative solution. Samples were taken during the May–August period.

2.2. Processing of samples

For the general histological description, ovaries were fixed in Bouin's solution and embedded in Histoplast. 5-μm thick sections were obtained and stained with hematoxylin–eosin (H–E). Four ovaries were fixed in a mixture of glutaraldehyde 2.5% and phosphate buffer 0.1 M at pH 7.4. After dehydration, they were embedded in epoxy resin to obtain 0.5- and 1-μm sections with an ultramicrotome and stained with Toluidine Blue (TB), which can infiltrate resin on a hot plate and reach the tissue. For determination of polysaccharides, mucopolysaccharides, glucolipids and glycoproteins, the ovaries were fixed in buffered formalin (pH 7.0) and stained using periodic acid Schiff plus H–E (PAS H–E). All slices were analyzed with an optical microscope.

2.3. Statistical analyses

Microphotographs were taken and ovary size and structure were determined with TSView version 6.2.4.5. Data are expressed as means ± standard error of the mean (SEM).

3. Results

The ovary is oval-shaped, with an average length and width of 3.41 ± 0.31 mm and 2.02 ± 0.36 mm respectively. It has two zones not clearly defined: the outer zone, the cortex and the inner zone, the medulla (Plate 1A).

3.1. Histomorphological characteristics of the ovary

The histological analysis of ovary sections stained with H–E reveals that the ovary surface is delimited by a flat epithelium that in some regions becomes cuboidal with cells with intensely basophilic nuclei. In all cases, the cytoplasm is acidophilous (Plate 1C). The epithelial cells have an average height of 2.85 ± 0.30 μm. The surface epithelium forms a continuous layer with the mesothelium lining the mesovary.

The layer of thick compact fibrous tissue under the epithelium, made up of collagen fibers and fibroblasts, is the tunica albuginea, with an average thickness of 26.26 ± 2.42 μm. This layer is thicker in the zone where the ovary meets the mesovary, its thickness being greater in older females. The direction of the collagen fibers immediately beneath the lining epithelium does not follow a uniform pattern throughout the ovary: In some regions vertical fibers prevail while in others horizontal fibers are more abundant (always with respect to the lining epithelium). These underlying fibers show a plexiform arrangement and numerous cells with oval or fusiform nuclei (similar to those in the rest of the stroma) can be observed among them. The tunica albuginea sends out trabeculae toward the inside of the ovary (Plate 1C).

A cellular stroma can be observed, with prevalence of extremely compact fusiform cells with oval nuclei. It is made up of connective tissue with mainly collagenous fibers radiating in all directions. All the elements that make up the ovarian parenchyma are immersed in the connective tissue or stroma.

In the zone corresponding to the medulla, nerves and large blood and lymphatic vessels (hilium of the ovary) can be seen. In addition, remains of the rete ovarii can be observed as a set of interconnected ducts lined by a simple or pseudostratified cuboidal epithelium surrounded by lax connective tissue. Inside these ducts secretory material can be found (Plate 1F and G).

Ovarian follicles at different developmental stages are located in the cortical stroma as well as luteal bodies of different sizes and follicles undergoing atresia. Both follicles and luteal bodies are surrounded by connective tissue with abundant collagen fibers (Plate 1A).

In the cortical zone, cell clusters or strings of cells different from the rest of the stromal cells can be observed (Plate 1D). These clusters, which are well irrigated, have secretory characteristics and are surrounded by connective fibers. Cells are eosinophilous and have lipid inclusions revealed by TB staining. These cell clusters are called interstitial glands. Interstitial tissue increases with the age of the females, occupying almost the whole stroma of the organ (Plate 1B).

In adult females the ovary presents follicles of all sizes. In general, the cortex is formed by a large proportion of very small follicles of the primordial and primary type. Toward the inside of the organ, we can find secondary preantral and antral follicles and preovulatory or mature follicles that return to the surface before ovulation occurs (Plate 1A). The ovary of senile animals (over 8 years old) shows few developing follicles (Plate 1B).

3.2. Description of the different follicle types

3.2.1. Primordial follicles (PrF)

These are the smallest follicles and are arranged in strings or groups in the ovarian cortical stroma, beneath the tunica albuginea. PrF are the prevailing type during all

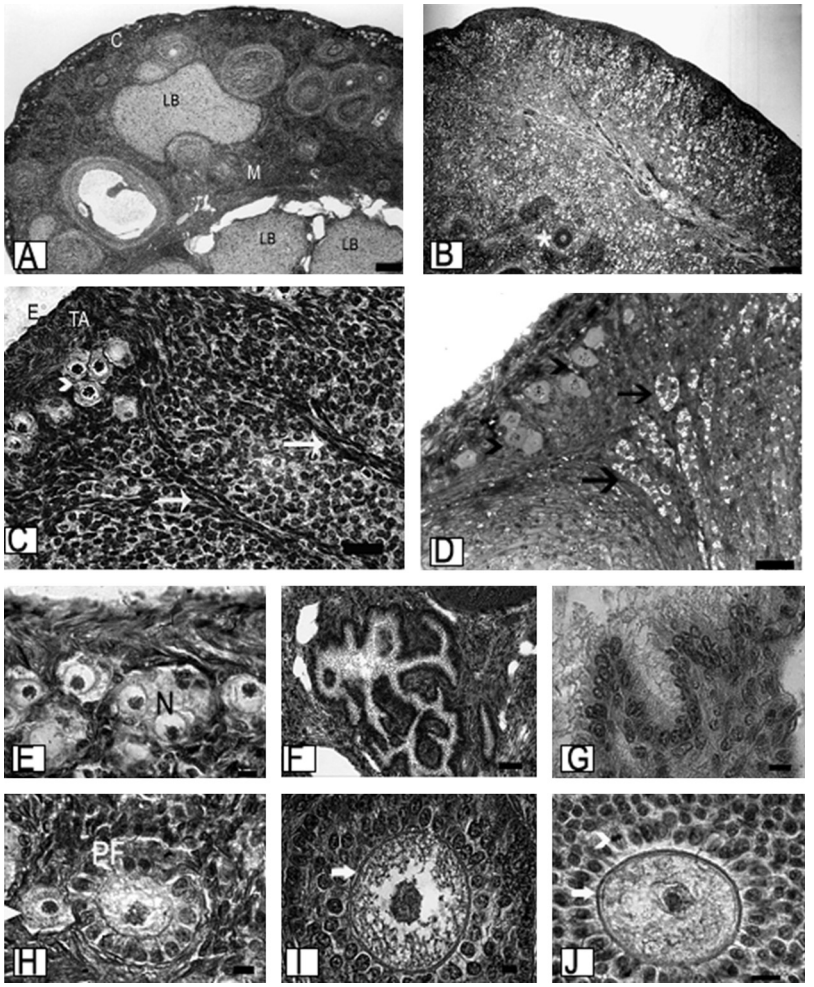

Plate 1. (A) Young adult female ovary, C: cortex; LB: luteal body; M: medulla. PAS H–E. Scale bar represents 121.18 μm. (B) The ovary of senile animals shows few follicles (asterisk). H–E. Scale bar represents 153.71 μm. (C) Connective tissue trabeculae (arrows). E: lining epithelium; TA: tunica albuginea; primordial follicle (arrowhead). PAS H–E. Scale bar represents 25.88 μm. (D) Interstitial glands (arrows); primordial follicles (arrowheads). TB. Scale bar represents 22.49 μm. (E) Primordial follicles in nest (N). H–E. Scale bar represents 10.38 μm. (F) Rete ovarii (200×). H–E. Scale bar represents 38.38 μm. (G) Rete ovarii at higher magnification (1000×). H–E. Scale bar represents 12.88 μm. (H) Primordial (arrowhead) and primary follicle (PF). H–E. Scale bar represents 7.56 μm. (I) Small secondary follicle with pellucid zone (arrow). H–E. Scale bar represents 6.18 μm. (J) Secondary follicle with granulosa cell in metaphase (arrowhead). H–E. Scale bar represents 16.69 μm (A, C, D, E, F, G, H, I and J correspond to young adult female ovary).

the months of the reproductive cycle with an average size of 25.76 ± 1.61 μm (Plate 1H).

The PrF is formed by a primary oocyte arrested in the diplotene of prophase I of meiosis, covered by a single layer of 3–6 flat follicle cells with oval nuclei supported on a basal layer. On some occasions, several oocytes are surrounded by the same follicle cells: These "oocyte nests" can have from 2 to 6 oocytes (Plate 1E). During this stage, oocytes are 21.46 ± 3.44 μm in size and present a voluminous nucleus centrally located with abundant heterochromatin.

3.2.2. Primary follicles

During the differentiation of primordial follicles, oocytes, follicle cells and the surrounding stroma undergo numerous structural modifications. Oocyte size increases and flat follicular cells proliferate and become cubical. When follicle cells form a monolayer of cubic-shaped cells, the follicle is called primary follicle and has an average size of 49.86 ± 4.00 μm.

The oocyte is located in the center of the follicle and its nucleus presents abundant heterochromatin. The nucleolus is prominent, with an average size of 28.88 ± 3.25 μm (Plate 1H). Between the oocyte and the follicle cells an extracellular matrix appears. It is specialized, homogeneous, extremely acidophilic, and is called pellucid zone. This extracellular matrix is formed by glycoproteins and plays an important role in fertilization.

Numerous primary follicles begin to develop at the same time, but only a few reach the ovulatory stage.

3.2.3. Secondary follicles

The single layer of follicle cells surrounding the oocyte undergoes mitosis and constitutes a stratified follicular epithelium resulting in the formation of a secondary follicle. Follicular cells proliferate until they have formed two

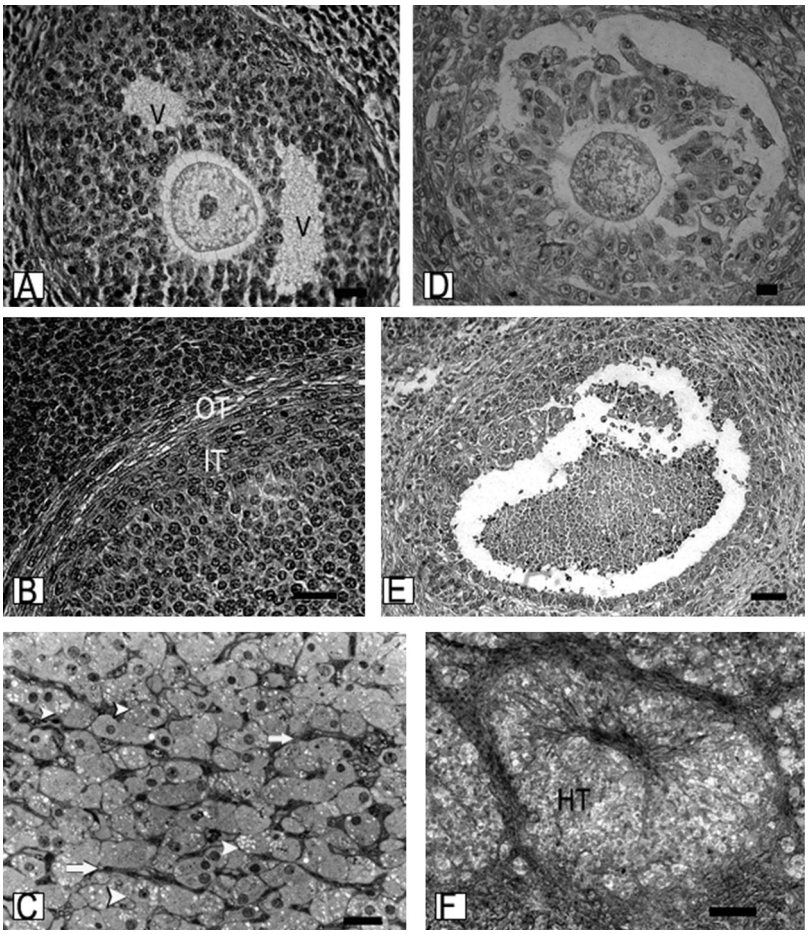

Plate 2. (A) Secondary follicle with vacuoles (V). H–E. Scale bar represents 21.88 μm. (B) Thecae large secondary follicle (IT: inner theca; OT: outer theca). H–E. Scale bar represents 26.84 μm. (C) Luteal body cells. Cells of lipid vacuoles (arrowheads); cells of fusiform shape and dark appearance (arrows). TB. Scale bar represents 18.21 μm. (D) Basal atresia. H–E. Scale bar represents 17.90 μm. (E) Antral atresia. H–E. Scale bar represents 43.84 μm. (F) Obliterative atresia with hyperplasia of the inner theca (HT). TB. Scale bar represents 46.19 μm.

or three layers that surround the oocyte. The external layer of follicle cells rests on the basal membrane to which connective tissue cells that form the follicular thecae are attached. These theca cells become gradually differentiated into inner and outer theca. The former has blood vessels and the latter is made up of dense connective tissue (Plate 2B). The stratified epithelium together with the basal lamina and the internal and external thecae form the follicle wall.

Secondary follicles show different stages of development according to the number of follicle cell layers that constitute them. Follicle cells modify their cytoplasm, which becomes granular, so that they are now called granulosa cells. Oocyte size increases, the nucleus becomes externally located, chromatin is laxer and the nucleolus is clearly visible.

Two types of follicles are distinguished according to their histological characteristics, preantral follicles (with no fluid) and antral follicles (with fluid). The mean diameter of preantral follicles is 150.82 ± 3.13 μm. The oocyte is larger than in the previous stage and remains so until the end of development. It is surrounded by 2–8 concentric layers of granulosa cells and has a diameter of 51.36 ± 4.6 μm (Plates 1I, J and 2B).

Antral follicles have an average size of 250.7 ± 11.06 μm, are made up of 9–15 layers of follicle cells and present one or several lacunae (Exner vacuoles) that coalesce into a single antrum, the follicular antrum. In both types of follicles granulosa cells present the same characteristics; most of them are polygonal cells with rounded nuclei, with the exception of the ones in the outer layer (in contact with the basal membrane), which are cylindrical and with ovoidal nuclei. We can see cells at different mitotic stages (Plate 2A).

The pellucid zone, about 1.5 ± 0.28 μm thick and clearly visible between the oocyte and the granulosa cells, is PAS positive. The follicle cells in contact with this zone send out prolongations that pass through it and contact the oocyte plasma membrane. Through these prolongations "communication" is established between the oocyte and the follicular cells that are fundamental for the development of the oocyte and the follicles (Plate 1J).

In large secondary follicles the inner theca is differentiated from the outer theca; it is formed by several

layers of polyedric cells with oval or rounded nuclei and is approximately 21.6 ± 2.3 μm. The outer theca is formed by fusiform cells with more flattened nuclei, among which there are numerous connective fibers and positive PAS material. Although it is difficult to determine the end of the outer theca since it is continuous with the stromal tissue (Plate 2B), its average size is 22 ± 2.8 μm.

3.2.4. Tertiary follicles

Tertiary follicles have a mean diameter of 656.2 ± 7.5 μm. They are larger than secondary follicles and have a well-developed antral cavity. Antrum liquid is eosinophilic and PAS positive (on occasion it appears precipitated due to a device of the histological technique).

The oocyte no longer occupies the central position. It is displaced toward one side of the antrum and surrounded by granulosa cells, thus forming the cumulus oophorus.

The basal membrane that delimits the follicle can be clearly seen and presents PAS positive material. The shape of granulosa cells is the same as in the previous stage, the cylindrical shape of the basal cells being more noticeable. The inner theca, with a thickness of 20.81 ± 2.23 μm and the outer theca, with a mean thickness of 30.01 ± 2.99 μm, are clearly visible. In both the characteristics of the theca of the large secondary follicles are more strongly marked.

3.2.5. Preovulatory follicles

The diameter of the preovulatory follicles (POF) ranges from 930 to 1200 μm. The size of the follicles is mainly due to the abundant secretion of follicular liquid.

The antrum is larger and the granulosa cells present the same characteristics as in the tertiary follicle. The theca, as in the tertiary follicles, is very well differentiated and irrigated by numerous blood capillaries.

The cumulus oophorus appears as a prominence in the antrum. The granulosa cells that form the cumulus are cylindrical, with rounded nuclei, and are arranged in 5 or 6 cell layers. These cells form the corona radiata surrounding the oocyte. The follicle walls become thinner due to the reorganization of the granulosa cells that no longer undergo mitosis.

3.2.6. Corpora lutea

In adult chinchilla females there are numerous large and medium-sized luteal bodies (Plate 1A). Cells present an eosinophilic cytoplasm of granular aspect with round nuclei and lipid vacuoles. Among these cells, other cells of fusiform shape and dark appearance can be observed. In the larger luteal bodies blood vessels are present (Plate 2C). Luteal bodies are well delineated by connective tissue that sometimes sends out trabeculae toward their inside.

3.2.7. Atresia

Follicular atresia is a degenerative process undergone by follicles that fail to reach complete maturation. Atretic follicles are evidenced because degenerative processes of the oocyte, the pellucid zone and the granulosa cells can be observed in them. Picnotic nuclei and vacuoles as well as thickening of the basal membrane can be seen.

Different types of atretic follicles exist in most chinchilla ovaries. In antral atresia, cellular alterations start in the granulosa cells of the most antral layers while the cells in the basal layers are still normal (Plate 2E). In basal atresia, on the other hand, the granulosa cells of the basal layers are the first to show alterations while the cells close to the oocyte exhibit normal morphology (Plate 2D).

Obliterative atresia can occur where there is marked hyperplasia of the inner theca that occupies practically the whole area of the former follicle. In this case, disorganized granulosa cells can be observed with vacuoles and PAS positive material, probably remains of the pellucid zone (Plate 2F).

4. Discussion

Despite the diversity of reproductive patterns observed in the suborder Hystricomorpha (Weir and Rowlands, 1974), the general morphology of the reproductive organs of chinchilla is similar to that observed in other South American hystricognath rodents (*Erethizon* sp., Mossman and Judas (1949); *Lagidium* sp., Pearson (1949); *Agouti paca*, Weir (1966, 1974); *Myoprocta pratti*, Rowlands et al. (1970); *Lagostomus maximus*, Weir (1971a,b); *Cuniculus paca*, Matamoros (1981); *Dasyprocta fuliginosa*, Mayor et al. (2011) and *Myocastor coypus*, Felipe et al. (1998, 1999). Our study agrees with the anatomical description of South American hystricognath rodents and, to a lesser degree, with the histology. The chinchilla ovary is oval-shaped, flattened, with a relatively smooth outer surface where translucent follicles may be found. It is only partially enclosed in the ovarian bursa, a structure that in other hystricognath rodents such as brush-tailed porcupine, *Atherurus africanus* (Jori et al., 2002), guinea pig (*Cavia porcellus*) and murine mouse opossum (*Marmosa murina*) (Weir and Rowlands, 1974) completely surrounds the ovary.

The ovary is composed of a cortical and a medulla zone without a clear demarcation between them. The cortical zone of the ovary consists of an epithelial monolayer cell below which the tunica albuginea and the population of follicles at different developmental stages are located. The trabeculae of the tunica albuginea that enter the ovary stand out.

Morphometric analyses showed that the diameter of the follicles and their associated structure is much larger than that reported by Flamini et al. (2009) in viscacha (*L. maximus*) and by Felipe et al. (1999) in coypu (*M. coypus*).

In peripheral areas of the ovary cortex, close to the tunica albuginea, primordial, primary and small secondary follicles were found as in *Hystrix africaeaustralis* (Van Aarde and Skinner, 1986). Primordial and primary follicles constitute the population of non-growing follicles as defined by Gougeon and Chainy (1987).

The transition of the primordial follicle to a primary follicle is independent of the hypophyseal hormones and takes place in response to autocrine and paracrine mechanisms between the oocyte and the somatic cells that surround it. In the ovary of chinchilla, these types of follicles were commonly observed.

Some primary follicles with two or more oocytes were found. This characteristic has also been observed in African porcupine (Van Aarde and Skinner, 1986) and *L. maximus* females (Flamini et al., 2009). Each oocyte in the follicle is surrounded by the pellucid zone. However, such polyovular follicles were not found in the other follicular development stages, suggesting that they do not develop or are eliminated.

In chinchilla only one or two large and three to five small corpora lutea or accessory CL (CLA) were identified. In this species the females usually have one and exceptionally two embryos that survive to term. The follicles from which ovulation did not occur undergo luteinization, forming accessory CL. The formation of CLA may respond to an adaptive strategy of reproduction in order to achieve the formation of mature offspring at birth, which would have a greater chance of survival compared to other rodent species. In this sense, several authors (Weir, 1971b; Weir and Rowlands, 1974 and Bowen-Shauver and Gibori, 2004) refer to the persistence of primary and accessory corpora lutea during pregnancy in the plains viscacha and suggest that in this species the placenta does not substitute the endocrine function of ovarian structures as it occurs in porcupine, degu, carisagua and rat. In the case of *A. paca* (Montes Pérez and Cabrera Baz, 2006) and viscacha (*L. maximus*) (Flamini et al., 2009), the formation of these CLA apparently occurs in order to create an environment conducive to maintaining gestation.

In chinchilla, CLA are smaller than the functional structures. However, all corpora lutea are histologically similar or have the same properties or the same types of cellular constituents. Luteal cells in true CL and accessory CL have a similar diameter.

Probably, as observed in the South American plains viscacha (Jensen et al., 2006), follicles from which ovulation does not occur become atretic due to suppression of follicular apoptosis and are transformed into accessory CL by luteinization of the granulosa cells.

In chinchilla, atretic CL was also present, showing signs of degeneration in luteal cells although no corpora albicans were observed.

Chinchilla ovary, in a similar way to that of viscacha (Gil et al., 2007), exhibits interstitial glands. These glands are derived from cells of the inner theca of almost mature atretic follicles. This interstitial tissue is considered as the third gland of the ovary since it produces androgens, especially testosterone and androstenedione (Gil et al., 2007).

One of the main histological differences that we found in *C. lanigera* with respect to other species is the large amount of interstitial cells distributed throughout the ovarian cortex, which raises the question of their origin and function in this species.

While in chinchilla and viscacha interstitial tissue is abundant, these glands do not seem to be present in some rodent species such as agoutis (*Dasyprocta aguti*) (Almeida et al., 2003) and coypu (Hillermann et al., 1958; Felipe et al., 1999). In the ovary of guinea pig, interstitial tissue is scarce (Rood and Weir, 1970; Weir, 1971c; Weir and Rowlands, 1974). In chinchilla, interstitial tissue, which is more abundant in senile females, becomes more evident with TB staining.

The rete ovarii develops from migrating cells of mesonephric origin in the developing gonad of the embryo (Wenzel and Odend'hal, 1985). In chinchilla and viscacha ovary (Flamini et al., 2009), the rete ovarii is generally constituted by groups of ducts with a cubical or columnar epithelium. These ducts are located in the hilum of the ovary and may extend through the medulla. The secretory capacity of the epithelium is retained, as evidenced by the presence of material secreted into the lumen of the ducts.

Follicular atresia is a degenerative process undergone by follicles that do not reach full maturation. The cells of atretic follicles have the morphological and biochemical characteristics of death by apoptosis. The classification of atresia into two types was made according to Irving-Rodgers et al. (2001): (1) Antral atresia, where cellular changes begin in the granulosa cells of the antral layers by initial destruction of those closest to the antrum, while the most basal layer cells remain intact and the inner theca has no major changes. (2) Basal atresia, showing destruction of the architecture of the basal granulosa cells. Apoptotic bodies were common in the basal granulosa cells, while the cells surrounding the oocyte showed normal morphology.

In chinchilla ovary antral atresia was observed in all sizes of antral follicles although basal atresia was confined almost exclusively to smaller follicles. In addition, macrophages were not observed in the granulosa layers of healthy follicles or in antral atretic follicles until the very late stages of degeneration.

In conclusion, in *C. lanigera* the general ovarian histological structure is similar to that of other hystricomorphs while the large number of primary and accessory corpora lutea and the abundance of interstitial tissue make them distinctive features in this species.

Conflict of interest

The authors declare that there are no conflicts of interest.

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