OVARIAN DIFFERENTIATION IN THE CAT AND DOG DURING THE PERINATAL PERIOD

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In this study the early perinatal development of cat and dog ovaries was studied using light microscopy. We observed that primordial germ cells migrated towards the gonadal anlage and became incorporated into the surface epithelium. Proliferating primordial germ cells represented a basal store of germ cells within the ovary cortex. These germ cells then lined up into a typical cord-like arrangement within the cortico-medullary region. The basal pool of follicular granulosa cells originated from the dividing cells of the surface epithelium. The appearance and the origin of these cells differed from the interstitial elements (cells of connective tissue) of the ovarian cortex. The original cortical elements formed a layer of *theca folliculi interna* around the growing ovarian follicles.

cat; dog; ovaries; development; surface epithelium; primordial germ cell; ovarian follicle

INTRODUCTION

The female gonad develops from three different tissues: 1) the coelomic epithelium, 2) the mesenchyme of part of the mesonefric ridge, and 3) the mesonefric tubules which grow towards the gonad, enter it and form the rete ovarii. The coelomic epithelium forms the surface epithelium of the ovary. Mesenchyme and rete tubules form the tissue of the medulla and they populate the cortex together with the germ cells. The granulosa cells, which become attached to the surface of the oocyte during the folliculogenesis, could therefore arise from cells of the surface epithelium, the mesenchyme, or the rete ovarii (Peters 1978).

Twenty or thirty years ago, some authors observed that the exterior of the mammalian ovary is covered by the ovarian surface epithelium. This epithelium is formed by peritoneal mesothelium descending from the mesovarium. At the same time, the presence of oocytes was described within this epithelium. Based on these reports, it was incorrectly assumed that the neoforma-

tion of oocytes occurred within the ovarian surface epithelium and that oocytes moved from the ovarian surface epithelium to the ovarian cortex. This hypothesis led some investigators to describe the surface epithelium as the germinal epithelium. This designation appears to be wrong, since the ovarian surface epithelium obviously does not represent the source of germ cells (Franchi et al., 1962; Odor, Blandau, 1969).

Several authors (Kurilo, 1980; Kurilo, Teplyakova, 1986; Kurilo et al., 1987) suppose the germ cells moved from the medulla to the cortex during the ovarian development. They assumed that germinal epithelium serves only as a covering epithelium and is not the source of germ cells.

In cattle, the formation of ovarian follicles is completed just before birth. At this moment (i.e. at the neonatal period), many atretic and degenerated follicles can be observed (Komárek et al., 1969).

According to Harrison and Weir (1977) primordial follicles start to develop in the rat during the neonatal period when resting oocytes grow and become associated with a single layer of granulosa cells which begin to proliferate.

Based on their exhaustive study, Makabe et al. (1989) state that primordial germ cells (PGCs) are present both in the ovarian cortex and the ovarian medulla when the ovarium is differentiated into these two parts during the advanced stages of ovarian development. Clusters of oogonia and oocytes then arise from the PGCs proliferating in the cortical part of the ovary. Both coelomic epithelium and the mesonephric cells contribute to the formation of early follicles. During this stage, the surface epithelium is separated from the underlying tissues by a basal lamina. Germ cells that had previously been asssociated with the most superficial area of the ovary, become incorporated into the surface epithelium. From this location they can be finally eliminated into the peritoneal cavity.

Korfsmeier (1983) studied the kitten ovary in the period from 2 to 16 weeks. He found many primordial follicles in the peripheral cortical regions. The chromosome arrangement in oocytes indicated they had undergone the later stages of meiosis.

In the dog, cells of the surface epithelium form cords which penetrate deeply into the ovary. Many of these cords lose their connection with the ovarian surface and they usually contain oocytes. Small follicles can form within these cords or in their close neighbourhood. Based on these data Andersen and Simpson (1973) suggested that the cord cells may differentiate into granulosa cells. At the same time, degeneration of oocytes and follicles was seen within the surface cords. This indicates that the surface epithelium can play an important role in the discarding of degenerated ovarian structures.

In their ultrastructural and quantitative study Wordinger et al. (1990) were concerned with the development of mouse neonatal ovarian surface epithelium. They described it as a simple squamous or a simple cuboidal epithelial layer with a distinct basal lamina. They also observed that primordial follicles located in the periphery of the ovary cortex interact with ovarian surface epithelium. Oocytes within the primordial follicles are surrounded by a single layer of squamous granulosa cells and they can migrate among the ovarian surface epithelial cells. Oocytes can pass directly into the periovarian space without loss of epithelium or granulosa. The portion of migrating oocytes reaches its maximum during the first week after the birth.

Hiura and Fujita (1977) investigated a similar situation in mouse germ cells from the ovarian surface. They considered the extrusion of germ cells into the coelomic cavity as one of the mechanisms for a reduction in the number of germ cells in the mouse ovary.

Jirásek (1992) investigated the development of human ovaries. The surface epithelium of fetal ovaries forms a single layer of cuboidal cells and contains numerous oogonia. The perinatal human ovary can be characterized by the presence of growing multilaminar primary follicles or secondary vesicular follicles.

Greenwald and Moor (1989) distinguished two types of primordial follicles: a) peripheral clusters of small oocytes with an incomplete investment of granulosa cells, and b) deeper lying individual oocytes, surrounded by a complete layer of pregranulosa cells. Makabe and Motta (1984) described a similar relationship between follicular cells and germ cells in the human embryonal ovary.

The aim of this study was to investigate the dynamics of ovarian surface epithelium in kitten and dog ovaries during the early perinatal period and to test the hypothesis that the ovarian surface epithelium can serve as a germinal epithelium during the transient period of ovarian development.

MATERIAL AND METHODS

Experimental ovarian tissue was removed from a newborn kitten (*Felis domestica*) on day 1 and day 10 and week 6 and week 11 after birth. After decapitation, the abdominal cavity was opened and the ovaries were removed and cut into very small pieces. These tissue blocks were immersed in a fixative solution (2.5% glutaraldehyde in 0.2 M phosphate buffer). Newborn female dogs (*Canis familiaris*) were sacrificed by decapitation several hours after birth. After opening the abdominal cavity, the ovaries were removed, cut into small tissue blocks and immersed in a glutaraldehyde fixation. Then the ovarian tissue was prepared for routine electron microscopy (postfixation

with 1% OsO_4 in the same buffer, dehydration in ascending concentrations of alcohols, infiltration with medium and embedding in Durcupan ACM). Semithin sections (1–1,5 µm) were prepared from the Durcupan blocks using a glass knife on an ultramicrotome Reichert ultracut E and these sections were stained with a 0.5% azure II. solution in a 0.2 M phosphate buffer (pH 8). These stained sections were observed and photographed in a Jenalumar light microscope (Carl Zeiss, Jena).

RESULTS

Analyzing the histological material, we focused especially on the ovarian surface epithelium and on the cortical part of the ovary just under this surface epithelium. We further observed the clusters of primordial germ cells (PGCs) and the primordial follicles.

Cat ovary – 1 day after birth

The surface of the neonatal kitten ovary is covered by simple cuboidal epithelial cells arranged in one or two layers. The cytoplasm of these epithelial cells stains very expressively. These cells contain a very pleiomorfic nucleus in which one or several prominent, excentrically placed, nucleoli are present. Within this surface epithelium, a small number of markedly greater and lighter cells can be distinguished (Fig. 1). The stainability of their cytoplasm rapidly diminishes, and their nuclei are conspicuous and dense. We observed distinct mitotic figures in the nuclei of these cells indicating their mitotic activity (Fig. 2). These light elements are taken to be PGCs. Concomitantly with PGCs division, the proliferative activity of neighbouring epithelial cells was also seen. During further ovarian development, the proliferating epithelial cells surrounded the daughter PGCs and formed a complex which entered the cortical part of the ovary. The interstitial elements of the ovary were derived from these cells of epithelial origin. Interstitial elements surrounded the clusters of light PGCs and separated them from the adjacent ovarian stroma. (Fig. 3, 4). At this stage of ovarian development, the cortical part was formed by the interstitial elements which were arranged in network-like structures and were accompanied by a few collagen fibers with small amounts of smooth muscle cells. The cords of big light germinal cells were closely surrounded with small, very dark elements, which penetrated this network. Comparing the number of mitoses within the PGCs and the surrounding interstitial elements, we have to state that the latter ones proliferated more intensively. Interstitial elements representing potential fibroblasts penetrated gradually into cords or clusters of PGCs and separated them.
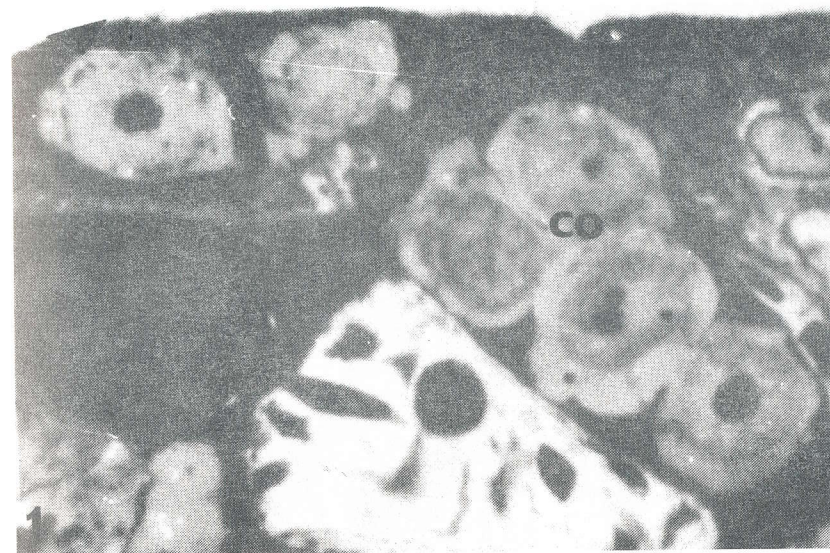
1. Kitten ovary, 1st day after birth. Light PGC (arrowhead) within the surface epithelium. A cord of daughter cells (co) emerges into the connective tissue; x 1 530

Completely separated germ cell represented the basis for the formation of primordial follicles. Interstitial quasi-fibroblasts are arranged into a single layer of granulosa cells which was separated by the distinct lamina basalis. During the 1st postnatal day, primordial follicles in the kitten ovary were observed only rarely. In several cases we observed the degeneration of big light germinal cells. Some of these cells also left their position within the ovarian surface epithelium and they were discarded from the ovary into the peritoneal cavity (Fig. 3).

Cat ovary – 10 days after birth

Germinal cells were present within the cuboidal surface epithelium and proliferated very intensely. Emerging daughter PGCs gradually penetrated the cortex (Fig. 4). In this ovarian region PGCs became surrounded with fibroblasts and primordial follicles, with a simple superficial layer of granulosa cells, were formed (Fig.5). At this stage, the potential of PGCs within the ovarian surface epithelium is reduced. Cells bulged above the ovarian surface and they left the ovary for the peritoneal cavity. PGCs liberated into the peritoneal cavity were degraded and absorbed.
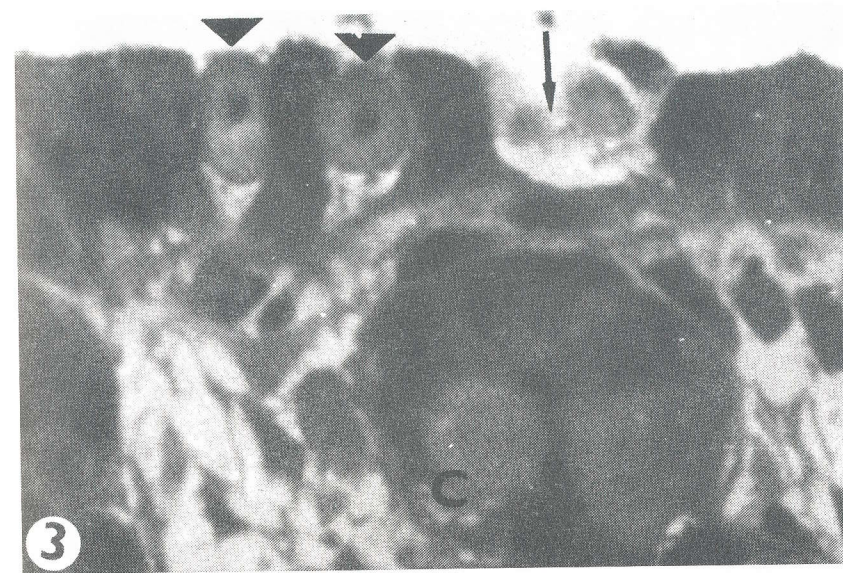
2. Kitten ovary, 1st day after birth. Dividing PGC with the mitotic figure (m); x 1 530

Cat ovary – 6 weeks after birth

Cuboidal epithelium at the ovarian surface became flattened. The surface epithelium contained only a limited portion of the big light PGCs and these cells were separated from the clusters of PGCs in the cortex. The cortical part of the ovary contained the primordial follicles, each of them being surrounded with a layer of flat connective tissue elements transforming into granulosa cells. In addition to primordial follicles, several unilaminar primary follicles, as well as multilaminar primary follicles, were seen.

Cat ovary – 11 weeks after birth

At this stage of development, the surface of the ovary was covered by flat epithelium with small regions of cuboidal epithelium and big light PGCs were not observed there. As the neonatal ovarian development continued, the surface epithelium became separated from the cortical part by newly formed and gradually thickening tunica albuginea, which contained fibroblasts, collagen fibers and a few scattered capillaries. The cortical part of the ovary was


3. Kitten ovary, 1st day after birth. The extrusion of two germ cells (arrowhead) from the surface epithelium into the peritoneal cavity; C – cluster of PGCs in the cortical part; degenerating PGC with a disrupted cell membrane (arrow); x 1 530

characterized by the presence of numerous primordial as well as unilaminar primary follicles (Fig. 6). There were numerous growing multilaminar primary follicles and a few secondary vesicular follicles with increasing antrum in the deeper regions of the ovarian cortex. Atretic follicles containing abnormal or degenerative oocytes were also observed in the cortex.

Dog ovary – 1st day after birth

The ovarian surface epithelium was formed by a continuous layer of squamous cells (Fig. 7). Clusters of PGCs were concentrated preferentially within the cortical part where strong proliferative activity was seen. The size of the clusters of PGCs increased. These clusters were surrounded with dark elements of connective tissue which separated individual PGCs. During further development these cells were transformed into typical granulosa cells. At the same time, primordial follicles began to form (Fig. 8). The cortical part of the ovary was rich in clusters of PGCs and was clearly separated from the surface epithelium by a layer of sparse connective tissue.
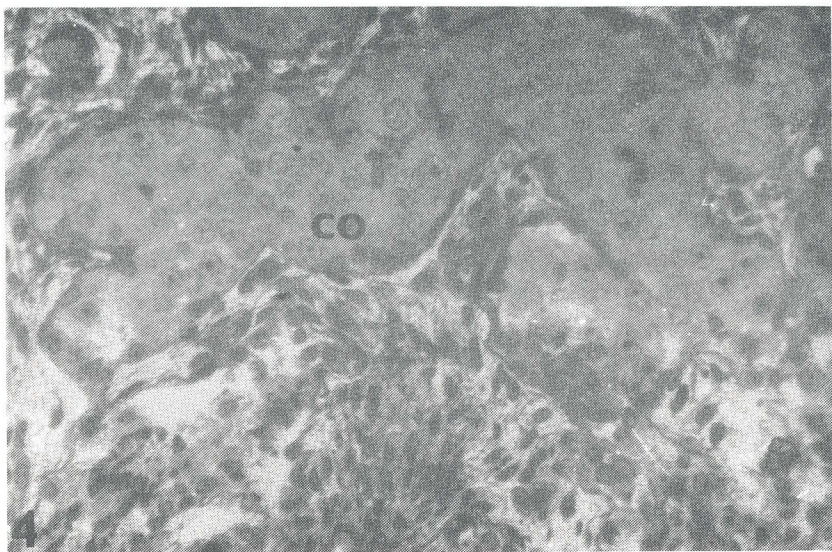
4. Kitten ovary, 10th day after birth. Cortical part with the cord (co) of proliferating PGCs. The whole cord is covered with many dark cells derived from the surface epithelium; x 600

5. Kitten ovary, 10th day after birth. Slightly flattened PGC (arrowhead) which progresses into the peritoneal cavity; CV – cluster of PGCs surrounded with dark cells derived from the surface epithelium, S – separation of a PGC from the epithelium is clearly visible, P – primordial follicle, empty arrow – primary follicle; x 1 530

DISCUSSION

Our morphological and light microscopical analysis of folliculogenesis in a newborn female cat and dog showed that the ovarian surface epithelium takes part in the formation of follicles. Our observations are in agreement with the hypothesis of M a k a b e et al. (1989). These authors postulated that the cells of coelomic epithelium may attract PGCs whereas mesonephric cells induce both migratory and proliferative activities of germ cells. When PGCs reach the gonadal tissue, they undergo rapid meiotic divisions and thus, increase in their numbers. After entering the gonads, proliferating PGCs become evenly scattered among the somatic elements. PGCs tend to occupy the most superficial areas of the ovary but some PGCs can also be observed in more internal regions of the developing ovarian medulla.

We found big light cells within the ovarian surface epithelium and we identified them as PGCs. We suppose that these big light cells migrate among the dark cells of the surface epithelium. The incorporation of PGCs into the superficial ovarian epithelium probably represents an impulse for the inten-

sive division of PGCs. Daughter cells derived from basal PGC then form a cord which penetrates the ovarian stroma (M a k a b e et al., 1989). F r a n - c a v i l l a et al. (1990) described a similar situation in the human fetus in the 7th week of intrauterine life. The cords of PGCs, lying within the ovarian cortex may show an amoeboid movement. The body of PGC may occasionally exhibit pseudopodial-like cell processes represented by one or two amoeboid prolongations. The amoeboid features of PGCs during the early stages of ovarian development suggest the possibility of active local migration of PGCs towards the epithelial covering the gonad. When PGCs complete their proliferation, some of them remain in the ovarian surface epithelium and become separated by connective elements from the cord of daughter PGCs. Many PGCs may be released from the ovary surface and finally lost. This phenomenon is most clear and most frequent just after the formation of tunica albuginea.

Our results directly correspond with the work of W o r d i n g e r et al. (1990). They reported that the number of oocytes migrating through the
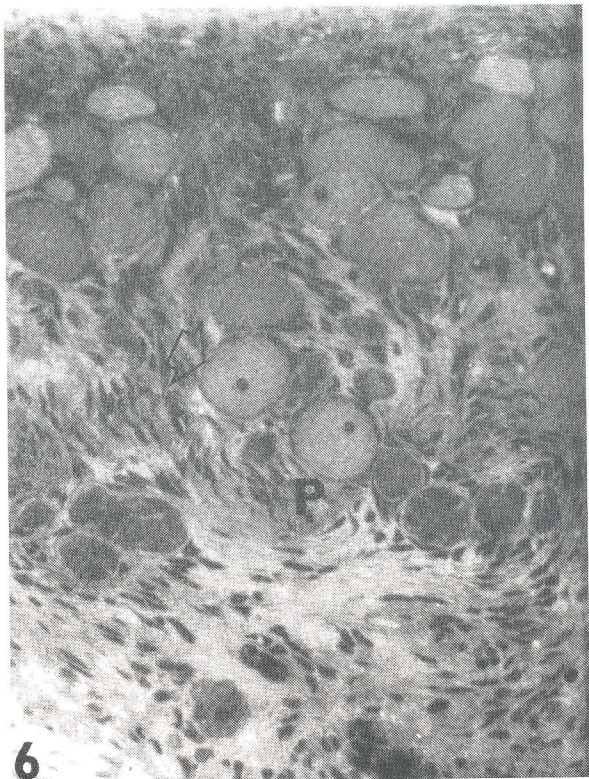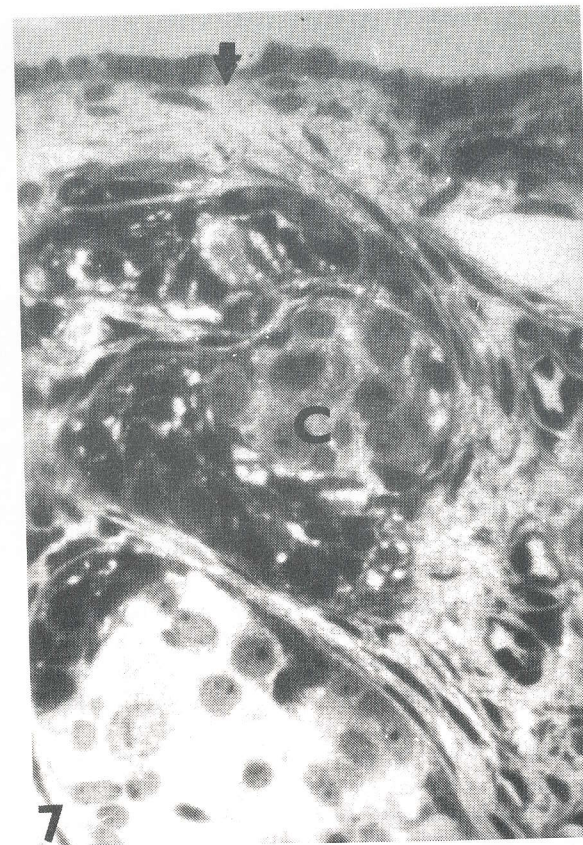
6. Kitten ovary, 11th week after birth. Cortical part contains the primordial follicles (P) as well as the primary follicles (empty arrow); x 850

7. Dog ovary, 1st day after birth. Ovarian surface epithelium (arrow) and cluster (C) of PGCs is surrounded incompletely with the dark cells; x 1 530

surface epithelium gradually increases from birth up to the age of several days after parturition. Then the oocyte migration starts gradually to decline. The oocyte migrate among the cells of the surface epithelium and is finally released into the peritoneal space. We observed that cells adjacent to the surface epithelium proliferate very intensely and their daughter cells begin to surround the cord of PGCs and thus separate this cord from the stroma.

B y s k o v (1986) described the same situation in deeper layers of mouse ovarian cortex. The "accompanying" somatic cells proliferate and separate the clusters of germ cells originated from the individual PGCs. This process represents the start of the development of primordial follicles. Accompanying cells are the source of granulosa cells, because they form a single layer on the surface of germ cells and they completely surround the oogonia. Lamina basalis, which is present around the whole follicle, separates it from the adjacent loose connective tissue of the ovarian cortex. During further development PGCs complete their proliferation. On the other hand, the cells adjacent to the PGCs proliferate in the ovarian surface epithelium without cessation. PGCs are gradually eliminated from the surface epithelium. A thin layer of connective tissue separates the surface epithelium from the cortex which is rich in newly formed primordial follicles (M a k a b e et al., 1989). The further differentiation of the ovary continues through the formation of new primordial follicles which increase in the number. When the development of primordial follicles is finished, several follicles begin to "wake up". They transform into unilaminar primary follicles and begin to grow. It must be emphasized, that the development of ovarian follicles is completed in the
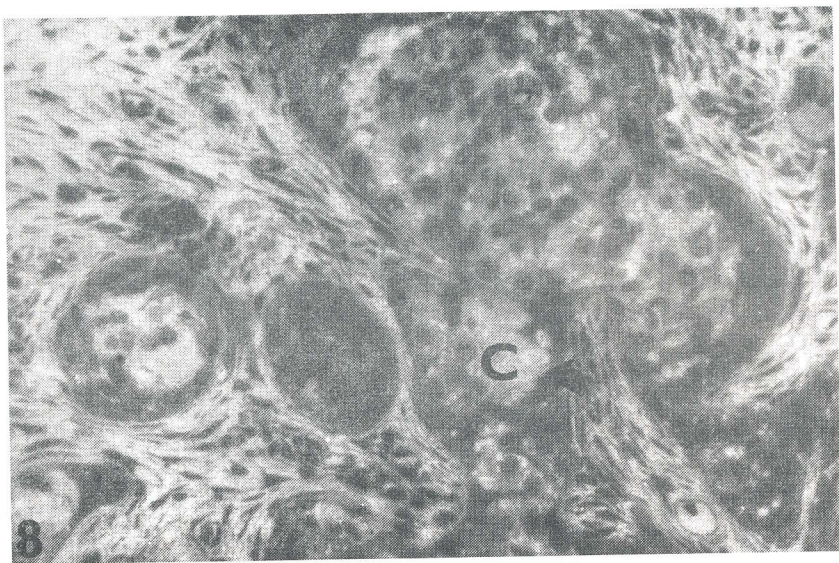
8. Dog ovary, 1st day after birth. In this case the clusters possess a complete cell layer on the surface. These flat cells (arrow) separate PGCs (C) from adjacent connective tissue; x 600

perinatal period in most species of mammals. Contrary to this, the early stages of folliculogenesis continue without cessation after parturition in the cat and in the dog the earliest folliculogenesis just before its completion at the moment of parturition. The cat is born in the stage when oogonia are formed from the PGCs. This means that the ovary in a newborn cat can be characterized by the multiplication and increasing of germ cells. On the other hand, Korfsmeier (1983) still found numerous primordial follicles in pubertal cat ovary.

In humans primordial follicles can be detected during the 18th week of intrauterine life (Makabe et al., 1989; Wartenberg, 1989). The stage of ovarian development in a newborn animal clearly affects the differentiation of ovarian follicles (Stein, Anderson, 1981). The cuboidal cells which form the surface epithelium in the cat ovary may be arranged in two layers just after birth. These cells gradually become flat and squamous. Flattening of the epithelium is clearly displayed 6 weeks after birth. Squamous surface epithelium is present in the cat ovary 11 weeks after birth. In the newborn dog, the ovarian surface epithelium is very flat yet from the 1st postnatal day.

In the cat, PGCs are present in the ovarian surface epithelium up to 6 weeks after birth. On the other hand, the dog ovarian surface epithelium does not contain PGCs after birth. During the subsequent stages of the development, the ovarian surface epithelium becomes separated from the ovarian cortical part by a thin layer of connective tissue which does not contain any follicles. In the cat this process takes place 6 weeks after birth. In the dog, a similar situation can be observed just before birth. In the cat ovary, the connective tissue elements begin to penetrate among individual oogonia arranged in clusters and these elements separate oogonia through their fine cell processes. The primordial follicles are formed with one layer of granulosa cells at the ovarian surface during the 6th week of postnatal development. Growing unilaminar primary follicles as well as multilaminar primary follicles can be seen very rarely. More intensive development of primary follicles appear during the 11th week of postnatal life. In the dog, the development of primordial follicles starts earlier and can be detected from the 1st day after birth.

Based on our data, we can conclude in agreement with Jirásek (1994 – personal communication) that the ovarian surface epithelium serves as a germinal epithelium. We also observed that PGCs begin to proliferate intensely and form cell cords after their first contact with the surface epithelium. These cords emerge from the surface into the cortical part of the ovary, which means that they migrate from the medulla part of the ovary into the cortex and give rise to the formation of primordial follicles within the cortex of the ovary.

Acknowledgements

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Vývoj vaječníků kočky a psa v perinatálním období.

Ovariální tkáň kočky a psa v časně perinatálním období (kočka – 1. a 10. den, 6. a 11. týden po narození, pes – 1. den po narození) byla studována na úrovni optického mikroskopu. Tkáňové bločky byly fixovány a zality do umělé pryskyřice, krájeny na ultramikrotomu na polosilné řezy (1–1,5 μm) a barveny roztokem azuru II. Na takto připravených preparátech byly hodnoceny: povrchový epitel ovaria s korovou částí ležící těsně pod ním, shluky a provazce primordiálních zárodečných buněk a formující se primordiální folikuly.

Povrchový epitel je tvořen kubickými, výrazně se barvícími buňkami uspořádanými do jedné, maximálně dvou vrstev. Bylo zjištěno, že primordiální zárodečné buňky, velice světlého vzhledu, se migrací přiblíží k základu ovaria a zapojí se do jeho povrchového epitelu (obr. 1). Na některých místech bylo pozorováno dělení těchto elementů s tvorbou mitotických figur (obr. 2). Proliferující zárodečné buňky vytvářejí shluky (obr. 3 a 5) a provazce (obr. 4) v korové části ovaria. Souběžně s dělením primordiálních zárodečných buněk se dělí i sousední buňky povrchového epitelu, postupně obklopují tyto shluky a provazce primordiálních zárodečných buněk a spolu s nimi postupují do korové části ovaria (obr. 3, 4 a 5). Kůru ovaria v časném perinatálním období tvoří vazivové buňky, síťovitě uspořádané, vazivová vlákna převážně kolagenní a malé množství buněk hladké svaloviny. Do této sítě se postupně zanořují zmíněné shluky nebo provazce primordiálních zárodečných buněk. Tmavé, menší buňky na povrchu těchto útvarů je nejen kryjí, ale pronikají i dovnitř do útvarů a jednotlivé zárodečné buňky tak od sebe oddělují. Zcela oddělená zárodečná buňka tvoří základ primordiálního folikulu (obr. 5). Z obklopujících elementů se formuje jedna vrstva plochých granulozních buněk. U koťat jsou 1. den po narození primordiální folikuly přítomny jen ojediněle, u štěňat jsou 1. den po narození přítomny zcela běžně. Potenciál zárodečných buněk v povrchovém epitelu ovaria je během perinatálního vývoje postupně redukován, a to tím způsobem, že některé primordiální zárodečné buňky se začnou vyklenovat z povrchového epitelu (obr. 3 a 5) směrem do peritoneální dutiny, postupně jsou z epitelu eliminovány a vstřebány v dutině břišní. U kotěte 6. týden po narození je pozorováno oplošťování povrchového epitelu. Kubický epitel se postupně mění na epitel plochý, dlaždicový. V tomto epitelu se ještě ojediněle vyskytují velké světlé zárodečné buňky. Korová část ovaria je charakterizována přítomností primordiálních a v malém množství i primárních folikulů s jednou vrstvou plochých granulozních buněk. 11 týdnů po narození je povrchový epitel již zcela oploštělý a nenacházíme v něm žádné primordiální zárodečné buňky. Mezi korovou částí ovaria a povrchovým epitelem se vytvořila vazivová *tunica albuginea*. V kůře jsou přítomny primordiální a primární folikuly, v hlubších vrstvách pak i malé množství rostoucích folikulů. Řada folikulů již podléhá atretickým změnám. Na povrchu rostoucích folikulů je tvořící se vazivová *theca folliculi interna*.

U psa lze konstatovat, že vývoj vaječníků je v okamžiku narození pokročilejší, neboť již první den po narození jsou v ovariu přítomny primordiální folikuly.

Z práce vyplynulo, že primordiální zárodečné buňky cestují od dřeně, resp. z hlubších vrstev kůry ovaria směrem k povrchovému epitelu a po kontaktu s ním se začínají intenzivně dělit. Tím vytvářejí provazce a shluky nových buněk rostoucích směrem od povrchu do kůry ovaria, kde se z nich formují primordiální folikuly.

kočka; pes; vaječníky; vývoj; povrchový epitel; primordiální zárodečná buňka; primordiální folikuly

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