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# Morpho-physiological features of endometrial and ovarian remodelling in cows during the oestrous cycle

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**Abstract.** The profitability of dairy farming directly depends on the intensification of reproduction indicators, which requires an increase in the percentage of calves per hundred cows and optimisation of milk productivity. Given the need to improve reproductive efficiency, the aim of the study was to identify the morphological and physiological changes in the ovaries and endometrium of cows during the oestrous cycle for the further development of evidence-based methods for correcting sexual cyclicity. Analysis of histological samples revealed a number of important changes. During the oestrus phase, the endometrium shows maximum swelling and blood filling of the arterioles, while the cells of the functional layer become decidual-like due to the active growth of stromal cells. Numerous uterine glands have a convoluted shape and enlarged cavities filled with secretions, while the epithelial cells of the glands become multinucleated with vacuolisation due to the accumulation of glycogen. Primary follicles with cubic-shaped follicular cells are recorded in the ovaries, indicating active replication and remodelling processes, as cubic cells divide faster than flat ones. During proestrus, the covering epithelium of the endometrium becomes wavy, and the uterine glands, although numerous, are located next to a small number of stromal cells, do not contain secretions and have a folded shape. Vascular changes include hyperplasia of the intima of arterioles with narrowing of the lumen and obliteration of thrombotic masses, which is the beginning of the desolation of vascular territories and remodelling of the connective tissue matrix. At this stage, the ovaries contain tertiary follicles without signs of atresia and corpus luteum in the stage of resorption. The metestrus phase is characterised by the formation of large, almost completely structured corpus luteum with large lutein cell nuclei, while the corpus luteum from previous cycles show signs of degradation. During metestrus, the endometrium simultaneously shows signs of hormone-dependent desquamation and active cell proliferation. The practical value of the study lies in the creation of a reliable morphological basis that reveals in detail the mechanism of hormone-dependent changes for the development of evidence-based diagnostic protocols and methods for correcting hormonal status and sexual cyclicity

**Keywords**: histological changes in the endometrium; ovarian follicles; ovarian reserve; corpus luteum; physiology of the sexual cycle

## Introduction

The physiological basis of cows' reproductive capacity is critically important for ensuring stable milk production and economic sustainability of dairy farms. Despite improvements in husbandry and feeding technologies, disorders of the sexual cycle and reproductive function remain one of the key problems in veterinary medicine. A detailed understanding of the morpho-functional dynamics of the ovaries and endometrium throughout the oestrous cycle enables veterinary specialists to substantiate and develop effective methods for the diagnosis, prevention and correction of reproductive disorders, which is a prerequisite for maintaining high herd fertility rates.

According to M. Lamanna *et al.* (2025) and R. Maculan *et al.* (2025), the issue of cattle reproduction, especially highly productive cows, which are characterised by singleton births, a long diestrus period, lactation dominance, and the prospect of infertility, will always remain relevant in both theoretical and practical terms. According to J.B. Santos *et al.* (2025), physiological data on the reproductive capacity of cows, including physiological and morphological changes in the ovaries and endometrium during the oestrus cycle, also make it possible to scientifically ensure planned livestock growth rates, sufficient milk productivity, and reduced production costs for raising replacement young stock, as they reflect the effectiveness of the technologies used on farms and highlight the economic feasibility of the cattle breeding industry in general.

To address these issues, a scientifically sound basis for the organisation of reproduction is needed, taking into account physiological indicators and the requirements of modern technologies for the development of dairy cattle breeding in Ukraine. The most common technologies for housing cows in Europe are tethered and untethered. According to S. Hassan *et al.* (2024), housing systems that assign service personnel to each specific cow (such as tethered housing) can have a positive effect on productivity. This simplifies individual feeding and ensures timely diagnosis of oestrus, since during the service period the animals are monitored not only by artificial insemination technicians, but also by service personnel, which is critical for restoring optimal ovarian function after calving. At the same time, as indicated by A. Pavlenko *et al.* (2023), loose housing better meets technological requirements but requires clear grouping based on the productivity and physiological condition of cows and complicates oestrus diagnosis due to limitations on the time staff can spend observing the animals.

In addition to timely indication of oestrus, the physiological state of the endometrium during the period of preparation of the body for implantation is extremely important, as it ensures not only nidation but also the further course of pregnancy. According to S.F. Sitko *et al.* (2024), cows with higher genomic fertility potential demonstrate better uterine condition and higher progesterone levels during synchronisation protocols, indicating a close relationship between genetics, hormonal status and morphological readiness of the reproductive organs for implantation.

Thus, the uterus has a multi-level regulatory system based on a hierarchical principle of interaction between the methods of controlling metabolic processes and the morphofunctional transformation of the functional layer of the endometrium, synchronised with the physiological work of the ovaries. which is why the study of the above-mentioned components in preparation for proestrus, oestrus, and zygote implantation is a pressing issue, the solution of which will contribute to the development of new approaches to the correction of reproductive function in cows. Therefore, given the need to improve reproductive efficiency, the aim of the research was to elucidate the morpho-physiological changes in the ovaries and endometrium of cows during the oestrus cycle for the further development of evidence-based methods for the correction of sexual cyclicity. To this end, the physiological and histological features of the morphological restructuring of the ovaries and endometrium of cows during oestrus, pro-oestrus and metoestrus were studied.

## Literature Review

The reproductive efficiency of dairy herds is inextricably linked to complex and cyclical morphofunctional changes in the reproductive system. Understanding these dynamics is critical for developing protocols to improve fertility. According to T. Sugiura *et al.* (2018), the uterus is a key organ that exhibits constant morphofunctional changes characteristic of the oestrus cycle. Under the influence of hormonal background, not only the height of the endometrium changes, but also the shape of its cells, the location of the nuclear apparatus, blood vessels and numerous uterine glands necessary for nourishing the embryo in the early stages of development are transformed.

Research by I.M. Sheldon *et al*. (2006) indicated that among the cells of the cylindrical epithelium of the uterine glands there are cells in a state of mitosis, wandering cells, large bubble-like cells located near the basement membrane and present in the endometrium during all stages of the oestrus cycle, especially when oestrogen levels rise, whereas in atrophic endometrium, "bubble cells" are not found. According to A. Pavlenko *et al*. (2023), throughout the entire oestrus cycle, the uterus is filled with fluid content formed as a result of transudation of various blood serum components, secretion of proteins, carbohydrates and other metabolic products, the synthesis of which is carried out in the cells of the glandular epithelium. Secretion from epithelial cells occurs asynchronously, in an apocrine manner. This structure of the surface epithelium ensures the implantation of the zygote during pregnancy. J.S. Stevenson & S.L. Pulley (2016) pointed out that under the covering epithelium there is a stroma, together with the uterine glands, containing a functional and deeper basal layer, whereas the former does not completely detach during the inhibition phase, and the basal layer, due to which the endometrium is restored during the next oestrus cycle, is preserved in its entirety.

According to P. Saini *et al.* (2019), the surface of the endometrium includes three morphologically and functionally distinct areas: the caruncular, intercaruncular, and glandular areas, in which the ducts of the uterine glands open. The histological specificity of these areas is quite heterogeneous, so the process of placentation in them is completely different. J.S. Stevenson & S.L. Pulley (2016) indicated that the connective tissue of the caruncle contains a large number of cells of the reticuloendothelial system and a well-developed capillary network, and with age and during pregnancy, their number and size increase. According to T. Taktaz *et al*. (2015), the covering epithelium of the caruncular zone undergoes lysis in places of direct contact with the tissues of the embryo, therefore, on the surface of the exposed endometrium, there are isolated islands of epithelium that have a wavy appearance.

M. Zargar *et al*. (2020) suggested considering the uterine gland, the stroma surrounding it, and the adjacent blood vessels as a structural unit of the endometrium. Such a structural unit is a multicellular system, the vital activity of which is ensured by intercellular interaction under the influence of steroid hormones and paracrine factors. The authors believed that the endometrium has a unique blood supply system: these are, first of all, the terminal vessels of the functional layer – spiral arterioles, which change depending on the phenomenon and stage of the oestral cycle, as well as hormonally independent arterioles of the basal layer, which ensure its constant blood supply and whose destruction leads to irreversible uterine infertility. According to A.G. Zhou *et al*. (2018), in addition to creating a nutritious and supportive environment for early pregnancy, the endometrium plays a role in suppressing the mother's immune response to the antigenically foreign foetus. The covering epithelium also secretes substances (steroids, growth factors, enzymes, cytokines, prostaglandins), the function and interaction of which have not been sufficiently studied.

M. Wang *et al.* (2018) noted that the cyclical transformations of the functional layer of the endometrium proceed in accordance with the ovarian cycle in several successive stages. The cyclical activity of the ovaries depends on the formation of two temporary endocrine structures: the mature dominant follicle (Graafian follicle) and the corpus luteum. T.B. Ault-Seay *et al.* (2022) noted that the functional state of the epithelial cells of the uterine glands and the cellular elements of the endometrial stroma during the oestrus cycle are characterised by heterogeneity. The biological value of the genotypic and phenotypic heterogeneity of a homogeneous cell population in the components of the endometrium lies in ensuring tissue homeostasis, since heterogeneity at all levels of organisation, starting from the molecular level, contributes to the adaptation of cells and tissues to changing environmental conditions by involving reserve structures in the process.

According to E. Tuckerman *et al.* (2010), morphological changes in the components of the endometrium during the oestrus cycle, which occur under the influence of 17b oestradiol and progesterone, allow to distinguish between the early and late stages of proliferation and secretion. Meanwhile, T.B. Ault-Seay *et al.* (2022) indicated that endometrial regeneration begins against a background of low (basal) levels of steroid hormones, and, more importantly, endometrial regeneration is significantly influenced by growth factors, which are polypeptides that interact with cell membrane receptors, initiating gene expression, metabolism, and cell division. According to these scientists, the functional layer of the endometrium is characterised by the connection between structure and function in various phenomena of the cycle: during oestrus, the structural and functional characteristics of the epithelial cells of the uterine glands are typical of growing and multiplying cells, while during ovulation and the inhibition phase, they are typical of cells that perform a secretory function.

According to T. Taktaz *et al.* (2015), it is during the proliferation stage in the glandular crypts that processes occur that demonstrate the growth and reproduction of cellular elements, as evidenced by an increase in nucleoprotein metabolism of epithelial cells of the glands and the accumulation of glycogen. Aerobic glycolysis processes predominate in the endometrial tissue. I.M. Sheldon *et al*. (2006) founded that at the time of ovulation, the maximum amount of proteolytic enzymes accumulates in the endometrium, and decidual transformations begin in the stroma (the cells of the compact layer increase in size, acquire a rounded or polygonal shape, glycogen accumulates in their cytoplasm), significant vascularisation of the stroma is observed, the endometrium transitions from the proliferation phase to the secretion phase, and the secretory activity of the uterine glands is stimulated.

According to M. Wang *et al*. (2018), the physiological reorganisation of the maternal part of the placenta before implantation is the most important prerequisite for physiological pregnancy, and the endometrium must be in a hormone-dependent state of receptivity during the self-regulating period, during which the blastocyst adheres to the functional layer. In the case of fertilisation of the egg, the epithelial layer of the endometrium undergoes degenerative changes: focal proliferation of the connective tissue stroma is observed, resulting in the growth of caruncles with the subsequent formation of septa and crypts on their surface, and hypertrophy of the uterine glands. These changes progress and become a factor determining the nature of placentation (Stevenson & Pulley, 2016). During the equilibrium stage, changes in the endometrium associated with the flourishing and regression of the corpus luteum consist in the disappearance of mitoses, changes in the tortuosity of the spiral arteries, and their location not only in the basal but also in the superficial sections of the functional layer of the endometrium.

P. Saini *et al*. (2019) believed that the division of the oestral cycle into stages and phenomena is rather arbitrary, since a high level of proliferation is maintained throughout the oestral cycle, only the maximum amount of progesterone after ovulation suppresses proliferative processes in the endometrium and ovaries. It is believed that progesterone production begins after puberty, mainly by the corpus luteum of the ovaries and, to a lesser extent, by the adrenal glands, as well as by the placenta during pregnancy (Nagy *et al.*, 2021). According to E. Labarta *et al*. (2021), the cellular composition of the parenchymal zone of the ovaries has also not been definitively determined. To determine the stage of the oestrus cycle during histological examination of the ovaries, it is important to determine the condition of the tertiary follicles and the preovulatory Graafian follicle against the background of the condition and functioning of the corpus luteum. In addition to the size of the follicles, informative signs of oestrus may include an increase in the number and ratio of atretic and primordial follicles. Also, the presence of a mature, resorbed, or residual corpus luteum is a marker of metoestrus and, in most cases, an indicator of stable, full-fledged oestrus cycles.

According to T. Pedersen & H. Peters (1968) and J.L. Ireland *et al*. (2008), there are small, medium and large follicles, which are in turn divided into groups according to the number of layers of follicular cells of the largest cross-section. Small primordial follicles contain inactive oocytes that are not surrounded by a layer of follicular cells. Medium primordial follicles are oocytes surrounded by a single layer of flat follicular cells. Large primordial follicles can be classified as medium-sized follicles, as they have between 2 and 80 layers of follicular cells, but no visually formed cavity. Large follicles have a fully formed oocyte surrounded by a large number of layers of follicular cells (from 201 to 400), but the follicle cavity is not completely filled with follicular fluid. Preovulatory or antral follicles have a cavity (antrum), and the follicular cells (from 401 to 600) are separated by several layers of follicular fluid. As the follicles grow and develop from primordial to preovulatory, quantitative and qualitative changes occur: the diameter of the oocyte increases, the shape and number of follicular cells change, the theca membrane appears, and its own vascularisation develops (Labarta *et al*., 2021).

The extracellular matrix plays an equally important role, influencing the morphology, proliferation and connection between follicle cells, forming paracrine and endocrine receptors. The basement membrane, which separates the follicular cell layer from the theca cells and externally separates the follicle from the brain matter, also changes. The transition from the primordial stage to the primary follicle stage is an irreversible process. A distinction is made between initial and cyclical follicular metamorphosis. Initial maturation occurs continuously throughout life, starting from birth, and is regulated by local growth factors. Cyclic maturation begins with the onset of sexual maturity, depends on the level of follicle-stimulating hormone (FSH) and the expression of its receptors, and is accompanied by follicular atresia, which is not characteristic of initial maturation (Kuru *et al.*, 2022). T.B. Ault-Seay *et al*. (2022) indicated that the increase in the diameter of a mature follicle occurs mainly due to the thickening of the layer of theca cells, on which receptors for luteinising hormone are formed. The growth of follicles until the appearance of a cavity in them is regulated by the interaction between follicular cells and theca cells, as well as follicle-stimulating and luteinising hormones.

The selection of the dominant follicle occurs at the beginning of metestrus and is caused by a decrease in FSH levels in the blood in response to increased oestradiol synthesis. After ovulation, the basement membrane between the granulosa and theca cells breaks down, the capillary vessels of the theca cell layer grow through the granulosa layer, creating a dense vascular network, and the granulosa cells transform into luteocytes. However, the process of follicular cell luteinisation can begin without follicle rupture, while ovulation and egg release do not guarantee the physiological development and functioning of the corpus luteum. Structural regression of the corpus luteum begins with the apoptosis of capillary endothelial cells, which leads to the destruction of the capillary barrier (Kuru *et al.,* 2022).

Immune cells play an important role in such important processes as follicular maturation, ovulation, luteogenesis, and luteolysis. According to B.S. Muasa (2010), under physiological conditions, the ovary contains immune cells such as macrophages, neutrophils, eosinophils, cytotoxic T cells, and NK cells. The populations of these cells vary depending on the cycle, increasing sharply before ovulation. According to a study by B. Nagy *et al*. (2021), macrophages do not affect the early stages of follicle growth (primordial and primary), but they promote their growth and development by regulating parenchymal cell proliferation, producing growth factors and cytokines, and at the same time suppressing follicular cell apoptosis. Thus, the cyclical histological remodelling of the ovaries and endometrium must be taken into account when fully assessing the reproductive system of a cow, as well as when choosing a method of stimulation and correction of reproductive function. This is why it is necessary to study in detail the morpho-histological transformation of the endometrium during the oestrus cycle.

## Materials and Methods

### Methodology for determining structural and morphological changes in the ovaries and endometrium based on the manifestation of the stages of the sexual cycle

The material for the research was samples of ovaries: selected from the middle part (the plane from the curvature to the gate); and endometrium – from the upper third of the uterine horns. Ovarian and endometrial tissue samples were taken from cows culled due to loss of productive qualities, without pathological changes in the reproductive system, aged 3-10 years: during oestrus (n = 5), metoestrus (n = 5), and prooestrus (n = 5). After collection, the tissue material was fixed in a 10% neutral formalin solution. Next, the endometrial fragments were washed in water, dehydrated, cleared in an alcohol-xylene solution, poured into paraffin blocks, and histological sections 4-10 μm thick were prepared on a Shandon Finnesse 325 (Thermo Scientific) rotary microtome. The samples were examined using a binocular light microscope with different magnifications, and digital images of the preparations were obtained using the "ZEN" digital imaging system for "Carl Zeiss" microscopes (Germany) at the Ukrainian-Swedish research centre SUMEYA (Medical Institute of Sumy State University). For review microscopy, histological preparations were stained with haematoxylin-eosin, and for the study of connective tissue structure, with a picrofuchsin mixture according to Van Gieson, using the methods described by L.P. Horalskyi *et al*. (2015).

### Method for determining the stages of the sexual cycle in cows

Oestrus was diagnosed in cows that clearly exhibited the immobility reflex at the peak of luteinising hormone secretion. Metestrus (the peak of corpus luteum activity) was diagnosed on the $7^{th}$-$8^{th}$ day of the oestrous cycle, since by the $7^{th}$ day the corpus luteum is formed and hormonally active. The progesterone secreted by the corpus luteum is sufficient for pre-pregnancy preparation of the uterus for embryo implantation. Proestrus was diagnosed on the $17^{th}$-$18^{th}$ day of the oestrous cycle in the presence of clinically pronounced hypertrophy and hyperemia of the external and internal genital organs (the beginning of proliferation under the influence of liberins, which enhance FSH production and indirectly activate the growth of primordial ovarian follicles).

**Object and conditions of the study**

The research was carried out in the laboratories of Sumy State University (contract No. 87.01.03.11 on the provision of scientific and diagnostic services dated 30 March 2011) and in the laboratory of LLC "Health Diagnostics" in Sumy. Despite the age of the material collected, the methods of histological processing and analysis used remain relevant. The morphological samples obtained are of scientific value as unique primary material that has retained methodological reliability and reproducibility of results. The results have not been published before. The current publication includes updated statistical processing and modern interpretation of data in the context of current scientific knowledge of the 2020s, which provides a new level of understanding of the structural and morphological features of the reproductive system.

For the clinical and experimental studies, meat and dairy breeds (Schwyz and Simmental) and dairy breeds (Holstein and Ukrainian Black-and-White) of cows were selected, aged 3 to 10 years, with a body weight of 400-600 kg. They were kept on dairy farms of various ownership forms in the Sumy region: JSC Breeding Farm "Mykhailivka" of Lebedynskyi District; PE "Vitaliya" of Burynskyi District; LLC AF "Vladana" of Sumy District; LLC AF "Lan" of Sumy District. The experimental farms used tethered and untethered systems for housing cows in typical cowsheds. With tethered housing, cows rested and ate in stalls on tether. Each animal had an individual feeder and drinker. Milking was carried out in stalls on tethers or in milking parlours. With tethered housing, cows moved freely inside the cowsheds and in the exercise yards. Feeders and drinkers were located at the end of the cowsheds. Cows were milked in a separate, specially equipped room.

Experimental studies, animal husbandry, and all manipulations with animals were carried out in accordance with modern methodological approaches, in accordance with the European Convention for the Protection of Vertebrate Animals Used for Research and Other Scientific Purposes (1986), Law of Ukraine No. 3447-IV (2006), and Order of the Ministry of Education and Science, Youth and Sports of Ukraine No. 249 (2012). The digital material obtained in the studies was processed using variational-statistical methods with the use of statistical techniques (STATISTICA 10.0 for Windows) to determine the arithmetic mean (M), the statistical error of the arithmetic mean (m), and the probability of difference (P) between two variation series according to Student's criterion with values $P \leq 0.05$; $P \leq 0.01$; $P \leq 0.001$.

## Results and Discussion

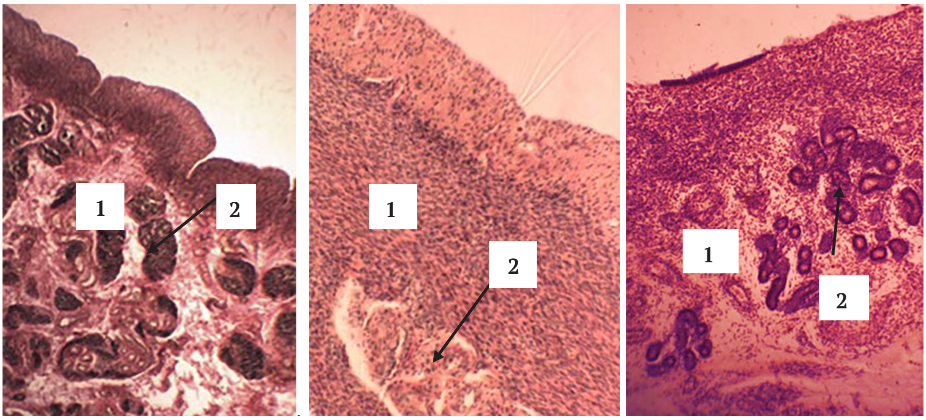
**Results of the study of histological, histochemical and structural-morphological changes in the endometrium**

During the study of structural and morphological changes in the functional layer of the endometrium during the sexual cycle, it was found that at all stages of the oestrus cycle, the endometrium is conditionally divided into basal and functional layers covered with epithelial cells. The stroma contains uterine glands. The surface of the endometrium contains morphologically and functionally different areas: glandular, intercaruncular and caruncular. The glandular area is covered with resistant, intensively secreting epithelium. It is on its surface that the ducts of the uterine glands open.

The caruncular zone contains a complex of decidual tissue capable of lysing microorganisms, inactivating their toxins, and synthesising carbohydrates, lipids, proteins, prolactin, and prostaglandins. These functional features complement the data of M.E. Diessler *et al*. (2023)

and M.J. Ruiz-Magaña *et al.* (2022). In the intercervical zone, the epithelium undergoes temporary degeneration, while the endometrial stroma does not change significantly.

Histological studies of the endometrium of cows conducted by the authors of this work complement and detail the findings of other researchers, in particular in the works of Y.A Amin & H.A. Hussein (2022) and Y.A. Amin *et al.* (2025), since it has been found that during oestrus: a clear division of the functional layer into spongy and compact remains, while the arterioles form maximally dilated and blood-filled clusters with swollen walls (Fig. 1a).




a b c

**Figure 1.** Caruncular zone, functional layer of the endometrium

***Note***: *a – oestrus; b – proestrus; c – metestrus; 1 – compact (superficial) layer; 2 – uterine glands. Coloured according to Van Gieson, x 400*

***Source***: *developed by the authors*

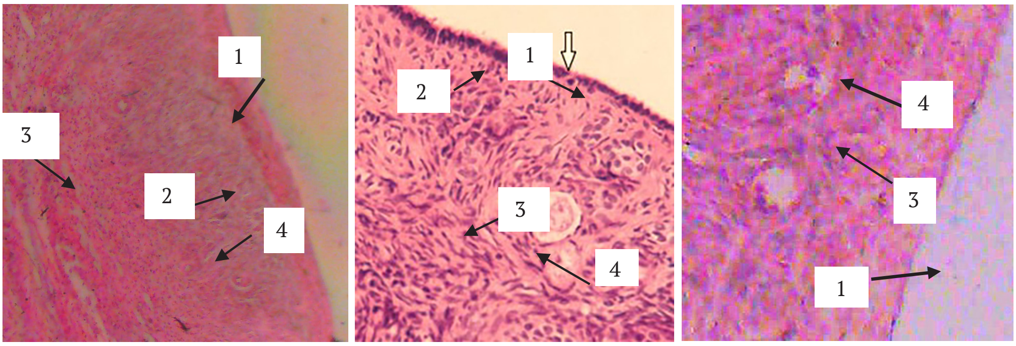
Mitotic activity of the epithelial cells of the uterine glands has also been detected. Pronounced oedema due to the growth of stromal cells reveals decidual-like elements of the endometrium (cells of the maternal part of the placenta appear). Increased secretory activity of endometrial cells leads to the formation of numerous uterine glands in the form of clusters, due to their elongated and sinuous shape. The latter acquire enlarged cavities and are filled with secretions rich in protein-carbohydrate compounds. The epithelial cells of the uterine glands are of uneven cubic shape, mainly multinucleated with uneven vacuolisation due to the accumulation of glycogen.

Histological examination of the endometrium during proestrus (17-18 days of the sexual cycle) supplemented and detailed the data obtained by Y.A. Amin & H.A. Hussein (2022), M.E. Diessler *et al*. (2023), as it established the presence of a clear division of the functional layer into compact and spongy. The covering epithelium was smooth, gathered in folds, or wavy (Fig. 1b). Numerous formed uterine glands were located in the functional layer of the endometrium next to a small number of stromal cells. The surface layer, on the contrary, contained isolated unformed glands. Located close to each other, the uterine glands did not contain secretions and had a folded shape. There were areas of separation between the stromal cells and the epithelial cells of the glands (Fig. 1b). The endometrial arterioles were dilated and excessively tortuous. There were changes in the vascular territories due to narrowing of the lumen of the vessels as a result of significant hyperplasia of the intima. There were signs of intravascular stasis, perivascular oedema with loosening around the vascular fibrillar connective tissue elements. Thrombotic masses appeared in the vessels and their obliteration was recorded, with the simultaneous formation of paravasal fuchsinophilic connective tissue fibres, indicating the onset of vascular territory desolation and the development of remodelling of the connective tissue matrix of the endometrium due to replacement by newly formed fibrillar elements.

Histological examination of the endometrium during metestrus (7-8 days of the sexual cycle) showed no clear division of the functional layer into compact and spongy. The covering epithelium was smooth or wavy, partially desquamated in the caruncle areas. The deep layer of the endometrium contained a small number of unformed uterine glands scattered in the stroma; there were almost none in the surface layer (Fig. 1c). There were dystrophic-degenerative changes in the functional layer of the endometrium, in the form of destruction of the compact and spongy layers with significant thinning and disappearance of the clear zoning of the latter. This is associated with hormone-dependent cellular desquamation of the compact and spongy layers of the endometrium. During metestrus, massive apoptotic death was observed in the cells of the functional layer, accompanied by karyopyknosis, karyorhexis, and hyperchromatosis of the cytoplasm. This is due to the development of hypoxic changes in the surface areas of the functional layer as a result of involution and desolation of vascular territories. Along with apoptosis of stromal cells, spindle-shaped cells with mitotic division were found, indicating simultaneous processes of cell proliferation with apoptosis. This may be related to the following fact: during the stage of corpus luteum development, against the background of dystrophic-degenerative changes, regenerative processes occur simultaneously.

**Results of the study of histological, histochemical and structural-morphological changes in the ovaries**

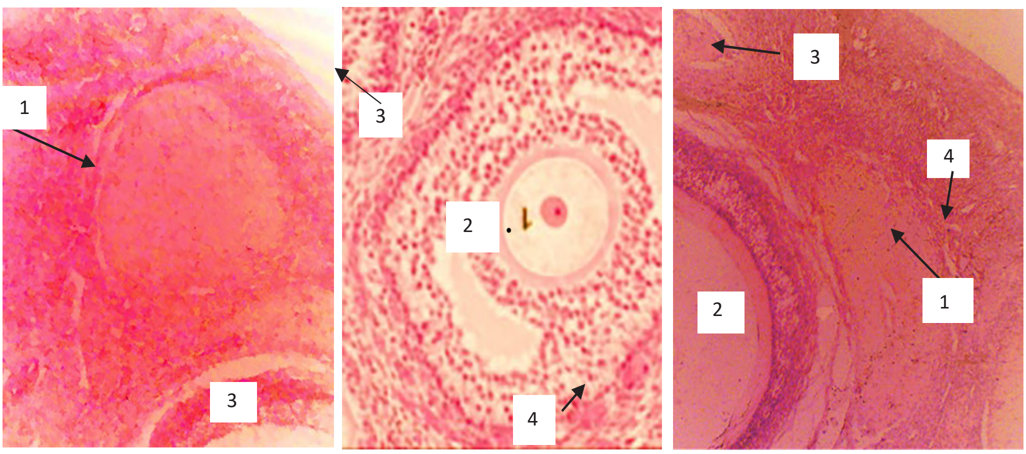
The study of structural and morphological changes in the ovaries is a widespread practice in scientific research, but the specifics of remodulation changes during the sexual cycle require well-founded additions, since the combined study of the ovaries and endometrium is diagnostically important in defining the stage of the oestrus cycle, because the histology of other organs of the reproductive system of cows is less informative. Histological examination of the ovaries of cows during oestrus revealed that the cortical substance is broad and contains mainly densely packed spindle-shaped connective tissue cells that form elastic fibres. A small number of stromal cells are subject to luteinisation. The medulla of the ovary consists of loose connective tissue that forms a well-developed connective tissue matrix and contains elastic smooth muscle fibres. Along the course of the nerve fibres, groups of polyhedral cells with oxyphilic cytoplasm were visible. A large number of elastic fibres of the medulla surrounded a dense network of ovarian vessels, nerve endings, and specialised cells similar to the interstitial cells of the testes, known as Leydig cells. The protein membrane, consisting of cells of dense connective tissue with admixtures of smooth muscle and elastic fibres, is clearly visible. The protein membrane lies under the covering epithelium (formed by cells of a low single-layer cylindrical epithelium) and the underlying cortical substance (Figs. 2a, 2b). The primordial follicles were ellipsoidal in shape and had no membrane. At the poles of the primordial follicles were flattened follicular cells surrounding a small oocyte.




a b c

**Figure 2.** Surface epithelium of the ovary
***Note***: *a – oestrus (x 100); b – prooestrus (x 100); c – metoestrus (x 400); 1 – covering epithelium; 2 – protein membrane; 3 – spindle-shaped fibres; 4 – primordial follicle. Staining according to Van Gieson*
***Source***: *developed by the authors*

Large tertiary follicles reached 5-8 mm in diameter and appeared under the microscope as large cavities filled with fluid (Fig. 3). The spherical inner layer of the tertiary follicle consisted of 5-6 layers of follicular cells. Some of the tertiary follicles located near the dominant follicle were atretic. The corpus luteum of the previous cycle appeared as wide strips of lutein cells in the stage of degeneration, as evidenced by foamy cytoplasm with large vacuoles. Fibrosis of the corpus luteum cells was observed. There were also corpus albicans without any clear remnants of corpus luteum cells. The latter contained loose connective tissue, intercellular substance with lutein cells located in it, and collagen fibres.




a b c

**Figure 3.** Corpus luteum, secondary and atretic follicles
***Note***: *a – metestrus; b – proestrus; c – oestrus; 1 – corpus luteum; 2 – secondary follicle; 3 – atretic follicle; 4 – ovarian vessels. Van Gieson staining, x 400*
***Source***: *developed by the authors*

The primary follicles contained a large oocyte surrounded by a membrane and a layer of cubic-shaped follicular cells. The cubic shape of the follicular cells is formed due to the onset of replication, as the latter acquire a cube-like shape in prophase and metaphase. This indicates active metabolic and remodelling changes in the ovary, as cuboid follicular cells divide faster than flat ones, as confirmed by the research of M. Kuru *et al*. (2022). After ovulation, the ovary contains a spherical layer of follicular cells with blood elements, which is a consequence of the ovulated Graafian follicle.

As a result of studying the ovaries during metestrus, data was obtained that clarifies the research of I. Nanas *et al*. (2021), as it was found that the main feature of this phase is the presence of one or more large corpus luteum in the cortical zone. The latter are almost completely structured, but sometimes there are cavities with blood cells in the centre (Fig. 3). The lutein cells had large nuclei with noticeable nucleoli and eosinophilic cytoplasm. Corpus luteum from previous cycles were also present in the ovary, but contained loose connective tissue, intercellular substance, collagen fibres, and sometimes remnants of lutein cells in the stage of degradation. In the ovaries of cows during proestrus (Fig. 3b), small tertiary follicles are observed, smaller in diameter than Graafian follicles. Most of these follicles show no signs of atresia, unlike in the metestrus stage. The corpus luteum is in the stage of resorption, but does not have wide bands of lutein cells, similar to the oestrus stage.

Follicular atresia (Fig. 4) was recorded in the ovaries during proestrus, oestrus and metestrus due to the fact that the follicular cells lost contact with the follicle wall, after which the follicle cavity was filled with fibroblasts. Due to the degeneration of follicular cells and theca cells, so-called hyaline eosinophilic masses are formed, since follicular cell atresia causes the death of the entire follicle, including the oocyte. In addition, atresia is accompanied by follicle resorption, which includes macrophage infiltration, phagocytosis,

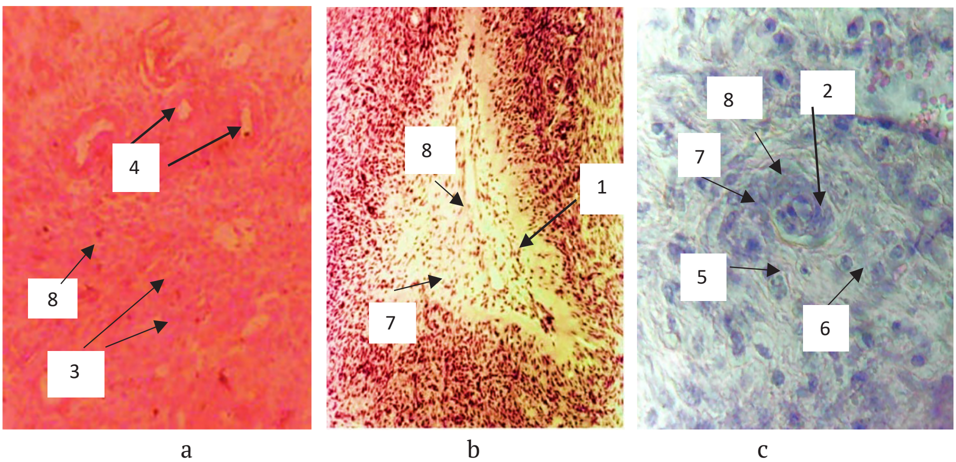



**Figure 4.** Ovarian follicular atresia

***Note***: *a – proestrus, atresia of primary follicles (x 100); b – metestrus, atresia of tertiary follicles (x 400); c – oestrus after ovulation, atresia of secondary follicles (x 1000); 1 – fibroblasts in the follicle cavity; 2 – atresia of the secondary follicle; 3 – hyaline eosinophilic masses; 4 – primary follicle at the stage of atresia; 5 – macrophage; 6 – lymphocyte; 7 – fibrocyte; 8 – fibroblast. a and b – Van Gieson staining; c – haematoxylin and eosin staining*

***Source***: *developed by the authors* migration of fibroblasts from the theca, and collagen accumulation. The above processes are similar to those observed during wound healing (Schultz & Wysocki, 2009).

Cell atresia is a physiological component of tissue homeostasis. There are several types of atresia. In the case of destruction of all layers of follicular cells, "antral (apical) atresia" and basal atresia (Rodgers & Irving-Rodgers, 2010) are diagnosed, characterised by the destruction of the follicular membrane of the follicles closest to the dominant follicle. Apical atresia was recorded during proestrus, oestrus and metestrus (Fig. 4), which are more extensive studies compared to the previously presented data from scientists. Numerous pyknotic nuclei are visible in the cells of the apical layer of follicular cells of primary, secondary and tertiary follicles (Fig. 3c). In the case of destruction of the basal layer of follicular cells, while maintaining the integrity of the inner layer, "basal atresia" is diagnosed, as described by W.M. Noseir (2003), which was recorded during proestrus and oestrus (Figs. 4a, 4c).

These studies necessitated the calculation of the ovarian follicular reserve of cows in tethered and untethered housing systems in a comparative aspect, since this indicator correlates with the data of J.B. Santos *et al.* (2025) with veterinary and sanitary housing conditions and can be used in assessing reproductive capacity. The results of the comparison are shown in Table 1. Tethered cows demonstrated a tendency towards a larger ovarian reserve than untethered cows. The number of follicles in the right ovary was slightly higher than in the left ovary in cows in both housing systems

**Table 1**. Influence of housing conditions on the average number of follicles in cows' ovaries in comparative terms

| Conditions for housing cows | Number of follicles in the ovaries | | |
|---|---|---|---|
| | Right ovary | Left ovary | Both ovaries |
| Tethered housing | 9.21 ± 0.27 | 8.87 ± 0.44 | 18.08 ± 0.31 |
| Untethered housing | 9.09 ± 0.18 | 8.71 ± 0.36 | 17.8 ± 0.24 |

***Source***: *developed by the authors*

There was a lack of scientific data on the difference in physiological activity between the left and right ovaries of cows in the available literature, but M.N. Purpera *et al.* (2009) claimed that the number of follicles in the right ovary exceeded that in the left ovary, which was confirmed by the current study. The data obtained also confirmed the results of N. Yimer *et al.* (2010), who claimed that the activity of the right ovary is due to better blood supply. A reasonable analysis of the ovarian reserve of tethered and untethered cows allows to conclude that the tethered method has obvious advantages, as it causes a stable tendency towards a greater number of follicles in the ovaries. It can be assumed that the tethered method of housing, which requires the assignment of personnel to care for each cow, has a positive effect on physiological reproduction indicators, since the formation of the main herd involves the participation of service personnel who are personally interested in obtaining the largest amount of high-quality products.

## Conclusions

The aim of the study was to investigate morphological and physiological changes in the ovaries and endometrium of cows during the oestrus cycle for the further development of evidence-based methods for correcting sexual cyclicity. Based on the histological and morphological analysis, it was confirmed that the reproductive organs of cattle are characterised by high plasticity and regenerative qualities. Their functional state is completely hormone-dependent, has autonomous regulation of its own enzyme apparatus, local immune system and is capable of steroidogenesis, which is the result of a regenerative-adaptive tissue response to constant hormonal changes.

In the course of the work, the physiological and histological features of the morphological restructuring of the ovaries and endometrium in the key phases of the cycle were studied in detail. During proestrus, the endometrium showed a folded form of the uterine glands without secretion, and the vessels were replaced by newly formed fibrillar elements. At this time, the ovaries were dominated by tertiary follicles without signs of atresia, while the corpus luteum from previous cycles was in the stage of resorption. The oestrus phase was characterised by maximally dilated and blood-filled arterioles of the endometrium, and the epithelial cells of the uterine glands were multinucleated with pronounced vacuolisation, indicating glycogen accumulation. At the same time, active metabolic and remodelling changes associated with preparation for ovulation were taking place in the ovaries. At the metestrus stage, fully structured corpus luteum were found in the cortical zone of the ovaries, while signs of hormone-dependent desquamation and intense cell proliferation were simultaneously observed in the endometrium.

The results obtained conceptualise the consistency and synchrony of morphological transformations of the endometrium and ovaries, emphasising the critical importance of timely detection and correction of dysfunctions at the tissue level. This holds practical significance for improving artificial insemination protocols and developing differentiated programmes for hormonal support. In view of this, a promising direction for further research involves a detailed analysis of the cyclical dynamics of hormone receptors in different layers of the endometrium, which will allow the creation of precise methods for correcting sexual cyclicity, taking into account the individual sensitivity of animals. Further research will focus on studying the dynamics of biochemical indicators of ovarian tissue during the oestrus cycle, which will allow for the rational correction of the reproductive capacity of cows.

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## Conflict of Interest

None.

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# Морфо-фізіологічні особливості ремодуляції ендометрія та яєчників корів за естрального циклу

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**Анотація.** Рентабельність молочного скотарства напряму залежить від інтенсифікації показників відтворення, що вимагає збільшення відсотку отримання телят на сто корів та оптимізації молочної продуктивності. З огляду на необхідність підвищення ефективності відтворення, метою досліджень було з'ясування морфо-фізіологічних змін яєчників та ендометрія корів протягом естрального циклу для подальшої розробки обґрунтованих методів корекції статевої циклічності. Аналіз гістологічних зразків виявив низку важливих змін. У фазу еструсу ендометрій демонструє максимальну набряклість і кровонаповнення артеріол, тоді як клітини функційного шару набувають децидуалоподібності за рахунок активного росту клітин строми. Численні маткові залози мають звивисту форму та розширені порожнини, наповнені секретом, при цьому епітеліальні клітини залоз стають багатоядерними з вакуолізацією через накопичення глікогену. В яєчниках реєструються первинні фолікули з кубічною формою фолікулярних клітин, що вказує на активні процеси реплікації та ремодуляції, оскільки кубовидні клітини діляться швидше, ніж плоскі. Протягом проеструсу покривний епітелій ендометрія стає хвилястим, а маткові залози, хоча й численні, містяться поруч із незначною кількістю клітин строми, не містять секрету та мають складчасту форму. Судинні зміни включають гіперплазію інтими артеріол зі звуженням просвіту та облітерацією тромботичних мас, що є початком запустіння судинних територій і ремодуляції сполучнотканинного матриксу. На цій фазі в яєчниках наявні третинні фолікули без ознак атрезії та жовті тіла на стадії розсмоктування. Фаза метеструсу характеризується утворенням великих, майже повністю структурованих жовтих тіл із великими ядрами лютеїнових клітин, тоді як жовті тіла попередніх циклів демонструють ознаки деградації. В ендометрії під час метеструсу одночасно наявні ознаки гормонозалежної десквамації й активної клітинної проліферації. Практична цінність дослідження полягає у створенні надійної морфологічної основи, яка детально розкриває механізм гормонозалежних змін, для розробки обґрунтованих протоколів діагностики та методів корекції гормонального статусу і статевої циклічності

**Ключові слова:** гістологічні зміни ендометрія; фолікули яєчника; яєчниковий резерв; жовті тіла; фізіологія статевого циклу