Basic Adaptation Mechanisms of the Woman's Body Ensuring Intrauterine Fetal Growth

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INTRODUCTION

Reproduction in humans is a unique natural phenomenon with many unexplained features. For example, why is the duration of human's pregnancy 40 weeks unlike that of animals? Or what is the aim of a complicated and time and energy consuming ovum fertilization and its movement towards the uterus, with undoubtedly rational targeted sperm delivery (directly to the external pharynx of the cervical canal) and the advancement of spermatozoa (in a huge amount) inside the uterine cavity through the fallopian tubes?

Scientists have not yet found the answers to these and many other questions about the characteristics of the reproductive process in humans. But many scientists are currently debating on such an important practical issue as the adaptation of the mother's body to an intrauterine developing fetus.

The purpose of our study was to investigate the adaptation mechanisms of a woman's body preparation for pregnancy as they will help to change the existing points of view on the pathogenesis of pregnancy complications.

The fact is that from the moment of conception, every prospective human has an individual set of adaptive mechanisms, i.e., reactions programmed in the genome that provide adequate responses to any stimuli within the physiological capabilities of the body. In this case we can speak about adaptation reactions, such as the innate adaptation of newborn organisms to the conditions of highlands, tundra, hot climate; adaptation to circadian biorhythms; adaptation of women to cyclical changes in the body during the reproductive period, etc.

If stimuli in strength and frequency exceed the physiological capabilities of a person, the body is to turn on (develop) protective mechanisms, somehow compensating the bioelectric (and some other indicators) homeostasis imbalance, thus, in this case we speak about protective compensatory reactions [1].

Such logical differentiation of these two concepts (terms) seems to be essential to choose the therapeutic measures for various diseases and pregnancy complications.

The sequence of the sexual cycle in women can be considered as one of many mysteries of human evolution. What external causes made it possible for millions of years to adapt the female body to a possible pregnancy during each month only on certain days?! If this is the result of the struggle for species survival, what is the reason for complicating all the subsequent stages of the reproductive process, i.e. the regulation of ovum fertilization duration, huge losses of valuable biological material - sperm for only one embryo (in majority of cases), a long (40 weeks) period of fetal development of the embryo (fetus) and complicated (placental) way of its nutrition? These and the vast majority of similar issues have not yet been studied by researchers, and in this connection it is important to clarify what adaptive mechanisms are involved in a woman's body to ensure a reproductive program encoded in the genome. The development and maturation of each ovum ready for fertilization lasts only 12-13 days, but only after ovulation on the 14th day of the cycle the body is about to prepare for a

possible pregnancy. The stimulus for such preparation is the exit of the ovum outside the ovary. The ovulation process lasts about 30-32 minutes and consists of several phases, including adaptation mechanisms to maintain the viability of the egg after it enters the abdominal cavity.

Shortly before the onset of ovulation the outward-facing wall of the follicle swells quickly, and a small area in the center of the follicle capsule, called stigma, begins to protrude outward like a nipple. During the next 30 minutes fluid begins to flow slowly out of the follicle through stigma, which is the first adaptation mechanism that facilitates the release of the ovum from the follicle.

Two minutes after, the stigma bursts allowing a large amount of viscous fluid to squeeze gradually out. This stage is possible due to two adaptation mechanisms contributing to the perforation of the follicle wall: a) a few hours before ovulation the capsule of the follicle (tecaexterna) begins to secrete proteolytic enzymes from lysosomes, which reduce the strength of the capsule wall and cause its swelling and stigma degeneration; b) simultaneously the rapid formation and germination of new blood vessels into the follicle wall begins and the production of prostaglandins causing vasodilation increases.

These mechanisms result in plasma transudation into the follicle, swelling (stretching) of its wall and the formation and degeneration of stigma. A viscous fluid flowing from the follicle entrains an ovum surrounded by several thousands of granulosa cells, which together make up the radiant crown (coronaradiata) [2].

By this moment, a mature egg increases almost by 10 times and reaches a diameter of 1-1.5 cm, while its mass increases approximately by 1000 times. The radiant crown, consisting of granulosa cells, helps to maintain the viability of the ovum after it leaves the follicle, that is the third adaptive mechanism involved in the preparation of the ovum for fertilization.

Just a few hours after the egg leaves the ovary, the remaining theca and granulosa cells quickly turn into luteal cells. It increases by more than 2 times and begins to be filled with lipid, the inclusions of which give these cells a yellow color. The corpus luteum region is vascularized properly, which ensures its rapid growth. As a result, its diameter reaches 1.5 cm for the period of 7-8 days after the ovulation.

Granulosa cells in the corpus luteum are provided with a developed smooth endoplasmic reticulum, which forms a large amount of progesterone and, to a lesser extent, estrogen. At the same time, theca cells form androgens (testosterone and androstenedione) to a greater extent than female sex hormones. However, most of these hormones are converted into female sex hormones under the influence of granulose cell enzymes. If the fertilization of the ovum has not occurred, the corpus luteum begins to suffer involution and in 30 days completely dissolves.

Along with the cyclic changes in the ovary in the uterus no less important processes are taking place, aimed at preserving vital functions and development of the ovum in case of its fertilization [3]. The role of progesterone is of great importance in these processes. It is believed to be responsible for secretory changes occurring in the endometrium, that is the accumulation of nutrients in the cells which are necessary to ensure the vitality of the ovum in case of its fertilization. Morphologically, these changes are manifested when the glands become convoluted, a large number of secreted substances accumulate in the glandular epithelial cells, and the amount of cytoplasm in the stromal cells increases, the blood flow through the endometrium continues to rise in proportion to the increase of secretory activity. Blood vessels become extremely convoluted. At the peak of the secretory phase (approximately one week after ovulation), the thickness of the endometrial layer is on average 14 mm.

If ovum fertilization does not occur, then due to a decrease of the stimulating effect of sex hormones, endometrial involution develops rapidly: its thickness decreases to 65% compared with the previous one. Then, within 24 hours before the onset of menstruation the spasm of the convoluted blood vessels of the endometrial mucosa occurs, apparently under the influence of one of the prostaglandins, which has a vasoconstrictor effect and is present in the surrounding tissues at that moment.

Vasospasm, a decrease in the amount of nutrients in the endometrium and the absence of hormonal stimulation cause the development of necrosis in it, especially of blood vessels. As a result, blood first seeps into the vascular layer of the endometrium and the volume of hemorrhage rapidly increases within 24-36 hours. Gradually, the necrotic inner layer of the endometrium is separated from the uterus and the entire mass of separated tissues and blood accumulated in the uterine cavity, under the influence of prostaglandins (or other substances in the decomposed desquamated endometrial layer) stimulating the contractions of the myometrium is expelled out of the uterus.

During normal menstruation, about 40 ml of blood and 35 ml of serous fluid are lost [4].

CHARACTER OF CHANGES IN THE ADAPTATION SYNDROME AFTER THE OVUM FERTILIZATION

In case of the fertilization of the egg and the formation of a zygote the adaptive mechanisms in the body of a pregnant woman become significantly complicated. Now they have to perform two functions: to maintain the physiological parameters of homeostasis of the pregnant woman and to form and maintain continuously new adaptive and protective-compensatory reactions leading to physiological intrauterine growth and development of the embryo.

It is obvious that the body can perform such complex functions only with initially balanced metabolic processes, where each system and organ has sufficient individual energy reserves to carry out these adaptive reactions. This is the main principle of survival of every prospective human. It is well known that in nature there are no absolutely identical individuals, since within each population there is significance and variability. This variability, along with genetic factors, are ensured by those individual adaptation reactions that protect the intrauterine stages (and also postnatal stages) of embryo development. According to the classical laws of biology, only some of those who are born survive, and only the most adapted of them subsequently participate in the continuation of the genus, which is the essence of the concept of the struggle for existence [5]. The effectiveness of adaptive reactions increases and depends on many factors:

1) the functional state of the female body;

2) the degree of readiness of a woman's reproductive organs: biocenosis and acidity of the vaginal environment, normal position of the cervix, lack of obstruction in the cervical canal, functionally viable endometrium, patency and sufficient peristaltic activity of the fallopian tubes, especially of their fimbriae; a mature, functionally active ovum with enough energy substances for moving freely in the pelvis if necessary. The eggs in the ovary are at the stage of the primary oocyte. Before an egg leaves the ovarian follicle, its nucleus is divided by meiosis, the first polar body is released from the nucleus, and the primary oocyte becomes a secondary oocyte. During this process, each of the 23 pairs of chromosomes loses its pair, which is included in the polar body and leaves the cell. As a result, 23 unpaired chromosomes remain in the secondary oocyte.

At this moment, ovulation occurs and the ovum at the stage of the secondary oocyte enters the abdominal cavity. But to prevent this the adaptation mechanism is activated: with sufficient body strength the fringe of the ovular ring of the fallopian tube tightly encircles the ovary, and the ovum enters the fallopian tube directly, which facilitates the next stage of the process of its fertilization. The inner surface of the fringe, located at the end of the tube, is covered with ciliary epithelium, the cilia of which are activated, as suggested, by ovarian estrogens. The rhythmic wave-like movements of the cilia are directed towards the entrance (ostium) of the involved tube. As a result, together with the flow of fluid from the bursting follicle, the ovum enters the tube. Studies have shown that 98% of the eggs enter the tube in this way.

If the adaptation mechanism does not function properly, the egg "falls out" into the abdominal cavity and begins to wander in it in the search of the ampullary end of the fallopian tube.

Clinical observations show that the outcomes in this case may be different:

1. The ovum enters the fallopian tube (possibly even on the opposite side of the uterus!) and the fertilization process continues as usual.

2. The ovum contacts the sperm in the tube, but after the fertilization it is not possible for it to move through the tube towards the uterus and a tubal pregnancy occurs.

3. For some reasons, a fertilized egg is not able to move through the tube and it falls into the abdominal cavity, where it is implanted in the omentum or in the serous membrane of the abdominal organs (abdominal pregnancy).

4. An ovum in the abdominal cavity cannot be fertilized and, due to the depletion of its own energy resources, loses mobility, dies and then dissolves.

It is believed that normal fertilization of the egg occurs in the ampoule of one of the fallopian tubes, shortly after the sperm cells and the egg enter it. A blastocyst is formed, which within 3-5 days passes the rest part of the fallopian tube and enters the uterine cavity. This advancement is supported by a weak fluid flow in the fallopian tube. It is important to note that the beating of the cilia is always towards the uterus. The peristaltic contractions of the fallopian tubes facilitate the movement of the fertilized egg.

After that some completely unexplained processes take place. The inner surface of the tube forms folds and crypts that delay the progress of the blastocyst along with the flow of fluid in the tube. In addition, the isthmus of the fallopian tube (the last 2 cm before the tube enters the uterus) remains in a state of spastic contraction for the first 3 days after ovulation. Then, the secretion of progesterone in the corpus luteum of the ovary rapidly increases, which, as commonly believed, initially provides a rise in the number of progesterone receptors in the smooth muscles of the fallopian tube wall. Progesterone-activated receptors cause relaxation of the smooth muscles of the tube and the blastocyst penetrates the uterine cavity [6].

While passing through the fallopian tube the fertilized egg manages to go through several stages of cell division and then the blastocyst, which already consists of about 100 cells, enters the uterus. It is believed that during all this time the secretory apparatus of the fallopian tubes produces a large amount of secretion which is used in the developing blastocyst as a nutrient [].

After the blastocyst enters the uterus 1-3 days pass before it is implanted in the endometrium. As a rule, the implantation occurs at least in 5-7 days after ovulation. Before this the blastocyst uses endometrial secretion – uterine leucorrhoea for nutrition.

The implantation process occurs with the active participation of trophoblasts located on the outer surface of the blastocysts. These cells produce proteolytic enzymes, metabolize and dilute the surrounding endometrial cells.

Meanwhile, some released dissolved nutrients are transported by trophoblastic cells to the blastocyst at the same place and serve as an additional source of nutrition for it [7].

Thus, the adaptive mechanisms of the mother's body prepare the egg for fertilization and the primary stages of its implantation in the uterus.

Before ovulation, the endometrial glands, mostly in the cervical region, produce fluid viscous mucus, which forms a mucous plug in the cervical canal, a lower pole of which is located at the external pharynx of the cervix (the well-known "symptom of the pupil"). The most important function of this "plug" is to protect the upper genital tract from the infection. Since the moment of ovulation this mucus liquefies, the "pupil" disappears, and the cervical canal becomes permeable to sperm cells. Thus, the mucus filaments stretch along the cervical canal of the uterus, forming inside the lumen of the cervix a route for the spermatozoa penetration in the desired direction from the vagina into the uterus. This proves an important role of mucus in the fertilization process success. One more fact which positively affects the fertilization process should also be noted. It is the woman's posture during the intercourse. The normal position of the cervix and uterus is anteversio, anteflexio, i.e., the external pharynx of the cervical canal is facing the posterior fornix of the vagina. Therefore, the physiological position for successful fertilization is the position of the woman with her back to the man, when the ejaculate is delivered directly to the external pharynx of the cervix. By the way, in this position, sexual intercourse occurs in the vast majority of representatives of the animal world.

Why is normally only one oocyte fertilized? A few minutes after fertilization the protective mechanism fixed in the phylogenesis of a person starts working, preventing other sperm cells from the penetration into the egg. The key role in this mechanism is played by Ca²⁺ ions, which, after the first sperm cell penetrates through the shiny membrane into the ovum, begin to diffuse inward through the oocyte membrane and cause release of many juxtamembrane vesicles into the surrounding space by exocytosis. Vesicle granules contain substances that permeate all parts of the shiny membrane and interfere with the interaction of other sperm cells with the ovum. Moreover, the attached sperm cells begin to fall off from the shiny membrane.

A fertilized egg (blastocyst) within 3-5 days passes the last section of the fallopian tube and enters the uterine cavity. Its progression is supported by a weak fluid flow in the fallopian tube. The composition of the fluid includes the secret of epithelial cells lining the surface of the lumen of the tube, as well as sperm metabolism products that were not involved in the act of fertilization.

For practical purposes it is necessary to consider one more adaptation mechanism that facilitates preparation for ovulation. Unfortunately, it is not described in the medical literature. It is the mysterious speed of delivery of sperm cells into the fallopian tube.

It is known that the intrinsic speed of sperm movement through the female genital tract (cervix, uterine cavity, fallopian tubes, the total length of which is not less than 17-18 cm), is 1-4 mm/min.

Simple arithmetic calculations make it possible to see that at this speed, sperm cells can be in the uterine tube ampoule after about 45 minutes. However, experimental studies show that some sperm cells are "at the finish line" 5 minutes after ejaculation?! The answer to this question can be obtained if we pay attention to two facts: 1) with the disappearance of the mucous plug from the cervical canal at the beginning of the second phase of the menstrual cycle and patency of the fallopian tubes, the abdominal cavity is connected with the external air environment; 2) during the respiratory movements of the chest, intra-abdominal pressure is constantly changing due to the movement of the diaphragm. Therefore, it is logical to claim that spermatozoa located near the external pharynx of the cervical canal quickly penetrate (suck) into the lumen of the fallopian tube due to a sharp decrease in intra-abdominal pressure. Penetration of "alien" biological material into the tube causes a woman's "stress" and a universal protective reaction — the spasm of the isthmic section of the tube, which, as we know, lasts for three days. Therefore, it becomes clear why of the 400 million sperm cells in the ejaculate, only about 1000 enter the fallopian tube.

The data analyzed by us indicate the necessity of synchronization and sequence of adaptive mechanisms of a **woman's organism** at all the stages of sexual intercourse in order to have successful egg fertilization.

As a result of an increasing concentration of progesterone, which has a property of relaxation, the spasm of the uterine tube isthmus ceases, and the dividing blastocyst enters the uterine cavity. However, the implantation of a blastocyst in the endometrium does not occur immediately, only after 1-3 days of its presence in the uterus. Implantation, as it is known, occurs along the "sperm path," that is, on the side of the uterus, along which the sperm cell moves towards the isthmus of the tube. It is believed that the main influence on the proper process of implantation is exerted by nutrients and other substances accumulated in the endometrium under the influence of progesterone in the second phase of the menstrual cycle. An active role in the implantation is played by trophoblasts – cells located on the outer surface of the blastocyst. Trophoblasts also produce proteolytic enzymes, "digest" and transfer adjacent cells of the endometrium into a liquid state.

After the blastocyst was implanted in the endometrium, the increased secretion of progesterone causes further swelling of the endometrial cells, contributing to the storage of more nutrients such as ejaculate, proteins, lipids, minerals, which provide nutrition to the embryo at the primary stages of its development. The accumulation of these cells is commonly called the decidual membrane. The nutrition of the embryo in this period is provided as follows. Trophoblasts capture the cells of the decidual membrane, "digest" and asymmetry them and then promote the use of the obtained metabolites for the growth and development of the embryo. This method of nutrition persists for the first 8 weeks after the implantation of the embryo. Though, the emerging placenta also begins to provide nutrition to the embryo from approximately 16th day after fertilization (a little more than a week after the implantation).

But the functions of trophoblasts are not limited by this. When the trophoblastic villi of the blastocyst penetrate the endothelium, the germination of blood capillaries from the embryonic elements of the vascular system of the forming embryo into the villi begins.

The essential role in the development of the vascular system of the future uterine-placental complex is played by convoluted (spiral) arterioles, which are functioning as direct participants in the first contacts of maternal blood with the emerging structures of the circulatory system of the embryo. As we know, the growth of spiral uterine arterioles continues throughout the entire stage of the advancement of the fertilized egg through the fallopian tube during its implantation. There is an opinion that the proliferation of arteries occurs under the influence of progesterone [8], but apparently this point of view cannot be considered fully true, since it is well known that progesterone does not have an anabolic effect. The invasion of trophoblast cells in the endometrium is always accompanied by local destruction of the walls of its vessels with the blood flow out and the formation of lacunae-like reservoirs for uterine blood, the components of which serve as an additional source of nutrition for the developing embryo before the uteroplacental vascular complex start functioning.

The trophoblast villi form branches, the accumulations of which eventually form the chorionic villi. Thus, the villi carrying the blood of the embryo (fetus) become surrounded by lacunae containing maternal blood. It should be noted that when the capillary walls are destroyed by proteolytic enzymes and hyaluronidase and the lacunae are formed there is a real risk of uterine bleeding that is prevented by trophoblasts in the cells (and metabolic products of spermatozoa located in the uterine cavity?). Fibrinogen, Ca²⁺ ions and prostaglandins cause the formation of local blood clots and contraction of the gaping vessels of the endometrium.

Therefore, if this adaptation mechanism is not sufficient, micro-uterine bleeding, rejection of the blastocyst (embryo), and an early "spontaneous miscarriage" occur, which is often considered as a menstrual cycle disorder.

The stage of implantation of a blastocyst in the endometrium is completed, as a rule, on the 7th day after the fertilization of the egg [9]. At this stage the blastocyst, formed on the 3rd day of two types of blastomeres: dark and light, takes the form of a hollow vesicle, in which the embryo begins to develop. The embryo body and all extra-embryonic structures except the trophoblast, are formed by dark embryoblasts. The trophoblast is formed by light blastomeres, which are small, light, rapidly dividing cells, which, during interstitial implantation on the 7th day, play a major role in blastocyst nidation both at the stage of adhesion (adjunction) and at the stage of invasion (penetration).

Meanwhile, chorionic villi form two layers: cytotrophoblast (internal) and simplastotrophoblast, which produces the previously described proteolytic enzymes that prepare the endometrium for blastocyst nidation. As a result, an implantation cell is formed in the uterine mucosa, into which the blastocyst enters. The implantation is considered to be finished when the embryo is completely immersed in the endometrium and the uterine mucosa is located above it. The next stage of embryo development begins. It is called gastrulation. In humans this stage proceeds in two phases. In the first phase (normally on the 7th day), as a result of separation of the embryoblast, two layers are formed: the epiblast (external) and the hypoblast (internal). In the second phase (on the 14th day), the primary structures of the future embryo — the mesoderm and chord — are formed. At the same time, the gastrulation stage involves the formation of extra-embryonic organs: amniotic, vitelline vesicles and chorion, which subsequently provide conditions for homosapiens to nourish and develop the embryo [10].

At the second stage of gastrulation (on the 15th - 17th days), an outgrowth (leg) of the amniotic vesicle grows a cord from the germinal part of the intestinal tube - allantois, which further ensures vascularization of the chorion. By this time the embryo has already formed three germinal layers, extraembryonic structures, the differentiation of germinal layers occurs and the foundation of the main primordial organs begins.

By the 35th day of life the embryo has clear signs of histo-and organogenesis and there are morphological signs of most organs. It is believed that by the end of the 8th week embryogenesis is completed and the fetal period of intrauterine development of the embryo begins. By this time the formed umbilical cord vessels of the embryo are completely connected with the capillaries of the embryonic villi and embryoplacental blood circulation is formed.

Besides, by 16-17 weeks another placental channel of metabolic products exchange of the organisms of the fetus and mother start functioning. It is formed by decidual tissue, cytotrophoblast and amniotic membrane. By these two ways, a constant energy and information exchange between the

organisms of the mother and the fetus is ensured throughout the pregnancy.

An important role in these processes belongs to the yolk sac, which is formed by the endoblastic vesicle during the period placentation. At the end of the third week after fertilization (on the 19th day), in the yolk sac foci of erythropoiesis forming the capillary network begin to form, delivering erythroblasts to the primary circulatory system of the fetus. In addition, in the fifth week after the fertilization, primary germ cells begin to be produced in the yolk sac, and then migrate to the forming gonadoembroys.

In addition, during this period, up to the sixth week after the moment of fertilization, the yolk sac functions as a primary liver and produces proteins necessary for the embryo: α -fetoprotein, α_2 -microglobulin, transferrins. In general, yolk sac tissues perform such numerous functions as metabolic, synthetic, hematopoietic, immunoregulatory, excretory until the formation of the corresponding organs and systems. Only at the end of the first trimester of embryogenesis the functions of the yolk sac as a participant in metabolic processes cease, it turns into a tiny cyst at the base of the umbilical cord.

If the embryogenesis process fails and the yolk sac stops functioning prematurely, and the corresponding fetal organs (liver, spleen, reticulum – endothelial system, etc.) are still not completely formed, then, as a rule, fetal death and spontaneous abortion occur [11].

At the beginning of the second trimester, the relationship between the mother and the fetus changes dramatically, becoming more complex. First of all, this relates to the method of plastic material delivery and energy supply processes for the growth of the fetus. It is worth comparing the size and weight of the fetus at the end of the first trimester and before the act of delivery. It will become clear that for such an enormous increase in body weight, it is necessary to have different conditions for the delivery of nutrients to the fetus as compared with the initial gestation period.

For placentation and embryogenesis the embryo uses several sources of energy: its own resources, nutrients stored in the cells of the endometrium, metabolic products of the yolk sac, as well as the energy components of maternal blood contained in the lacunae. But, it is obvious, that all of these mentioned sources can provide energy only for the processes of nidation of a fertilized egg and its multiple division, the differentiation of cells for laying future organs and systems of the developing embryo.

Therefore, for the rapidly increasing demands of the developing embryo some other suitable sources of nutrition are needed. In homosapiens, this function is performed by placenta which is a temporary functional formation that regulates the volume and nature of the metabolic processes between the organisms of mother and fetus during the 29 weeks of the gestational period.

CONCLUSION

To summarize, the following key points can be formulated.

- I. Basic adaptation mechanisms of the pregnant woman body ensuring fetal development
- 1. The provision of trophism, development and protection of the embryo in the first trimester of pregnancy by the

accumulation of nutrients in the cells of the decidual membrane.

- 2. The predominant changes in the intensity of blood flow in the uterus on the side of implantation.
- 3. The active formation of placental structures and constant feto-dependent correction of its fractions.
- 4. The preservation (optimization) of vital parameters of the woman's physiological homeostasis.
- II. Adaptation reactions of the fetus providing its life activities and development
- 1. The accumulation of nutrients in the blastocyst for the trophism in the initial phases of embryogenesis.
- 2. The protection from external media by the formation of a shiny shell.
- 3. The creation of trophoblast structures involved in implantation, trophism and self-defense at the early stages of embryogenesis.
- The modulation of the endocrine balance of the mother with the synthesis of specific proteins and hormones by the chorion.

The combination and synchronization of these and some other mechanisms make up the adaptation syndrome concept.

In case of disorder of at least one of the adaptation mechanisms in the body, a great number of protectivecompensatory reactions instantly turn on. As a result, parameters of physiological homeostasis can be restored, that is, the pregnant woman's body, despite the presence of an intrauterine developing fetus, preserves, to some extent, her self-regulation functions.

However, with periodically recurring and even chronic stress factors, the compensatory mechanisms of the mother's body are depleted, and it starts forming compensatory, but pathological mechanisms that can make conditions acceptable for the continuation of the fetal life but damaging to its own health. In other words, the conditions called complications of pregnancy can be developed.

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